

Random walks in a metapopulation: how much density dependence is necessary for long-term persistence?

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Summary

1. We describe analytical and simulation models of metapopulations consisting of local populations that obey a random walk between a reflecting upper boundary (population ‘ceiling’) and an absorbing lower boundary (local extinction).
2. We present analytical results for the expected time to local extinction, expected size of local populations, and incidence of density dependence. The latter is defined as the frequency of hitting the ceiling per generation per population.
3. With these models we examine the proposition that a metapopulation consisting of random walk local populations would persist without density dependence.
4. Long-term persistence of a metapopulation is not possible without local populations occasionally becoming large and hence being affected by density dependence. But it is possible to construct examples in which a metapopulation persists for a long time with a low incidence of density dependence, in which cases local populations typically have very short expected lifetimes.
5. We demonstrate that, paradoxically, a persisting metapopulation may consist of only ‘sink’ populations (negative average growth rate in the absence of migration). Contrary to some previous suggestions, increasing migration rate generally increases density dependence in persisting metapopulations.

Key-words: metapopulation, density dependence, stochastic model, species survival, sink population.

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Introduction

The vast majority of natural populations show conspicuous fluctuations in size (Andrewartha & Birch 1954; Taylor & Woiod 1980; Connell & Sousa 1983; Schoener 1986; Hanski 1990), often without any clear indication of density dependence (Dempster 1983; Strong 1986; Gaston & Lawton 1987; Den Boer & Reddingius 1989). Ecologists have disagreed for decades on the implications of such findings. One school of thinking, implicitly focusing on the dynamics of local populations in isolation, has emphasized the logical necessity of density dependence, whatever the data may suggest: random walks cannot remain, forever, between finite positive limits. The opposing opinion admits that extinctions are inevitable; but extinctions may be compensated for by colonizations, and a metapopulation of density-independently fluctuating local populations might persist, if not forever, at least for so long that the practical distinction between density-dependent and density-independent persistence becomes academic (Den Boer 1991).

Our purpose here is to describe and analyse appropriate random walk models for metapopulation dynamics in order to answer the question: how much density dependence is necessary for long-term persistence of a metapopulation consisting of local populations modelled as random walks?

Analytical results

This section describes an analytical metapopulation model, which is based on Foley’s (1994) random walk model of local dynamics. Let us define N_t as the size of a local population at time t (or in generation t) and let $n_t = \log_e N_t$. Changes in the size of a local population are given by

$$n_{t+1} = n_t + r_t, \quad \text{eqn 1}$$

where r_t is a normally distributed random variable with mean r_d and constant variance v_r . For convenience, we define $s = r_d/v_r$. Population size N cannot exceed a ‘ceiling’, K , and the population goes

extinct if N becomes equal to or less than one (n equal to or less than zero). The following analysis will use both K and its natural logarithm, $k = \log_e K$. The $\log_e$ -transformed population size n thus takes a random walk over the interval $(0, k]$, with reflection at the ceiling k . More precisely, if n_{t+1} as given by equation 1 is greater than k , it is instantaneously 'reflected' to the value $2k - n_{t+1}$. Note that the only density dependence in this model is due to this reflection from the ceiling, in contrast to the logistic model, for example, in which there is pervasive density dependence, the expected per capita growth rate decreasing gradually with increasing population size. It is not known which type of density dependence is most frequent in natural populations, but the 'ceiling' model used here may well be a reasonable choice for at least some species.

LOCAL DYNAMICS

Assuming that a local population obeying equation 1 is established at size n_0 , which is called the propagule size, the expected time to extinction is given by (Foley 1994: Appendix)

$$T_e(n_0) = \frac{1}{2sr_d} [e^{2sk}(1 - e^{-2sn_0}) - 2sn_0] \quad \text{eqn 2a}$$

$$\approx \frac{n_0}{r_d} [e^{2sk} - 1], \quad \text{eqn 2b}$$

where the approximation given by equation 2b holds best when n_0 is small.

In Appendix A we derive the following approximation for the expected value of N over the lifetime of the population

$$EN \approx \frac{2s(K^{2s+1} - 1)}{(2s + 1)(K^{2s} - 1)}. \quad \text{eqn 3}$$

This approximation is used below when assembling a metapopulation of random walk local populations.

INCIDENCE OF DENSITY DEPENDENCE

We define the incidence of density dependence as the probability, $P(K_{hit})$, of hitting the ceiling K per generation per population. A good approximation of $P(K_{hit})$ for $4v_r > r_d^2$ is given by (Appendix B)

$$P(K_{hit}) \approx \frac{e^{2sk}}{e^{2sk} - 1} \frac{2r_d}{\sqrt{2\pi v_r}}. \quad \text{eqn 4}$$

RANDOM WALK IN A METAPOPOPULATION

Let us now consider an environment consisting of H habitat patches with equal size k . Assuming that H is large, changes in the fraction of occupied patches p can be approximated by Levins's (1969) metapopulation model,

$$\frac{dp}{dt} = mp(1-p) - ep, \quad \text{eqn 5}$$

in which the equilibrium fraction of occupied patches is

$$\hat{p} = 1 - \frac{e}{m}, \quad \text{eqn 6}$$

where e and m are the extinction and colonization rate parameters. We assume that population size in each newly colonized patch increases instantaneously to n_0 , the propagule size, due to immigration. The extinction rate e is given by the inverse of the expected time to extinction, $1/T_e$. We assume that the colonization rate m increases proportionally to the average size of local populations, that is $m = \mu EN$, where EN is the expected population size and μ is constant. With these assumptions, the equilibrium fraction of occupied patches is given by

$$\begin{aligned} \hat{p} &= 1 - \frac{1}{T_e \mu EN} \\ &\approx 1 - \frac{r_d(2s+1)(e^{2sk} - 1)}{2s(e^{2sk+k} - 1)\mu n_0(e^{2sk} - 1)} \\ &= 1 - \frac{v_r(2s+1)}{2\mu n_0(e^{2sk+k} - 1)} \\ &= 1 - \frac{2r_d + v_r}{2\mu n_0(e^{2sk+k} - 1)} \end{aligned} \quad \text{eqn 7}$$

Let us first observe that long-term persistence of a metapopulation is not possible in this model without some density dependence. To see this, we calculate the expected number of reflections from the ceiling during the lifetime of a local population in a deterministically persisting metapopulation ($\hat{p} > 0$),

$$T_e P(K_{hit}) \approx \frac{2n_0 e^{2sk}}{\sqrt{2\pi v_r}}. \quad \text{eqn 8}$$

Expression 8 is always positive, and hence some density dependence will always occur in a persisting metapopulation.

With a finite number of habitat patches, the Levins metapopulation with local turnover has a finite lifetime, though it may be very long for a large number of patches. Nisbet & Gurney (1982) give the following approximation for the expected lifetime of a metapopulation, T_m , with H patches,

$$T_m \approx T_e e^{H\hat{p}^2/[2(1-\hat{p})]}. \quad \text{eqn 9}$$

RELATIONSHIP BETWEEN METAPOPOPULATION PERSISTENCE AND DENSITY DEPENDENCE

Equations 4 and 9 give the incidence of density dependence in, and the expected lifetime of, a metapopulation. We have already seen that some density dependence is always associated with long-term persistence (eqn 8). In this model, the expected lifetime T_m increases with the number of habitat patches H , emigration rate μ , and propagule size N_0 . As these parameters do not affect density dependence, one

could increase metapopulation persistence time while keeping the level of density dependence constant by increasing the values of these parameters. However, as we have not modelled migration explicitly, we have implicitly assumed small values of μ and N_0 . A very large H is not consistent with the spirit of the Levins model, which assumes that all patches are equally accessible (Hanski 1991).

We have examined numerically the relationship between metapopulation persistence time T_m and the incidence of density dependence $P(K_{hit})$ for various combinations of r_d , v_r and K (Fig. 1). Increasing K and

decreasing r_d decrease density dependence, while the effect of v_r depends on the value of r_d : density dependence increases with v_r for negative and small positive values of r_d , whereas density dependence decreases with increasing v_r for larger, positive r_d (Fig. 1c, d). The extreme combination of long persistence time with little density dependence is obtained with large K , small negative r_d and small v_r (Fig. 1a, c). We used the arbitrary limit $\log_e T_m > 10$ ($T_m > 22000$) to characterize 'persisting' metapopulations. The average value of $P(K_{hit})$ for the persisting metapopulations in the simulations in Fig. 1, which cover a realistic

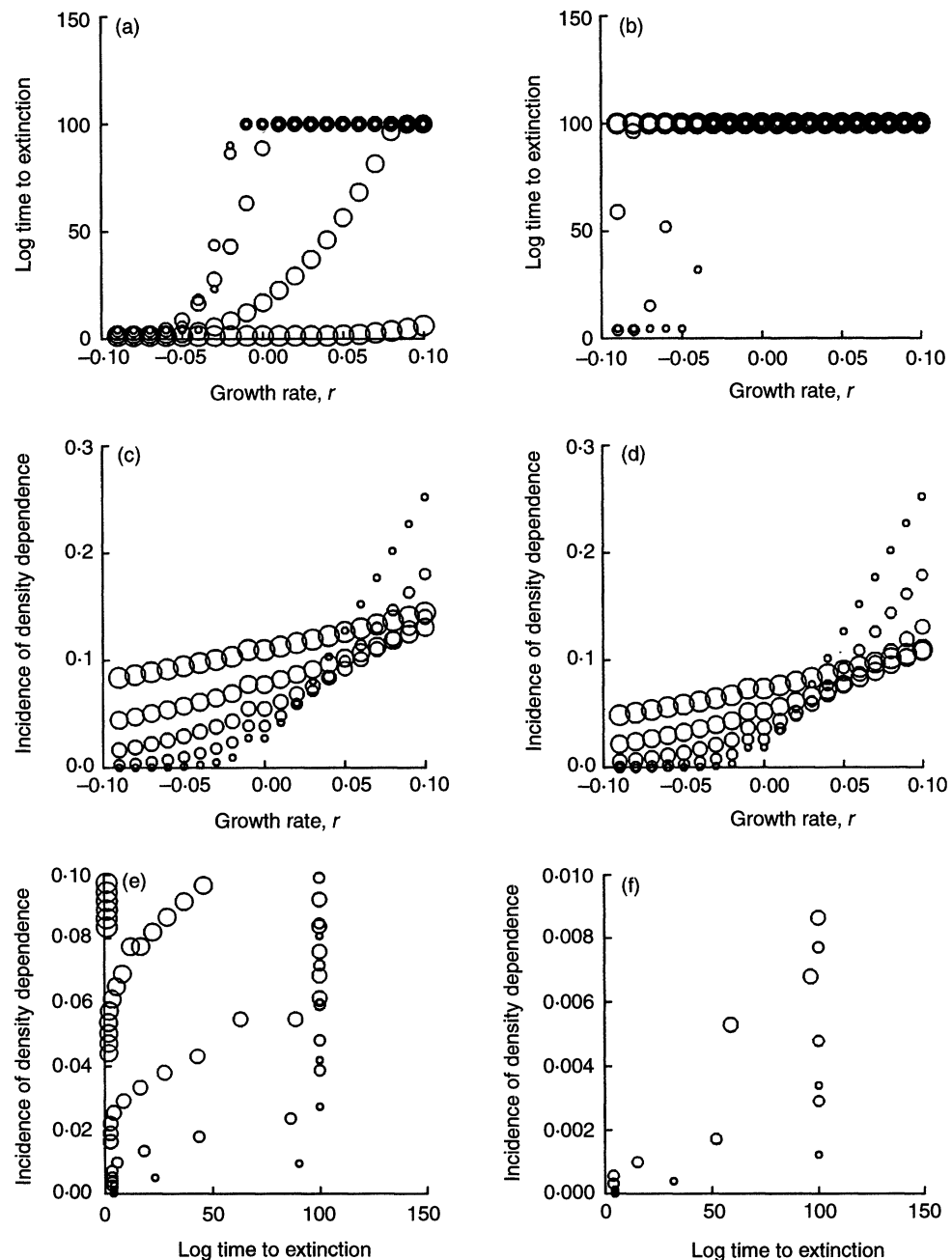


Fig. 1. Relationships between expected time to metapopulation extinction (T_m ; equations 9, 2a and 7) and the average growth rate r_d (a and b); between incidence of density dependence ($P(K_{hit})$; equation 4) and r_d (c and d); and between incidence of density dependence and time to extinction (e and f). The left-hand panels give the results for $K = 100$, the right-hand panels for $K = 1000$. The size of the circle is proportional to the value of v_r (the actual values were 0.1, 0.2, 0.4, 0.8 and 1.6). Other parameter values were $H = 100$, $\mu = 0.01$ and $N_0 = 2$. Note that only small values of $P(K_{hit})$ are shown in (e) and (f).

range of parameter values, was 0.09 for $K = 100$ and 0.07 for $K = 1000$. The respective minimum values were 0.005 and 0.0004. Equations 3 and 7 show that, at equilibrium, variation in the parameters of local dynamics, s and K , affect both EN and $\hat{p}$ but variation in the parameters of metapopulation dynamics, μ and n_0 , affect only $\hat{p}$. This result follows from the Levins model assumption that migration is weak enough not to affect the dynamics of the existing local populations. Gyllenberg & Hanski (1992), Hanski & Gyllenberg (1993) and Hanski & Zhang (1993) analyse metapopulation models in which migration does affect local dynamics.

Simulation results

In this section we investigate two simulation models, which differ in the way migration is modelled. Model 1 is identical to the analytical model in the previous section. It is used to check the accuracy of the analytical approximations. In this model, each empty patch is colonized with a probability proportional to the total number of individuals alive in the metapopulation. If a new population is established, it is started with a small, constant propagule size. Model 2 includes a more mechanistic description of the migration process. Each habitat patch is now assigned a set of spatial coordinates. In each time interval, a constant fraction c of individuals emigrates from each patch, and these individuals are distributed among the other patches in such away that the migration distances are negative exponentially distributed with a parameter d . In this model, emigration and immigration affect the dynamics of existing local populations, and colonization of an empty patch is a mechanistic consequence of individuals arriving at that patch. The propagule size is determined by the numbers of individuals arriving at a patch, which varies both between patches and in time.

MODEL 1

Table 1 gives the parameter values which were used in the simulations. The model has been run for a maximum of 1000 time intervals, and any meta-

population which persisted for the entire length of the simulation was scored as ‘persistent’. We first observe that the analytical result for density dependence (eqn 4), measured by the number of reflections from the ceiling per generation per population, is a very good approximation for even large values of sk (Fig. 2). The approximation for the expected size of local populations (eqn 3) is equally good for all parameter combinations used in the simulations (Fig. 3). Figure 4 shows that metapopulation size at equilibrium tends to be underestimated by equation 7. The simulated maximum values of $\hat{p}$ are around 0.4, which agrees with the stochastic result of equation 9, where long-term metapopulation persistence ($T_m > 100T_e$) requires that $\hat{p} > 0.35$. The analytical result given by equation 7 is based on the Levins model, which does not take into account colonization-extinction stochasticity (Hanski 1991). Turning then to the main concern of this paper, Fig. 5 shows the relationship between time to metapopulation extinction and the incidence of density dependence in the simulation results. Several points in this figure are worth noting. First, there is a positive

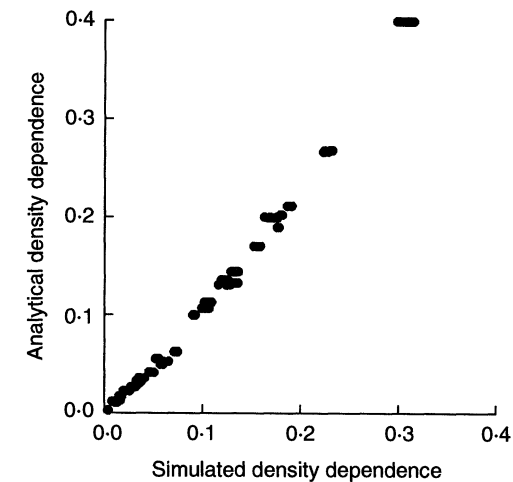


Fig. 2. Comparison between the analytical result for the number of reflections per generation per population (equation 4) and the result obtained by simulation of Model 1. This figure includes results for all the parameter combinations in Table 1 for which the simulated time to extinction was > 1000 time intervals and for which $sk < 20$.

Table 1. Parameter values used in the simulations of Models 1 and 2. Metapopulations were started with half of the habitat patches occupied at half density. Models were iterated for a maximum of 1000 time intervals

Parameter	Model 1	Model 2
r_d	−0.2, −0.1, 0.0, 0.1, 0.2	−0.3, −0.2, −0.1, 0.0, 0.1
v_r	0.04, 0.16, 0.36, 0.64, 1.0	0.16, 0.36, 0.64, 1.0, 1.44
K	100, 1000	100
μ	0.002, 0.004, 0.008, 0.016, 0.032	—
N_0	2	—
c	—	0.01, 0.10, 0.20, 0.30, 0.40
d	—	0.5, 1, 2, 4, 8
H	50	20

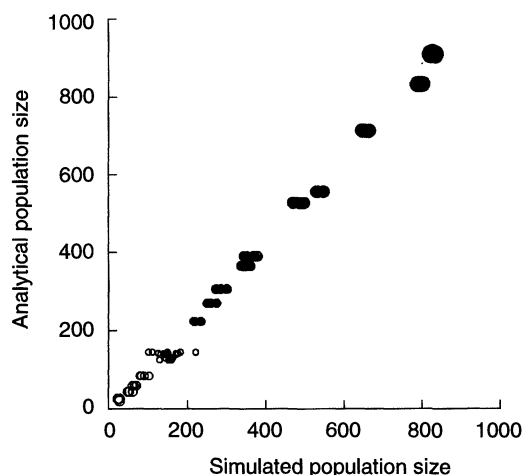


Fig. 3. Comparison between the analytical result for the expected population size (equation 3) and the result obtained by simulation of Model 1 (using data for time intervals from 900 to 1000). This figure shows results for all parameter combinations in Table 1 with $K = 1000$ and for which the simulated time to extinction was > 1000 time intervals (similar results were obtained for $K = 100$). Negative values of sk are shown by open circles, positive values by dots. The size of the symbol indicates the magnitude of the absolute value of sk .

relationship between the time to extinction and the level of density dependence: higher persistence times are generally associated with more density dependence. Secondly, as found in the analytical model, for a given level of density dependence, persistence time increases with K and μ . And thirdly, long-term persistence (> 1000 time intervals) was always associated with density dependence (Fig. 5). The average value of $P(K_{hit})$ in the runs that persisted for the entire length of the simulation (1000 time intervals) was 0.17 for

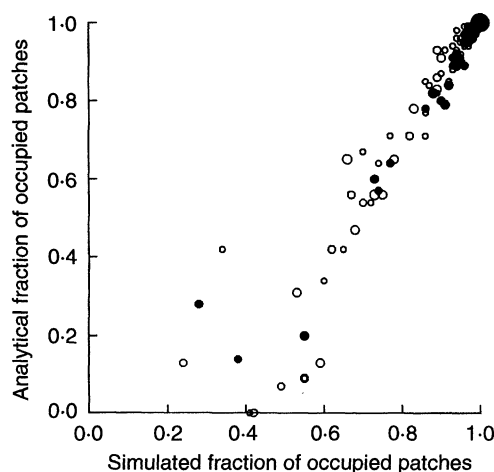


Fig. 4. Comparison between the analytical result for metapopulation size (equation 7) and the result obtained by simulation of Model 1 (using data for time intervals from 900 to 1000). This figure includes all the parameter combinations in Table 1 for which the simulated time to extinction was > 1000 time intervals. Negative values of sk are shown by open circles, positive values by dots. The size of the symbol indicates the magnitude of the absolute value of sk .

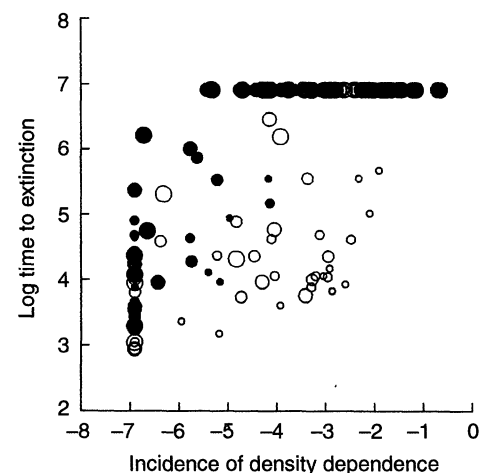


Fig. 5. Relationship between time to metapopulation extinction and the frequency of hitting the ceiling, $P(K_{hit})$, in the results of Model 1. Both axes have been log-transformed (after adding 0.001 to $P(K_{hit})$). Open circles are for $K = 100$, dots for $K = 1000$. The size of the symbol increases with the magnitude of the colonization rate μ .

$K = 100$ and 0.14 for $K = 1000$. The respective minimum values were 0.014 and 0.003. Naturally, it would be possible to obtain even lower values by carefully selecting parameter values, or by using an unrealistically large value of K , but values of $P(K_{hit})$ thus obtained would be of little relevance to the situation in natural populations. Incidentally, note that the lowest values of $P(K_{hit})$ are obtained with small values r_{db} for which the analytical approximations are most accurate.

With the incidence of density dependence as low as a few percentage per generation per population, one may ask whether this could be discerned using the current techniques of detecting density dependence. Figure 6 gives an example for a parameter combination where $P(K_{hit})$ is around 5% and T_e is 18 time intervals. Bulmer's (1975) method to detect density dependence has been used and, as expected, the frequency of detecting significant density dependence increases with the length of the time series (Fig. 6). In time series longer than 20 time intervals (years), significant density dependence at 5% level was detected in 40% of the series.

MODEL 2

The difference from Model 1 is that we now model emigration and immigration explicitly. For that purpose, simulations were conducted with a system of patches with explicit spatial coordinates. For each simulation, the required number of patches was placed randomly within a square area. In each time interval, a fraction c of individuals leave their patch and are distributed (without mortality) among the other patches. The emigrants from patch i are distributed among the other patches in such a way that the distribution of migration distances is a negative

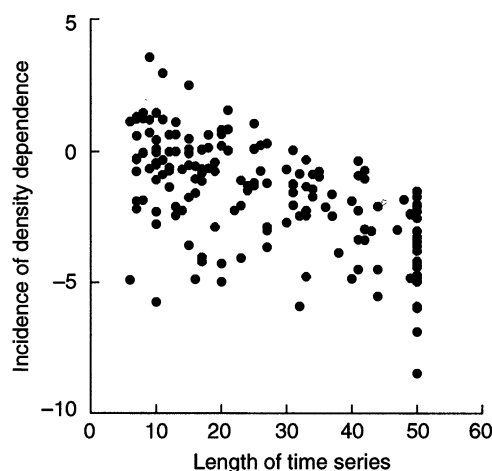


Fig. 6. Relationship between the probability of rejecting the null hypothesis of density independence and the length of the time series in the results of Model 1. The vertical axis gives the logit transformed probability of rejecting the null hypothesis of no density dependence (as in Woiwod & Hanski 1992; using Bulmer's 1975 method to detect density dependence). Values smaller than -2.9 are significant at the 5% level. The results were obtained for the following parameter values: $K = 100$, $r_d = 0$, $v_r = 0.36$, $\mu = 0.016$, $N_0 = 2$ and $H = 50$. The incidence of hitting the ceiling is low for these parameter values, around 5% per generation per population, but the metapopulation persists for a very long time ($T_m < 18e^{100}$, equation 9). The time series for the analysis were obtained by locating randomly, in the simulation results, a positive starting density for a local population, then including the subsequent series of numbers until the population went extinct or the time series was 50 time intervals long.

exponential, with parameter d . Note that the absolute numbers of migrants to any patch j from patch i depend both on the distance between patches i and j and on how many patches there are at different distances from patch i . Parameter values used in the simulations are given in Table 1.

As with Model 1, we scored metapopulations which survived for the entire length of the simulation (1000 time intervals) as 'persistent'. In general, the results are qualitatively very similar to the results of Model 1. In the set of simulations described in Table 1, the average value of $P(K_{hit})$ was 0.142, and the minimum value was 0.032. The latter value is somewhat higher than the minimum obtained with Model 1. This was expected because in the former case colonizations represent an extra input of individuals to the metapopulation, whereas in Model 2 the colonists are extracted from the existing local populations.

The main interest in Model 2 is the effect of migration rate on metapopulation persistence and density dependence. Increasing migration distances (parameter d) had a similar, but weaker, effect than increasing emigration rate (parameter c) on the results, and we here focus on the latter. In metapopulations persisting for > 1000 time intervals, $P(K_{hit})$ increased with increasing migration rate when the positive effects of r_d and v_r had been taken into account. But in metapopulations which did not persist

for 1000 time intervals, time to extinction increased but $P(K_{hit})$ decreased with increasing emigration rate (Fig. 7). The lowest values of $P(K_{hit})$ were between 0.03 and 0.04; these values were obtained for negative r_d and high emigration rates (0.2–0.4), or with r_d about zero and emigration rates lower or with low variance v_r .

Discussion

It is impossible to have long-term persistence in a metapopulation without some density dependence, if population sizes are realistically restricted below some upper value K . In this respect there is no difference between the dynamics of a single population and the dynamics of a metapopulation, and no special analysis is really needed for the latter. The interesting question is about the frequency of density dependence in persisting metapopulations. We have shown that it is possible to construct examples in which a metapopulation persists for a very long time with so little density dependence that even long series of data, say 50 years or more, might fail to demonstrate significant density dependence in local dynamics. The difference in the levels of density dependence necessary for the persistence of a single random walk population and a metapopulation is very clear. To take a representative example, assume a local population with $K = 100$, $N_0 = 2$ and $v_r = 0.3$. Equation 2a shows that r_d must exceed 0.1 for the expected lifetime of the population to exceed 100 time intervals, in which case the incidence of density dependence as measured by equation 5 is around 0.15. A higher value of v_r would yield a higher level of density dependence. Den Boer (1991) reported $v_r = 0.7$ for carabid beetles, in which case persistence for $c. 100$ time intervals requires $r_d \approx 0.3$ and gives the frequency of hitting the ceiling as ≈ 0.3 . In contrast, a random walk metapopulation with realistic parameter values, for instance $H = 50$ and $\mu = 0.001$, would easily persist for much longer than 100 time intervals with density dependence reduced by an order of magnitude. Our results suggest that the incidence of density dependence in a random walk metapopulation may often be around 5% or even less.

Woiwod & Hanski (1992) have recently examined the incidence of significant density dependence in several thousand time series of annual density estimates for British moths and aphids. They found that 79 and 88% of the moth and aphid time series, respectively, longer than 20 years showed significant density dependence at the 5% level (using Bulmer's 1975 method to detect density dependence). These values are clearly higher than the possible minimum values consistent with metapopulation persistence in the present models, suggesting that moth and aphid populations have relatively persistent local populations.

Kuno (1981) first pointed out that migration among independently fluctuating local populations enhances the average growth rate r_d . A metapopulation may

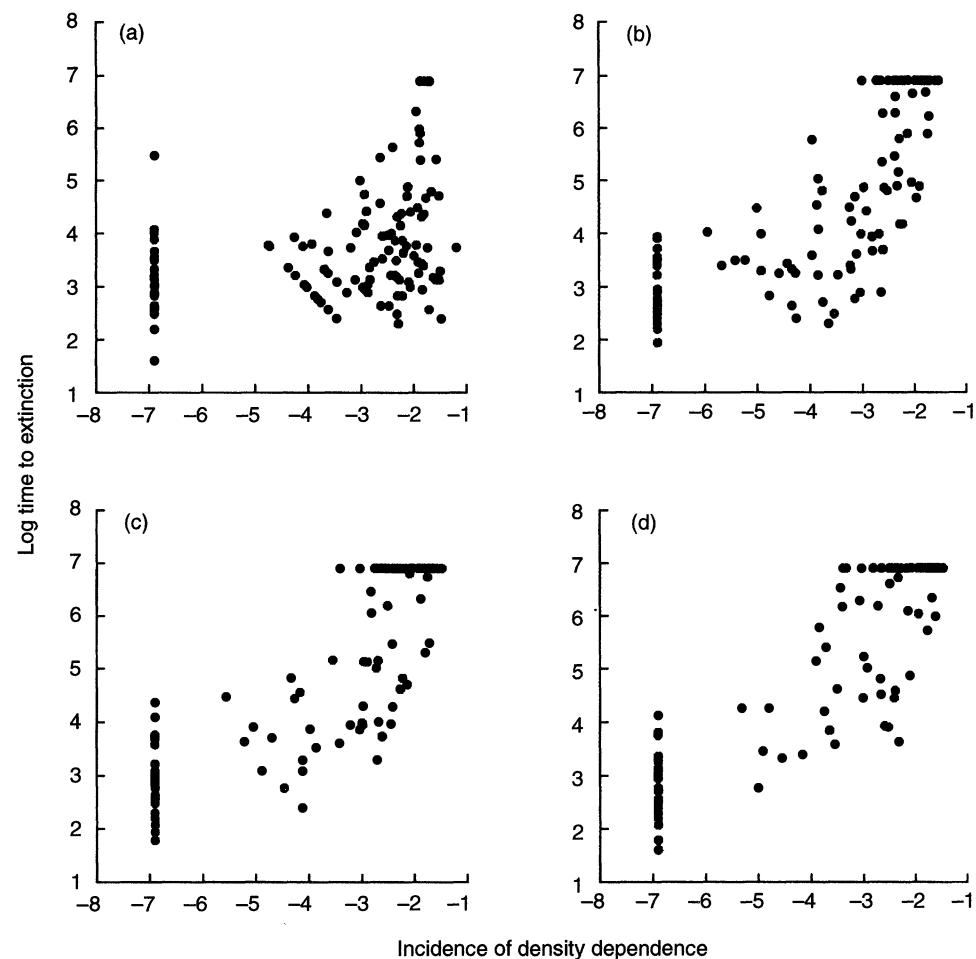


Fig. 7. Relationship between time to metapopulation extinction and the frequency of hitting the ceiling, $P(K_{hit})$, in the results of Model 2. Both axes have been log-transformed (after adding 0.001 to $P(K_{hit})$). The four panels give the results for four levels of emigration rate c , (a) 0.01, (b) 0.11, (c) 0.21 and (d) 0.31. $K = 100$.

persist even if r_d is negative; that is, even if all local populations, when isolated, would show a deterministic trend to extinction. Although the positive effect of migration on growth rate is diminished in real metapopulations by spatial synchrony in the dynamics of local populations, probably largely caused by spatially correlated environmental stochasticity (Hanski & Woiwod 1993), this result has important implications for the study of metapopulation dynamics. Most real metapopulations are thought to consist of 'source' and 'sink' populations. In source populations (habitats), the average number of birth events exceeds the average number of death events, and emigrations exceed immigrations, whereas in sink populations (habitats) the reverse is true (Pulliam 1988). But if we have a metapopulation in which r_d is negative, each population, *if isolated*, would function as a sink! In this sense, paradoxically, a persisting metapopulation may include only sink populations (habitats).

The spreading of risk argument of Den Boer (1968 and later papers) implies that migration may allow

metapopulation persistence without density dependence. Our Model 2, which explicitly includes migration, shows that, keeping other things unchanged, increasing migration rate indeed increases metapopulation persistence time and decreases the level of density dependence, but only in metapopulations which have relatively short persistence times. In the case of more persistent metapopulations (T_m large), increasing migration rate actually *increases* the incidence of density dependence.

In conclusion, long-term persistence of a metapopulation is not possible without some density dependence, contrary to suggestions by Den Boer (1968, 1991) and others. However, the incidence of density dependence may be very low in some persisting metapopulations, in comparison with the incidence of density dependence that is necessary for long-term persistence of an isolated local population. In metapopulations, the combination of long persistence time and low incidence of density dependence is associated with a high rate of population turnover, that is, frequent local extinctions and colonizations.

But even in these cases long-term persistence is not possible without some local populations occasionally growing to a large size, and hitting the population ceiling, which an ecologist would record as an instance of density dependence.

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Appendix A

EXPECTED VALUE OF N

The density of n (over the lifetime of the population) can be obtained by the formula

$$f(n; n_0) = \frac{t(n; n_0)}{T_e(n_0)}. \quad \text{eqn A1}$$

By using equations A17 and A18 in Foley (1994: Appendix) in equation A1 we get

$$f(n; n_0) = \frac{2se^{2sn}(1 - e^{-2sn_0})}{e^{2sk}(1 - e^{-2sn_0}) - 2sn_0}. \quad \text{eqn A2}$$

If n_0 is close to 0 (populations are established by a few individuals only), then this becomes

$$f(n; n_0) \approx \frac{2se^{2s(n-k)}}{1 - e^{-2sk}}. \quad \text{eqn A3}$$

To obtain the density of N we use the change of variable formula (Bickel & Doksum 1976; p. 448). Since $N = e^n$, we use $g(n) = e^n$, $g' = e^n$ and $g^{-1}(N) = \log_e N$ in the formula, to get

$$f(N) = \frac{f(g^{-1}(N))}{|g'(g^{-1}(N))|} \quad \text{eqn A4}$$

$$\begin{aligned} &\approx \frac{2sN^{2s-1}}{e^{2sk} - 1} \\ &= \frac{2sN^{2s-1}}{K^{2s} - 1}. \end{aligned} \quad \text{eqn A5}$$

The expected value for N is now given by

$$\begin{aligned} EN &\approx \int_1^K Nf(N) dN \\ &= \frac{2s(K^{2s+1} - 1)}{(2s+1)(K^{2s} - 1)} \end{aligned} \quad \text{eqn A6}$$

Appendix B

INCIDENCE OF DENSITY DEPENDENCE

To find out the fraction of time a population hits the population 'ceiling', that is, bounces off the reflecting barrier K , requires a different sort of approach. To hit K , $n_t + r_t$ must be equal to or greater than k . The probability of a hit, $P(K_{hit})$, is then given by

$$\begin{aligned}
P(K_{hit}) &= \int_0^k p(r) \int_{k-r}^k f(n) \, dn \, dr \\
&\approx \int_0^k \frac{e^{-(r-r_d)^2/2v_r}}{\sqrt{2\pi v_r}} \frac{e^{2sk}(1-e^{-2sr})}{e^{2sk}-1} \, dr \\
&= \frac{e^{2sk}}{e^{2sk}-1} \int_0^k \frac{(1-e^{-2sr})e^{-(r-r_d)^2/2v_r}}{\sqrt{2\pi v_r}} \, dr \\
&\approx \frac{e^{2sk}}{e^{2sk}-1} \left[1 - 2 \int_{r_d}^{\infty} \frac{e^{-r^2/2v_r}}{\sqrt{2\pi v_r}} \, dr \right] \\
&\approx \frac{e^{2sk}}{e^{2sk}-1} \frac{2r_d}{\sqrt{2\pi v_r}}.
\end{aligned}$$

eqn B1

The limit of equation B1 as r_d approaches zero is

$$P(K_{hit}) = \frac{\sqrt{v_r}}{k\sqrt{2\pi}}.$$

eqn B2

The approximation of B1 works because in realistic situations, k is large in comparison with the square root of v_d , r_d is much smaller than k , and r_d is less than

the square root of v_d . Although there appear to be three parameters here, the dynamics and the formulas can all be put in terms of two parameters, k' and r_d' , defined by:

$$\begin{aligned}
k' &= \frac{k}{\sqrt{v_r}} \\
r_d' &= \frac{r_d}{\sqrt{v_r}}.
\end{aligned}$$

Numerical comparisons show that the final approximation of equation B1 works reasonably well when $k' > 3$, $|r_d'| < k'/3$ and $|r_d'| < 1$. The approximations are then within 17% of the original integral of B1. When $|r_d'| < 0.2$, the approximation is less than 1% off. To improve $P(K_{hit})$ for larger r_d' values, the error function $\text{erf}(x)$ can be used. This function, available on some spreadsheet programs, returns the area under a Gaussian curve which is not analytically obtainable (Abramowitz & Stegun 1972). For r_d not equal to 0,

$$P(K_{hit}) \approx \left| \frac{e^{2sk}}{e^{2sk}-1} \right| \text{erf} \left(\frac{|r_d|}{\sqrt{2v_r}} \right).$$

eqn B3

Local extinction in a metapopulation context: an empirical evaluation

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Metapopulations are classically viewed as sets of populations persisting in a balance between local extinction and colonization. When this is true, regional persistence depends critically upon parameters influencing extinction and colonization rates, e.g. the number of habitat patches and populations, the rates and patterns of interpatch migration, and propagule establishment probabilities. A review of relevant empirical literature identifies few metapopulations which fit this description well. Instead, three qualitatively different situations are found to be more common: (1) mainland-island and source-sink metapopulations, in which persistence depends on the existence of one or more extinction-resistant populations; (2) patchy populations, in which dispersal between patches or sub-populations is so high that the system is effectively a single extinction-resistant population; (3) non-equilibrium metapopulations, in which local extinction occurs in the course of a species' overall regional decline. This suggests a modified view of metapopulation dynamics in which local extinction is more an incidental than a central feature.

KEY WORDS: Extinction – metapopulations – persistence – dispersal – colonization – population dynamics.

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INTRODUCTION

Although the theory of single-species metapopulation dynamics is well developed (see review in Hanski, 1991), and metapopulation ideas have permeated many areas of ecological and evolutionary theory, many empirical questions remain to be answered about how metapopulations function. The extinction of local populations is a central aspect of most metapopulation models and ideas. This review examines local extinction from an empirical perspective,

comparing the role it is given in metapopulation theory with evidence from relevant field studies.

Field observations of local extinctions, especially in plant and insect populations, were an important early stimulus to the ideas which later became known as metapopulation theory (Andrewartha & Birch, 1954). From such observations, it was argued that species may persist as regional ensembles of transient populations, through dispersal and (re-)colonization of vacant habitats. Such a 'shifting mosaic' mode of demographic persistence was proposed by some theorists as an alternative to stabilizing or regulatory factors acting within local populations (Andrewartha & Birch, 1954; Ehrlich & Birch, 1967; see also Ricklefs, 1979).

Mathematical theory in this area began with the model by Levins (1969, 1970). Hanski (1991) and Hastings (1991) review the development of metapopulation models. Levins's and other simple metapopulation models depict an either finite or infinite set of populations, all of which are subject to extinction with equal and temporally independent probabilities. More complex models (e.g. Hastings & Wolin, 1989) incorporate such refinements as spatially structured dispersal and continuous rather than binary population dynamics within patches. However, most retain the feature of Levins's (1969, 1970) model that local extinction affects all populations, more or less equally. This is true as well in the majority of models concerned with the regional coexistence of locally unstable combinations of competitors or predators and prey (e.g. Horn & MacArthur, 1972; Slatkin, 1974; Hastings, 1978; Hanski, 1983).

There are important implications to this extinction-centred view of metapopulations. If all populations are subject to extinction, regional persistence depends critically upon colonization. In turn, persistence depends on the parameters controlling colonization rates, such as the number of vacant patches and extant populations, the rates and patterns of dispersal (Hansson, 1991) and propagule establishment probabilities (Ebenhard, 1991). Another key determinant of metapopulation persistence is the degree of temporal independence among local populations in their chances of extinction (Harrison & Quinn, 1989; Gilpin, 1990).

Other metapopulation models present modified views of the role and importance of extinction. The mainland-island metapopulation structure of Boorman & Levitt (1973; see Fig. 1B) contains a central population, immune to extinction, which supplies colonists to transient marginal populations. In the model by Hanski (1985) local populations may alternate between susceptibility and resistance to extinction. In a different vein, metapopulation models by Roff (1974), Chesson (1981) and Roughgarden & Iwasa (1986; Iwasa & Roughgarden, 1986), emphasize spatio-temporal variability in population dynamics, rather than extinction and colonization. These models assume such a high degree of dispersal between the patches on which recruitment and growth take place that local extinction is unlikely to occur. Similarly, Levin (1974) and Comins & Noble (1985) find that competitors or predators and prey can coexist in a fugitive fashion without local extinction; coexistence is facilitated by the spatially localized nature of competitive exclusion and/or predation, combined with limited dispersal.

This brief review of theory provides a background against which to contrast the empirical evidence on local extinction in metapopulations. Although the

causes of local extinction will be briefly discussed, below, more emphasis will be placed on its consequences, especially with respect to demographic persistence. First, it will be necessary to define local extinction and to distinguish among the various ways the terms 'extinction' and 'metapopulation' are used in the literature.

DEFINITION AND CAUSES OF LOCAL EXTINCTION

'Local extinction' is sometimes used to denote the disappearance of a species from any arbitrarily defined sampling plot (e.g. den Boer, 1970). At the other end of the scale, it may signify a species' extirpation from any region less than its entire range (e.g. Chew, 1981). Here, local extinction is defined more narrowly as the disappearance of a population, where the term population is used in the demographic (Ehrlich, 1965) or genetic (Wright, 1969) sense. Admittedly, this definition presents practical difficulties, since not all species are organized into discrete, identifiable groups within which 'nearly all' mating, reproduction and interactions take place. In considering metapopulation dynamics, one possible definition of a local population is the minimal unit which once extirpated, may remain extinct for more than one or a few generations. This at least serves to exclude sub-populations so tightly coupled to others that their 'extinction' is likely to be followed immediately, e.g. within one generation, by 'recolonization'.

The causes of local extinction may be stochastic or deterministic. The stochastic aspects of extinction have been categorized by Shaffer (1981) as demographic, genetic and environmental stochasticity, and catastrophes. Stochastic local extinction has received a great deal of theoretical attention, beginning with MacArthur & Wilson's (1967) work on island colonization. More recently it has become a central theme in conservation biology (Shaffer, 1981; Wright & Hubbell, 1983; Shaffer & Samson, 1985; Gilpin & Soulé, 1986; Simberloff, 1988). Only a brief summary of theory and relevant empirical work is attempted here.

Demographic stochasticity (MacArthur & Wilson, 1967; Richter-Dyn & Goel, 1972; Gilpin & Soulé, 1986; Ebenhard, 1988, 1991) concerns the changes in population size caused by randomness in the order of occurrence of births and deaths. Theory suggests that this only adds significantly to the risk of extinction in populations which are below a relatively small threshold size (MacArthur & Wilson, 1967; Richter-Dyn & Goel, 1972), though the exact magnitude of the threshold depends on specific demographic traits of the species (Ebenhard, 1988, 1991). Because of the existence of a threshold, it might be expected that demographic stochasticity will play a more significant role in the success or failure of colonizing propagules, and the final extinction of declining populations, than in the extinction of established populations. Empirical studies of demographic stochasticity mainly concern colonization (e.g. Crowell, 1973; Ebenhard, 1988 and references therein).

Genetic stochasticity refers to the loss of heterozygosity through drift and the loss of fitness due to inbreeding. Empirical work connecting these genetic processes to the demography of small populations is almost non-existent. However, theory predicts that genetic stochasticity enhances the risk of extinction mainly in populations that have recently declined in size and that

lack histories of severe fluctuations. In species that are naturally subject to frequent population turnover, genetic stochasticity is expected to affect persistence relatively little (Gilpin, 1987, 1991; Lande, 1988; Sjögren, 1991).

Environmental stochasticity is temporal variation in the net rate of population growth, driven by variation in external factors such as weather or food supply. The magnitude of population variability depends on life-history traits that determine how well reproduction and mortality are buffered against environmental change. Theory predicts that in species with highly variable rates of population growth, even large populations have short expected lifetimes (Leigh, 1981; Goodman, 1987). Studies of insular faunas confirm this prediction: after correcting for different population sizes, the species with the greatest variability in population growth rates are the most prone to extinction (Leigh, 1981; Karr, 1982; Schoener & Toft, 1983; Pimm, Jones & Diamond, 1988).

When the environmental events causing populations to fluctuate are infrequent and severe, or so-called catastrophes, risks of extinction are only weakly dependent on population size (Ludwig, 1976; Hanson & Tuckwell, 1978, 1981; G ripenberg, 1985). Environmental catastrophes which have been observed to cause local extinction in insects include droughts (Ehrlich *et al.*, 1980; Thomas, 1984), aberrant freezes (Ehrlich *et al.*, 1972; Strong, Antolin & Rathbun, 1990) and fires (Cryan & Dirig, 1978; Givnish, Menges & Schweitzer, 1988).

Of the various stochastic causes of local extinction, environmental stochasticity and catastrophes are probably the most important in natural metapopulations, based on both the balance of empirical evidence (below) and the theoretical expectation that they can affect populations of a large range of sizes. Environmentally-driven local extinction raises a potential problem for metapopulation theory. Many of the environmental factors which cause population fluctuations and extinction act at a regional scale. Weather is the most obvious example. It is likely to affect all populations in a metapopulation simultaneously, and thus to create temporal correlation in their chances of extinction. Correlated local extinction (or 'regional stochasticity', Hanski, 1991) can sharply reduce the expected persistence time of metapopulations (Harrison & Quinn, 1989; Gilpin, 1990).

Direct evidence on correlated extinction in metapopulations is very limited. However, Pollard, Hall & Bibby (1986) examined 10-year relative abundance data for British butterflies, and documented that conspecific populations often fluctuate in synchrony. Ehrlich *et al.* (1972) and Ehrlich *et al.* (1980) observed the extinctions of multiple conspecific butterfly populations in two environmental catastrophes, a spring freeze and a drought respectively.

Thus, local extinction in many species is caused by large-scale environmental events. Theory suggests that in such circumstances, classical metapopulations are unlikely to persist. This enhances the potential significance of refuges, habitats in which certain populations are protected from catastrophes and act as sources for recolonization (see below), to persistence in such cases. Also, many species are adapted to large-scale adversity through 'escape in time' strategies, such as environmentally cued seed dormancy in plants or facultative diapause in insects (for a review of the latter, see Hanski, 1988). These adaptations have the effect of making local, as well as regional, extinction less likely.

Deterministic local extinction characterizes species of temporary habitats, such

as successional vegetation. These species continually disappear from local habitats as these become unsuitable. However, whether these local disappearances can be usefully regarded as local extinctions, in the sense defined above, depends critically upon the lifetime of the habitat and the frequency and range of individuals' movements (this issue is also discussed below under 'Patchy Populations'). The other major source of non-random local extinction is human pressures on species and their habitats (Ehrlich & Ehrlich, 1981).

LOCAL EXTINCTION IN A METAPOPOPULATION CONTEXT

There are far fewer case studies of local extinction in a metapopulation context than of local extinction *per se*. Of the empirical studies that have quantified patterns of local extinction in multiple populations, nearly all come from the field of island biogeography (see reviews in Schoener, 1983; Diamond, 1984). The sets of insular populations in these studies are not maintained by mutual recolonization, but by repeated immigration from a mainland. Apart from island studies, most cases of extinction reported in the literature are single observations from which little can be deduced about metapopulation structure, such as where colonists come from and how often (e.g. Washburn & Cornell, 1981; Svensson, 1985).

Studies documenting rates and patterns of local turnover within entire, closed population systems are limited in number. However, examining the available literature, it is possible to identify several major types of metapopulations, in terms of the different roles which they imply for local extinction. I have categorized these as follows (see also Hanski & Gilpin, 1991): (1) Mainland-island and source-sink metapopulations (Fig. 1B), the distinction between which is clarified below. Local extinctions occur mainly among a subset of populations, the islands or sinks, and have little effect upon regional persistence since the extinction-resistant mainland or source populations are the major providers of colonists. (2) Patchy populations (Fig. 1C), which are distributed over a patchy and/or spatiotemporally variable habitat, but in which high rates of dispersal effectively unite the patches into a single demographic entity. There is thus little potential for the extinction of discrete local populations. (3) Non-equilibrium metapopulations (Fig. 1D), among which recolonization is either absent or insufficient to balance extinction. Local extinction occurs as part of an overall regional decline, usually a product of the reduction, fragmentation or deterioration of the habitat. (4) Classical metapopulations (Fig. 1A), sets of conspecific populations persisting in a dynamic regional balance between extinction and colonization, as represented by the standard metapopulation models. There appear to be relatively few cases conforming well to this description; I will speculate on the reasons for this, after illustrating each of the types of metapopulation with examples.

Mainland-island and source-sink metapopulations

In the equilibrium theory of island biogeography (MacArthur & Wilson, 1967), local extinction affects the distribution of local populations, but not the regional persistence of the species. Extreme differences in patch sizes make some terrestrial metapopulations very similar in their dynamics to true mainlands and

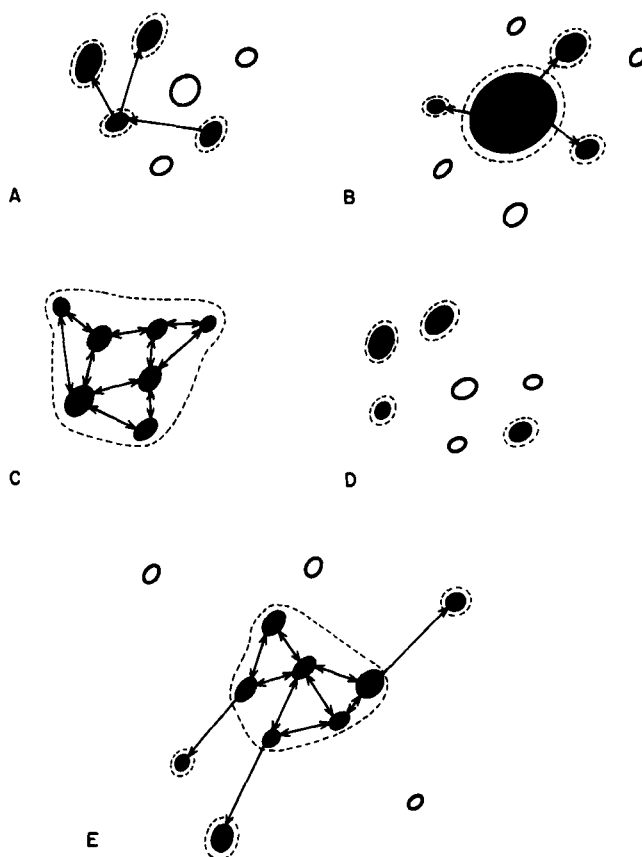


Figure 1. Different kinds of metapopulations. Closed circles represent habitat patches; filled = occupied, unfilled = vacant. Dashed lines indicate the boundaries of 'populations'. Arrows indicate migration (colonization). A, Levins metapopulation. B, Core-satellite (Boorman-Levitt, 1973) metapopulation. C, 'Patchy population'. D, Non-equilibrium metapopulation (differs from A in that there is no recolonization). E, An intermediate case that combines B and C.

islands. One example is the metapopulation of the Bay checkerspot butterfly (*Euphydryas editha bayensis* Boisduval) that I studied (Harrison *et al.*, 1988; Harrison, 1989). It consisted, in 1987, of a population of on the order of 10^6 adult butterflies on a 2000-ha habitat patch, and nine populations of 10–350 adult butterflies on patches of 1–250 ha. Of 27 small habitat patches in the region which were found to be suitable, only those closest to the large patch were occupied (Fig. 2). This pattern of patch occupancy could not be explained by differences in habitat quality. Instead, the distance effect appeared to indicate that the butterfly's capacity for dispersal is limited, and that the large population acts as the dominant source of colonists to the small patches. From this and other evidence, it appears that persistence in this metapopulation is relatively unaffected by population turnover on the small patches.

Thus, local extinction may be frequent and yet may be relatively trivial in terms of regional dynamics, as Williamson (1989) has previously noted. For this to be true, there need not be a mainland population of extreme size. High variance in patch or population size means that most local extinctions will

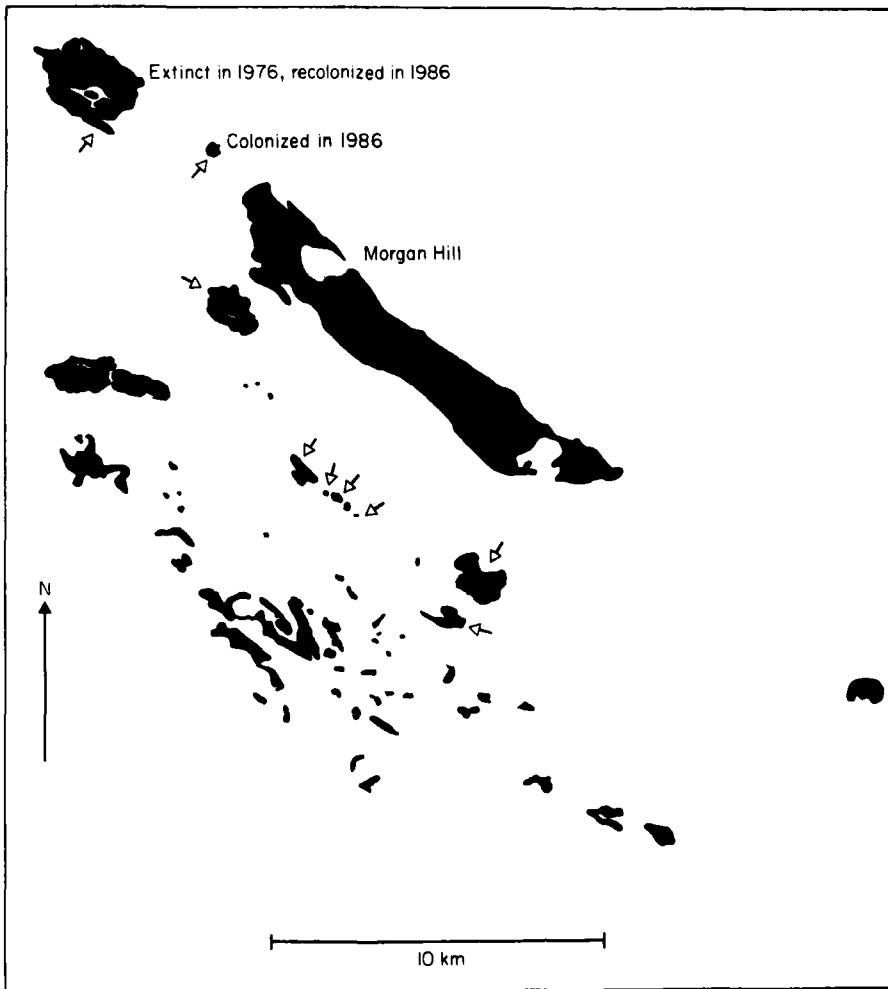


Figure 2. Metapopulation of the Bay checkerspot butterfly, *Euphydryas editha bayensis* (from Harrison *et al.*, 1988). The black areas represent patches of the butterfly's serpentine grassland habitat. The 2000-ha patch labelled 'Morgan Hill' supported a population of in the order of 10^6 adult butterflies in 1987. The nine smaller patches labelled with arrows supported populations of in the order of 10^1 – 10^2 butterflies in that year. Eighteen other small patches were found to be suitable but unoccupied.

probably be unimportant, as they will tend to strike the smallest populations with the least influence on the metapopulation. Schoener & Spiller (1987) found this to be the case in Bahamian orb spider metapopulations. In populations of five spider species on 108 islands (distant from the continental mainland), which were monitored for 5 years, local extinction affected only the 10–40% (depending on species) smallest populations. Many of the larger populations appeared to be effectively immortal, in that their expected lifetimes (were these populations isolated) would be much longer than the timescale of interisland dispersal.

Metapopulation dynamics have seldom been quantified as directly and thoroughly as in the study of Schoener & Spiller (1987). However, it is probably common for metapopulations to contain similarly high variation in population

and patch size and to function as constellations of mainlands and islands. The Solomon Archipelago, on which avian colonization-extinction dynamics were studied by Gilpin & Diamond (1976, 1981), spans a five-to-six order of magnitude range in island size. A population size range of up to three orders of magnitude was reported by Thomas (1984) in a review of population studies of endangered British butterflies. Fritz (1979) estimated lifetimes ranging from 2 to 100 years for the local populations in a spruce grouse metapopulation, based on patch sizes, bird densities and a demographic model. In the Concho water snake, Soulé & Gilpin (1991) noted a mainland-island effect caused by variation in local densities of river riffles.

High variation in local population size may arise for other reasons than patch size, including chance. Metapopulations of aphids on fireweed (Addicott, 1978) consisted of ensembles of local colonies, lasting in total for the duration of the summer growing season (4–8 aphid generations). The majority of colonies were much shorter-lived than the metapopulation as a whole, but a few were large enough to last the entire season, leading Addicott (1978) to conclude that metapopulation persistence did not depend on the ongoing founding of new colonies. The variation in colony size appeared to be produced by chance factors in the process of colony establishment.

From the point of view of regional dynamics, it is not the variation in patch or population size *per se* that is significant so much as the variation in the persistence of local populations. Heterogeneity in the quality of the habitat may have this effect. In the source-sink systems discussed by Pulliam (1988) there is a net flow of migrants from persistent populations in good habitats ('sources') to populations in inferior habitats which act as sinks. The difference between these and mainland-island metapopulations lies in the nature of the peripheral, extinction-prone habitats. While islands are merely smaller than mainlands, sinks are qualitatively different from sources, being unsuitable in some way for survival and reproduction.

An example of a source-sink metapopulation is the checkered white butterfly (*Pieris protodice* Boisduval & LeConte) in the Central Valley of California (Shapiro, 1979). The source population occupies a riparian area, which is the only part of its regional range in which the butterfly can overwinter successfully. Every spring, emigrants found numerous smaller colonies on outlying patches of the host plant, sometimes at considerable distances from the source population. However, these colonies persist for about five generations, at most, before becoming extinct at the onset of the following winter. Similarly, a population of *Euphydryas editha wrightii* in Southern California was observed to undergo an explosive increase in numbers, following a series of especially favourable years. A number of peripheral colonies appeared on patches of marginal-quality habitat and subsequently disappeared (Murphy & White, 1984).

Peripheral or sink areas may be occupied only infrequently, while the source areas are always occupied, as in the examples above. From such situations, a continuum extends to metapopulations in which peripheral areas are occupied most of the time, but populations retract to core areas during adverse conditions. Emigrants from these refuge habitats then recolonize the extinction-prone habitats when favourable conditions return. An example is the Amargosa vole, a microtine subspecies endemic to an isolated desert marsh. Vole populations are widespread throughout the marsh in most years, but during occasional flood

years the vole survives only as disjunct populations on isolated hilltops (Freas & Murphy unpublished). Similarly, Strong *et al.*, 1990) found that populations of a leafhopper and its parasitoid in a coastal marsh survived a rare winter freeze under scattered piles of beach wrack.

Species coexistence may also be mediated by mainland-island or source-sink dynamics. In some insect predator-prey systems, it appears that the prey species is able to persist, despite the ability of the predator to drive it locally extinct, because of habitat refuges in which it is invulnerable to the predator (Beddington, Free & Lawton, 1978; Murdoch, Chesson & Chesson, 1985). Iwasa & Roughgarden (1986) model coexistence in locally competing intertidal organisms by assuming that for each species there is a source habitat in which it outcompetes the others. Regional sources or refuges constitute a qualitatively different explanation for coexistence than the extinction-colonization dynamics proposed in classical patch models (e.g. Horn & MacArthur, 1972; Slatkin, 1974; Hastings, 1978; Hanski, 1983; Bengtsson, 1991).

Hanski (1983) and Gilpin (1987) have previously noted the unrealism of the assumption that all local populations in a metapopulation are equally subject to extinction and contribute equally to colonization. To the extent that this assumption is violated, metapopulation processes (extinction and colonization) become less crucial to regional persistence. Persistence may depend more upon the local factors, such as large size or favourable habitat, that permit mainland or source populations to resist extinction.

Patchy populations

The kind and degree of connectedness between patches or populations is a critical feature in models of spatially structured populations. The classical metapopulation concept of Andrewartha & Birch (1954), Ehrlich & Birch (1967), and Levins (1969, 1970) portrays sets of relatively independent demes undergoing turnover on a timescale of years to generations. In contrast, models concerned with the effects of spatio-temporal variability on population stability (e.g. Roff, 1974; Chesson, 1981; Crowley, 1981; Roughgarden & Iwasa, 1986), though superficially similar to metapopulation models in that they depict local population units fluctuating independently, differ in that these units are coupled by very high dispersal (see also Taylor, 1988). In the extreme, complete mixing of progeny among patches is assumed. Here the designation 'patchy population' is used for such demographically united systems of patches. High interpatch dispersal means that the differentiation between local and regional timescales, a principal attribute of metapopulations, is diminished, and so is the potential for local extinction.

In practice, of course, it is impossible to draw a sharp distinction between metapopulations with true local extinction, and patchy populations in which extinction is absent or unimportant. However, if the average individual inhabits more than one patch in its lifetime, the patches clearly do not support separate populations. The fauna of patchy and ephemeral habitats, such as the insects that specialize on fallen fruit, rotting logs or water-filled treeholes, are often regarded as forming metapopulations. But such species are typically highly mobile; each patch usually supports only one generation of the insect, and adults oviposit on numerous patches (Kitching, 1971; Hanski, 1987). Similarly,

butterfly species which specialize on weedy host plants typically show high vagility compared with species using more permanent habitats (Scott, 1975; Blau, 1980). Gerrid water bugs (Kaitala, 1987) move frequently among the ephemeral ponds which they inhabit. In general, high interpatch dispersal may be said to be common trait in species of unstable, transient, and/or patchy habitats (see Hanski, 1987 for a review).

A considerable number of other 'metapopulations' in the literature appear to lie toward the high dispersal end of the continuum. A case in point is the classic study in which den Boer (1970, 1981) found asynchronous fluctuations in the numbers of carabid beetles trapped at various sampling points within a continuous habitat, on the scale of tens to hundreds of metres apart. Den Boer (1970, 1981) theorized that the beetle population is stabilized by the movement of individuals over distances greater than the scale of localized environmental fluctuations. Within-habitat dispersal also appears to enhance the persistence of populations of *Euphydryas editha*. Larval survival varies among different slope exposures, because the suitability of host plants is affected by an interaction between topography and yearly weather patterns. Both larvae and ovipositing adult butterflies disperse among slopes within continuous habitat (Weiss, Murphy & White, 1988). Many sessile marine organisms appear to spread their propagules widely in comparison to the scale of the patches on which recruitment and growth occur (Strathmann, 1974). Random dispersal may be a very general means of population persistence in spatiotemporally varying environments (Goodman, 1987).

Local differences in the abundance of predators or competitors are another source of spatiotemporal variation in population dynamics. High dispersal by a prey species or an inferior competitor may allow it to coexist with a predator or superior competitor. However, since the dynamics of predators and prey are coupled, the relationship of prey dispersal rates to coexistence may be complex; see Taylor (1988, 1991) for recent reviews of theory.

Thus, patchy population dynamics arise when dispersal takes place on a spatial scale greater than that of the local events causing population fluctuations. This may be expected to be the case in many species of patchy, transient or otherwise risky habitats; or such species may 'escape in time' through dormancy. High dispersal means that patches or sub-populations are united into a relatively persistent population in which there is little potential for local extinction. Local 'turnover' on patches, in such systems, is more the product of the movements of individuals than of mortality.

Non-equilibrium metapopulations

A great number of local extinctions take place, not in the context of a regional colonization-extinction equilibrium, but in the context of the regionwide decline of a species. Recolonizations may occur infrequently or not at all. This usually occurs as the species' habitat is undergoing long-term fragmentation, reduction or deterioration. Habitat fragmentation leaves local populations more prone to extinction, because they are isolated from 'rescue' by immigration, and also to limit or prevent recolonization. One natural example is the series of extinctions of mountain mammal populations, caused by the reduction and isolation of mountaintop habitats during post-Pleistocene warming (Brown, 1971; Taylor,

1991). Much more abundant, however, are cases of regional declines caused by human impacts on natural habitats. Wilcove, McLellan & Dobson (1986) and Rolstad (1991) provide reviews of habitat fragmentation and local extinction in temperate birds and mammals. Arnold (1983), Thomas (1984) and Cappucino & Kareiva (1985) provide similar examples from butterflies.

Conservation of species in fragmented habitats is an important area for the application of metapopulation models. This issue is discussed by Gilpin (1987) and Hanski (1989, 1991), and only a few additional points are raised here. First, fragmentation may very often result in mainland-island situations in which a single remnant population is of overwhelming importance (e.g. the grizzly bear in the United States, Gilpin, 1987). Second, fragmentation may be fine-grained in relation to the range of movement of individuals; this appears to be true in many cases involving birds in forest fragments (Rolstad, 1991). Fine-grained fragmentation is perhaps better thought of as altering habitat quality than as leading to the isolation and extinction of local populations.

Third, unstable regional extinction-colonization dynamics may be induced by anthropogenic habitat changes other than outright fragmentation. For example, species dependent on disturbance-generated habitats are sensitive not only to reduction in the amount of the habitat matrix, but also to changes in the disturbance regime. This is the situation for a number of endangered butterflies in Britain and the United States. In Britain, several species requiring sunny openings in woodlands are declining not only due to deforestation, but also to the cessation of traditional forest coppicing, which generates forest clearings (Warren, Thomas & Thomas, 1984; Warren, 1985). Another British species is declining because of the demise of peat-cutting, which opens up patches in heathlands (Thomas, 1985). In the U.S., the combination of fire suppression and habitat loss to urbanization threaten the Karner blue butterfly (*Lycaeides melissa samuelis* Nabokov) which depends on a host plant characteristic of post-fire succession (Cryan & Dirig, 1978; Fried, 1987; Thomas, 1983).

Because of reduced disturbance, new habitats are generated for these butterflies at insufficient rates. When new habitats do appear, they are increasingly unlikely to become colonized by the butterflies (Thomas, 1984). These cases are similar to the disturbance-driven population dynamics which have been frequently studied in intertidal communities (e.g. Paine & Levin, 1981; Caswell & Cohen, 1991), with the important difference that the butterflies' rates of dispersal between disturbed patches are low, quite possibly too low to prevent eventual regional extinction. An interesting application for metapopulation models would be to predict the minimum size of the disturbance mosaic (Pickett & White, 1985) required to support these species. This has been attempted for the Karner blue butterfly by Givnish *et al.* (1988).

Classical metapopulations and intermediate cases

Waterflies (*Daphnia* spp.) in rockpools (Bengtsson, 1988, 1989, 1991) and pool frogs (*Rana lessonae* Camerano) in successional ponds (Sjögren, 1988, 1991) form metapopulations in which there is neither extreme variation in population sizes or other determinants of persistence, nor extremely high rates of movement among patches. These appear to represent close approximations to Levins

metapopulations, sets of discrete local populations which are subject to local extinction and persist regionally because of (re-)colonization.

Of course, the distinction between these and the other types of metapopulations is largely a function of the timescale being considered. There is sufficient variation in persistence among pool frog populations that this metapopulation could probably persist for decades without recolonization, despite numerous extinctions (Sjögren, personal communication). Similarly, Pajunen (1986) has suggested that certain *Daphnia* pools support mainland populations considerably more persistent than those in other pools. But metapopulations such as these, with moderate levels of variation in population size and moderate dispersal among patches, may provide the majority of real-world cases in which local extinction both occurs and has regional significance.

Other intermediate cases may arise from the spatial arrangement of patches. There is widespread evidence in island biogeographic studies for rescue effects (Brown & Kodric-Brown, 1977; see review in Ebenhard, 1988), in which a patch is more likely to be occupied the nearer it is to other occupied patches (see also Ray *et al.*, 1991). This suggests the possibility of a metapopulation (Fig. 1E) combining features of the mainland-island and patchy population structures: dispersal unites central patches into a single population, but is low enough to allow local extinctions on peripheral patches. A possible example of this is the metapopulation of hyraxes on kopjes (rockpiles) studied by Hoeck (1982, 1989). Another intermediate case, one which combines mainland-island and classical metapopulation structure, is exemplified by the archipelago vole populations studied by Ebenhard (1988). With increasing distance from the mainland, insular populations are influenced less by the mainland population and more by among-island dynamics.

SUMMARY

A critical examination of the metapopulation literature reveals that local extinction does not have the same role or degree of importance in all situations. Local extinction may not occur at all, if interpatch dispersal is always high, or it may only affect populations in small patches or poor habitats. Local extinctions may be a manifestation of a species' regional decline. Only in a subset of metapopulations in the empirical literature does the analogy of a 'population of populations', existing in a balance between birth (colonization) and death (extinction), seem to apply well.

The birth-death analogy arose from a simple model which did not include such refinements as variation in population persistence, explicit spatial structure of patches and temporal correlation in extinction. When such real-world features are considered, a general result may be to shift importance away from regional process (extinction and colonization) and more toward local factors, such as large population size, habitat heterogeneity and within-population dispersal, in determining persistence.

Of course, the empirical evidence is far too limited for secure generalizations to be made. There is undoubtedly a research bias toward systems with rapid local turnover, and too little evidence on the extinction and colonization dynamics of long-lived organisms. However, there may also be real biological reasons for the seeming scarcity of cases of classical metapopulations. It is reasonable to expect

that most organisms are adapted to escape, in space or time, from the environmental risks they normally face, and a side effect of such adaptations will be to make the extinction of local populations less likely to be a routine part of population dynamics.

If these empirical considerations suggest a diminished role for local extinction in metapopulations, they are not intended to downplay the significance of metapopulation dynamics broadly defined. The interplay between local and regional processes can promote the regional persistence of locally unstable species, and the regional coexistence of locally incompatible combinations of species, with or without the complete extirpation and refounding of separate local populations.

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RESPONSES OF SIBERIAN FERRETS TO SECONDARY ZINC PHOSPHIDE POISONING

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Abstract: The hazard of operational-type applications of zinc phosphide (Zn_3P_2) on a species closely related to the black-footed ferret (*Mustela nigripes*), was evaluated by feeding 16 Siberian ferrets (*M. erversmanni*) rats that had been killed by consumption of 2% zinc phosphide-treated bait or by an oral dose of 40, 80, or 160 mg of Zn_3P_2 . All ferrets accepted rats and a single emesis by each of 3 ferrets was the only evidence of acute intoxication. All ferrets learned to avoid eating gastrointestinal tracts of the rats. Subacute zinc phosphide toxicity in the ferrets was indicated by significant decreases (18–48%) in hemoglobin, increases of 35–91% in serum iron, and elevated levels of serum globulin, cholesterol, and triglycerides. Hemoglobin/iron, urea nitrogen/creatinine, and albumin/globulin ratios also were altered by the treatments. This study demonstrated that Siberian ferrets, or other species with a sensitive emetic reflex, are afforded a degree of protection from acute zinc phosphide poisoning due to its emetic action. The importance of toxicity associated with possible respiratory, liver, and kidney damage indicated by altered blood chemistries is not known.

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Black-footed ferrets probably were never abundant and now may be nearly extinct (Fortenbery 1972). Apparently the original range of this species corresponded closely to that of prairie dogs (*Cynomys* spp.), its principal food (Hillman 1968, Fortenbery 1972, Sheets et al. 1972). As prairie dog populations were suppressed by control measures and habitat changes, black-footed ferret populations also declined (Hillman 1968, Tietjen 1976). Along with reduction of their food source, ferrets were subjected to possible poisoning with rodent control chemicals such as sodium monofluoroacetate (1080) and strychnine as the result of eating poisoned animals (Rudd and Genelly 1956, Hillman 1968, Schitoskey 1975, Tietjen 1976). Zinc phosphide (Zn_3P_2), an efficacious rodenticide (Schoof 1970, Dimmick 1972, Hilton et al. 1972, Hood 1972) that appears comparatively free of secondary hazard (Bell and Dimmick 1975, Schitoskey 1975, Tietjen 1976), has been evaluated and registered as a substitute for more hazardous tox-

cants because of the potential secondary hazard associated with the use of these chemicals for prairie dog control. However, direct evaluation of secondary poisoning risk to endangered black-footed ferrets was not possible. Therefore the present study was conducted with closely related Siberian ferrets as research surrogates.

Our primary objective was to determine if rodents killed by operational concentrations of zinc phosphide-treated bait (steam-rolled oats containing 2% Zn_3P_2 by weight) are hazardous to a species of presumed physiologic similarity to the black-footed ferret. Other objectives were to determine subtle physiologic responses of ferrets to secondary zinc phosphide poisoning and attempt to estimate the probable margin of safety for ferrets fed operationally killed rodents.

The concept of the experiment was proposed by R. C. Stendell and L. F. Stickel. H. P. Tietjen provided technical assistance. P. A. Harker assisted with all aspects of the experiment and B. I. Wil-

liams provided husbandry support. The manuscript was reviewed by E. H. Dustman, W. C. Eastin, Jr., and H. P. Tietjen.

METHODS

Thirty-seven Siberian ferrets (2 females and 35 males) were live-trapped near Voronezh, U.S.S.R., in 1975. All males were considered young-of-the-year at the time of capture. Eighteen of the original males (3 years old) and 2 male offspring (1 2-year-old and 1 1-year-old) were selected at random and placed in individual pens consisting of a 2-compartment nest box adjoining a vinyl-coated wire mesh (2.2 cm) run (50 × 42 × 31 cm high) for the duration of the experiment. The light regime was 12 L : 12 D and ambient temperatures were 18–23 C. Water was available *ad libitum*.

Following a 7-day conditioning period during which ferrets were fed dead laboratory rats, each was anesthetized with ketamine hydrochloride (25 mg/kg intramuscularly) containing 10% acepromazine maleate, weighed, and given a physical examination. A baseline scan of selected blood chemistries was obtained (Carpenter and Hill 1979).

Laboratory rats ($\bar{x}$ weight = 210 g, SD = 14 g) were conditioned on a diet of 4% corn oil-fortified oat groats for 1–2 weeks before exposure to zinc phosphide. At 1500 hours on the day before exposure, randomly selected rats were assigned to a treatment group and fasted overnight. At 0830, rats received either a 1-ml oral dose of 40, 80, or 160 mg zinc phosphide (technical grade, 94% AI) in a corn oil suspension, or were given (*ad libitum*) a 4% corn oil-fortified bait containing 2% zinc phosphide. Treatments are hereafter referred to as control, RT-40, RT-80, RT-160, and RT-2%. Oral dosing of rats was performed on the morning

they were to be fed to the ferrets. However, the bait was presented to the rats on the morning preceding the day they were to be fed to the ferrets because it took longer for the rats to die from feeding on bait than from dosing. Control rats were killed with CO₂ gas; all other rats died from exposure to zinc phosphide.

Treatment of rats with zinc phosphide was based on a preliminary feeding trial in which laboratory rats weighing about 200 g died from eating 2–3 g of 2% bait (40–60 mg Zn₃P₂) and on a study showing that 3–3.6 g of 2% bait (60–72 mg Zn₃P₂) was lethal to adult prairie dogs (Tietjen 1976). The 40- and 80-mg doses represent maximum quantities of zinc phosphide likely to be encountered in operationally poisoned rodents, and the 160-mg dose provided a margin of safety exposure. Rats fed 2% bait and those dosed with 40 mg received equivalent zinc phosphide exposures and provided the tie between operational poisoning and our controlled laboratory studies.

Ferrets were stratified by weight and 4 (2 above and 2 below median weight) were randomly assigned to each treatment group and fed 1 rat every 2nd day for a total of 5 feedings. Feeding records for each ferret included the quantity and anatomical portions of rats consumed. Care was taken to determine if the gastrointestinal (GI) tract had been eaten because of the possible presence of unaltered zinc phosphide. Each ferret was carefully observed at least 3 times daily for evidence of toxic signs and vomitus (Zn₃P₂ is an emetic). At the end of the experiment, ferrets were anesthetized, weighed, and examined. A 2nd blood chemistry scan was performed. Postmortem examinations were performed on 2 randomly selected ferrets from treatments RT-40, RT-80, and RT-160.

Ferrets were fed on alternate days to ensure that the majority of each rat carcass would be eaten, thereby helping to equalize overall feeding behavior and zinc phosphide exposure among treatment cohorts. Pretreatment conditioning showed that over one-half of nearly all carcasses were eaten by the 2nd day, and that no putrefaction of the remnants occurred. We therefore considered consumption >105 g as normal feeding.

Blood chemistry values were determined for all ferrets by collecting sera before and after treatment to assess possible physiologic and pathologic responses to zinc phosphide. Ten ml of blood were obtained via cardiac puncture of each anesthetized ferret. One ml of whole blood was placed in a tube containing an anticoagulant (EDTA) and the remainder was placed in a tube without additives and permitted to clot at room temperature and then centrifuged at 3,000 rpm for 10 min before serum was removed. Hematocrit (Hct) and hemoglobin (Hb) were determined from the EDTA blood samples. Hct was measured by the microhematocrit method; centrifugation was for 5 min at 7,500 rpm. Hb was determined on whole blood by the cyanomethemoglobin procedure (Hycel kits 116 and 117, Hycel Inc., Houston, Tex.).

Serum samples were refrigerated and transported to a commercial laboratory (Vet-Lab, A Division of Metpath, Hackensack, N.J.) within 2–4 hours of separation for analysis on computer process-controlled equipment. Blood chemistries determined were glucose, creatinine, blood urea nitrogen, uric acid, total and direct bilirubin, total protein, albumin, globulin, total lipids, cholesterol, triglycerides, alkaline phosphatase (EC 3.1.3.1), γ -glutamyl transpeptidase, (EC 2.3.2.2), aspartate aminotransferase (EC 2.6.1.1),

alanine aminotransferase (EC 2.6.1.2), lactate dehydrogenase (EC 1.1.1.27), calcium, chloride, iron, phosphorus, potassium, and sodium. Specific procedures were reported previously (Carpenter and Hill 1979).

Body weight comparisons were made on the basis of pre- to post-treatment changes for individuals as well as on post-treatment differences among experimental groups. Blood chemistries were treated similarly, except that individuals were also compared to the pretreatment baselines, i.e., individual values exceeding ± 2 SD of the mean were considered abnormal (Copeland 1974). Statistical procedures were parametric (paired *t* test, 1-way analysis of variance) or non-parametric (Wilcoxon rank sum, 2-tailed) (Wilcoxon and Wilcox 1964) as appropriate and indicated for various comparisons in text. Separations for significant *F* tests ($P = 0.05$) were by Duncan's (1955) procedure. $P = 0.05$ was considered significant for all statistical procedures.

RESULTS

All 20 ferrets accepted the rat diet during pretreatment and 18 regularly ate more than one-half (>105 g) of each rat carcass presented. Feeding behavior (e.g., time of feeding, anatomical preference) varied considerably among individuals during the 2-day feeding periods, but each ferret readily ate entrails including the gastrointestinal tract. By the end of the pretreatment period overall average consumption was 149 g (SE = 8.6) of rat carcass per ferret per feeding, or, on the basis of the ferret's weight, 77 g/kg/day (SE = 5.3).

In the experimental phase of the study, overall consumption (mean g/kg body weight/day) for controls was similar to that observed during pretreatment. Ferrets receiving zinc phosphide-treated rats

Table 1. Feeding performances and body weight changes of Siberian ferrets fed rats killed with different zinc phosphide treatments.

Rat treatment (Zn ₃ P ₂)	Consumption rate (g/kg ferret wt/day)				Number of feedings on GI tract	Weight change (%)	
	Pretreatment (7 days)		Experimental (9 days)			$\bar{x}$	SE
	$\bar{x}$	SE	$\bar{x}$	SE			
Control	78	15.3	76	14.7	14 ^a	-4.0	2.6
RT-2%, 2% bait	85	9.4	62 ^b	11.3	10	-6.4	1.3
RT-40, 40 mg	65	8.7	58	3.4	12	-14.9	5.0
RT-80, 80 mg	84	2.7	59 ^b	5.4	9	-11.0	1.2
RT-160, 160 mg	74	19.9	67	21.6	6	-10.8	6.7

^a Total feedings on GI tract during 16 feeding bouts per treatment (4 replicates × 4 2-day bouts).^b Different from pretreatment ($P < 0.05$, paired t test).

had lower consumption rates compared to pretreatment (Table 1). These decreases in consumption were significant ($P < 0.05$) for ferrets on RT-2% ($\bar{x} = -27\%$) and RT-80 ($\bar{x} = -30\%$). Ferrets fed RT-40-poisoned rats (the dose equivalent of RT-2%) consumed quantities similar to ferrets that were fed RT-2%- and RT-80-poisoned rats, but the average decrease of only 11% from pretreatment consumption was not significant. Random chance of treatment assignment appeared to contribute to this result because ferrets on RT-40 ate an average of 21–24% less than other groups during pretreatment. Ferrets on RT-160 rats consumed total quantities comparable to controls throughout the study, however, ferrets on RT-160 rats fed on the gastrointestinal tract in only 6 of 16 feeding bouts (38%) compared to 14 of 16 (88%) for controls. During pretreatment, feedings on gastrointestinal tracts occurred 89 and 92% of the time for RT-160 and control ferrets. Ferrets on other zinc phosphide treatments ate gastrointestinal tracts in 56–75% of the feedings.

Time-related changes in feeding behavior occurred for ferrets on all zinc phosphide treatments over the 1st 4 2-day feeding periods (Fig. 1). The 5th feeding period was only 1 day and was

omitted from these comparisons. In the 1st feeding period, 82% of the ferrets fed poisoned rats ate more than one-half of the carcass; this frequency decreased to 44, 44, and 56% for the 2nd, 3rd, and 4th periods. Control frequency was 100% for the 1st period and 75% thereafter. Although 94% of the ferrets fed poisoned rats ate all or a major portion of the gastrointestinal tract during periods 1 and 2, only 31 and 12% of these ferrets ate any of the gastrointestinal tract in periods 3 and 4. There was no apparent dose-response relationship between rat treatment and avoidance of gastrointestinal tracts. Control animals ate gastrointestinal tracts 75–100% of the time. Although zinc phosphide stimulates emesis (Lisella et al. 1971), evidence of vomitus was found only 3 times, once each on treatments RT-2% (ferret #40), RT-40 (#26), and RT-160 (#41). Overt signs of toxicity were not observed for any ferret during this study.

The average weight of the ferrets at the beginning of the study was 987 g (extremes 722–1,605 g, median 980 g). Nineteen of the ferrets lost weight during the experiment (Table 1). Average losses were 4.0% for controls and 6.4–14.9% for ferrets on zinc phosphide treatments. Within-treatment variances were large

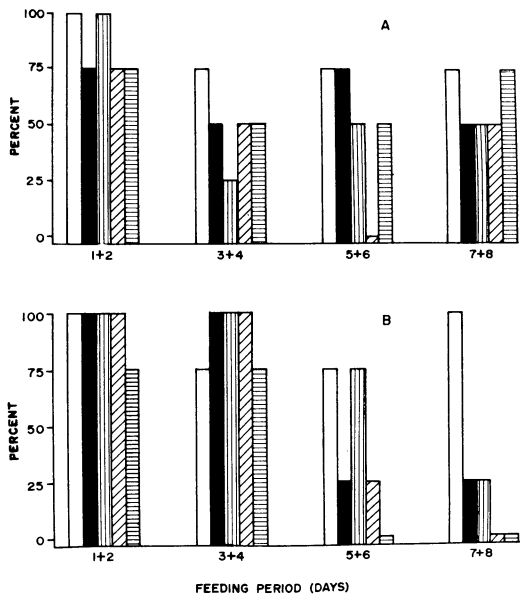


Fig. 1. A. Percentage of ferrets that ate >105 g of rat carcass during a 2-day feeding period. B. Percent of times all or a portion of the GI tract was eaten during a feeding. Control (open bar); Zn₃P₂, RT-2% (solid); RT-40 (perpendicular lines); RT-80 (diagonal lines); and RT-160 (horizontal lines).

for all groups and statistical separation of means was not possible. These variances are exemplified by ferrets on the extreme treatments (control and RT-160). Control #38 ate 16–67% less per feeding than the other 3 control animals, even though it was 20% heavier than 2 of them at the start of the study. This animal experienced a 12% weight loss while the other 3 controls remained within 3% of their pretreatment weights. Ferret #50 on RT-160 increased in weight by 3.1% while the other animals in the group lost 6.9–29.1% of their weight. Ferret #50 completely devoured every rat during the pretreatment period and the 1st poisoned rat it was offered; thereafter it ate all but the gastrointestinal tract. Average consumption rates for ferrets on RT-160 varied from 17.7 (#31) to 121.2 g/kg/day

(#50) compared to controls which varied from 40.8 (#38) to 102.9 g/kg/day (#14).

Concentrations and ratios of certain blood chemistries were altered ($P < 0.05$) from control values for ferrets fed zinc phosphide-poisoned rats (Table 2). Hemoglobin was reduced by averages of 18–48%; serum iron was increased by 35–91%. These concomitant changes yielded hemoglobin/iron ratios that averaged 69, 61, 72, and 56% less than controls for treatments RT-2%, RT-40, RT-80, and RT-160, respectively. Triglyceride concentrations were elevated for ferrets on RT-2% and RT-40 by averages of 83 and 93% compared to controls ($P < 0.01$). Triglyceride levels for ferrets on RT-80 and RT-160 averaged 57 and 111% higher than controls, but these high dose treatments were subject to large within-treatment variances and were not statistically separable.

Other ratios of possible clinical importance that were altered during this experiment were urea nitrogen/creatinine and albumin/globulin. The urea nitrogen/creatinine ratios for ferrets fed poisoned rats were increased by 2–2.6 fold over controls, but the differences were significant only for RT-2% ($P < 0.01$) and RT-160 ($P < 0.05$); RT-40 and RT-80 probabilities were $0.05 < P < 0.10$. By themselves, neither urea nitrogen nor creatinine were separable from controls for any zinc phosphide treatment. Albumin/globulin ratios decreased ($P < 0.05$) for ferrets on treatments RT-40 and RT-160, but not for other treatments. Ratios that were calculated and shown unaffected were aspartate aminotransferase/alanine aminotransferase, lactate dehydrogenase/aspartate aminotransferase, and sodium/potassium.

Hemoglobin, globulin, cholesterol and triglycerides were the only chemistries

Table 2. Significantly altered blood chemistries of selected ratios of Siberian ferrets fed rats killed with different zinc phosphide treatments.

Variable	Zn ₃ P ₂ treatment (rat exposure)									
	Control		RT-2% (2% bait)		RT-40 (40 mg)		RT-80 (80 mg)		RT-160 (160 mg)	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Hemoglobin, g/dl	18.5	0.4	10.9 ^a	1.6	9.8 ^a	2.9	9.7 ^a	3.0	15.2	1.5
Iron, μ g/dl	125	25.3	239 ^a	46.8	169	12.4	238 ^a	40.5	234 ^a	30.0
Hemoglobin/iron	148 ^b	28.9	46 ^a	4.3	58 ^a	14.8	41 ^a	15.2	65 ^a	5.3
Creatinine, mg/dl	1.3	0.1	1.2	0.15	1.3	0.1	1.2	0.1	1.2	0.3
Urea nitrogen, mg/dl	29.8	11.1	43.0	1.8	52.5	10.4	34.8	4.8	52.5	12.3
Urea nitrogen/creatinine	14.0	2.1	35.2 ^a	3.9	37.1 ^a	10.3	30.8 ^a	6.3	28.1	2.9
Globulin, g/dl	2.9	0.9	3.1	0.2	3.3	0.1	2.7	0.1	3.3	0.3
Albumin, g/dl	3.6	0.1	3.4	0.2	3.3	0.1	3.5	0.1	3.3	0.1
Albumin/globulin	1.3	0.01	1.1	0.1	1.0 ^c	0.1	1.3	0.1	1.0 ^b	0.1
Triglycerides, mg/dl	100	8.1	193 ^b	13.4	183 ^b	15.0	157	41.0	157	41.0

^a Different from controls ($P < 0.05$).^b Hemoglobin/iron ratio is in units $\times 1,000$, e.g., 148 = 148,000.

that were consistently altered from the baseline norm for individual ferrets (Table 3). All ferrets on RT-2% and 3 of 4 on RT-40 had depressed hemoglobin and elevated triglycerides. Each of these ferrets ate gastrointestinal tracts from poisoned rats at least twice. Globulin was elevated in 3 ferrets on RT-40, 2 on RT-2%, and 2 on RT-160, but was normal for those on RT-80. Cholesterol was elevated in 3 ferrets on RT-160 and only 1 animal on each of the other treatments. Ferrets with all of the aforementioned determinations outside the norm were #40 (RT-2%), #25 (RT-40), and #41 (RT-160), as

they were associated with 2 (#41), 3 (#25), or 4 (#40) feedings on gastrointestinal tracts.

DISCUSSION

The only overt evidence of acute intoxication of Siberian ferrets fed zinc phosphide-poisoned rats was a single emesis by each of 3 ferrets. That they were able to consume poisoned animals and not be affected more adversely was probably due to their avoidance of chemicals by not eating gastrointestinal tracts of the rats. Whether this avoidance was a response to the emetic property of zinc

Table 3. Altered blood chemistry of individual Siberian ferrets fed rats killed with different zinc phosphide treatments.^a

Variable (norm)	Zn ₃ P ₂ treatment (rat exposure)																			
	Control				RT-2% (2% bait)				RT-40 (40 mg)				RT-80 (80 mg)				RT-160 (160 mg)			
	14 ^b	30	38	43	19	23	28	40	18	24	25	26	17	36	46	81	31	41	42	50
GI tract feedings ^c	4	4	2	4	2	2	2	4	3	3	3	3	3	2	2	2	1	2	2	1
Hemoglobin (16.7–20.3 g/dl)					↓	↓	↓	↓	↓	↓	↓	↓	↓			↓		↓		↓
Globulin (1.8–3.1 g/dl)						↑		↑	↑	↑	↑	↑						↑	↑	↑
Cholesterol (151–142 mg/dl)								↑	↑	↑	↑	↑				↑		↑	↑	↑
Triglycerides (82–142 mg/dl)					↑	↑	↑	↑	↑	↑	↑	↑			↑	↑		↑	↑	↑

^a An individual is classed as a respondent (↑ = elevated, ↓ = depressed) when its value for a given blood chemistry is outside the baseline norm as reported by Carpenter and Hill (1979).^b Individual ferret identification number.^c Number of times all or a portion of the GI tract was removed and eaten during a feeding bout.

phosphide or to the taste or odor of the chemical could not be determined by this study. However, the pungent, garlic-like odor of the phosphine (PH_3) was conspicuous in the viscera of rats that had been eviscerated by ferrets. None of the 3 ferrets that vomited during a feeding bout ate gastrointestinal tracts thereafter.

Similar studies of secondary poisoning have also demonstrated the emetic properties of zinc phosphide and have shown other carnivores to be grossly tolerant of the poison, but there is evidence that certain species may be seriously affected. Kit foxes (*Vulpes macrotis*) that were fed kangaroo rats (*Dipodomys* sp.) killed with high doses of zinc phosphide (equivalent to 282 mg/kg/day per fox, for 3 days) consumed the entire rat, regurgitated, and reconsumed vomitus without apparent ill effect (Schitoskey 1975). In contrast, single dosages of zinc phosphide of 33–96 mg/kg were administered to 6 domestic cats through poisoned rats. Five of the cats accepted the rats, all vomited, 3 died, and 2 recovered; the 6th cat refused to eat (Chitty 1954). In comparison, maximum potential zinc phosphide dosages per feeding in our ferret studies were 40–49 mg/kg for RT-2%, 41–45 mg/kg for RT-40, 75–115 mg/kg for RT-80 and 155–214 mg/kg for RT-160. It is likely that reported dosages are biased high because there were certainly different time lapses between exposure and death of rodents fed to carnivores in all of these studies. Nonetheless, some of the ferrets probably received exposures comparable to those causing serious toxicity for other species.

Direct comparisons of acute peroral zinc phosphide toxicity were not possible between carnivores because these species possess a vomiting reflex which makes single-dose trials with strong emetics difficult to assess. The only LD₅₀ reported for a carnivore was 93 mg/kg for kit foxes

(Schitoskey 1975). Most rodents are highly susceptible to zinc phosphide toxicity because they do not have a vomiting reflex. This susceptibility is indicated by the following LD₅₀'s: nutria (*Myocastor coypus*), 5.6 mg/kg (Hood 1972); prairie dog, 18.0 mg/kg (Tietjen 1976); and Norway rat (*Rattus norvegicus*), 40.0 mg/kg (Schoof 1970). Zinc phosphide therefore appears to be at least 2–15 times more toxic to rodents than to carnivores.

Clinical findings of zinc phosphide toxicity in the ferrets in this study were alterations in certain blood chemistry values. Whereas acute zinc phosphide toxicity is primarily due to gastric production and absorption of phosphine gas that may result in respiratory (Janda and Bosseova 1970) or heart failure (Chitty 1954), the etiology of the subacute effects is unknown. However, our observed hemoglobin depressions coupled with increased circulating iron suggest that an additional mechanism of action may result from ionic zinc. Ionic zinc may result as a breakdown product during formation of phosphine gas (Hilton et al. 1972).

Excess zinc ions have been shown to increase the rate of cellular heme degradation by inducing synthesis of heme oxygenase in the liver. This heme degradation, in turn, may deplete cellular heme proteins such as microsomal respiratory cytochromes, e.g., P-450 (Maines and Kappas 1977). Also, increased heme degradation could depress hemoglobin synthesis because heme is essential to the formation of hemoglobin. Iron levels in the blood may be elevated because iron from degraded heme or cytochrome is retained for reuse (Harper 1973). The biological significance of these possibilities are (1) impairment of oxygen transport due to reduced hemoglobin levels and (2) altered detoxicating potential if cytochrome P-450 is degraded.

Zinc phosphide has been associated

with damage to liver, kidney, and heart tissue (Chitty 1954, Stephenson 1967, Janda and Bosseova 1970). Serum urea nitrogen/creatinine ratios above 20 in our ferrets on all toxic treatments may be indicative of renal damage (Sullivan et al. 1972). Elevated serum iron, globulin, triglycerides, and cholesterol may all be indicators of liver disorders (Zimmerman 1974). However, the elevated triglyceride and cholesterol levels in our animals could have been caused by food deprivation because most ferrets on zinc phosphide treatments reduced their food consumption and lost considerable amounts of body weight.

Our ferret study supports previous toxicity studies in which species with a sensitive emetic reflex are afforded a degree of protection from acute zinc phosphide poisoning because of its emetic action. Thus, occasional feeding on prey poisoned by zinc phosphide would not appear to be an acute hazard to species such as the Siberian ferret or its close relative the black-footed ferret, provided alternative prey is also available. However, the importance of toxicity associated with possible respiratory, liver, and kidney damage from repeated exposure to zinc phosphide as indicated by observed alterations in blood chemistries is not known at this time and warrants additional study.

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FIELD OBSERVATIONS OF BLACK-FOOTED FERRETS IN SOUTH DAKOTA¹

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The black-footed ferret (*Mustela nigripes*) an endangered species, has been under investigation in South Dakota since 1962 (Henderson *et al.*, 1968; Progulske, 1968). The present study was conducted from April 1966 through December 1967 to learn more of the ferret's life history and ecology.

My observations were restricted to western Mellette County in southwest South Dakota, but ferrets have been seen by others throughout the western part of the state where ranching is the primary industry.

DESCRIPTION OF STUDY AREA

All black-footed ferrets that were observed inhabited six black-tailed prairie-dog (*Cynomys ludovicianus*) towns which varied in size

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from 15 to 100 acres. Five towns were on rolling grassland and one was located on low terraces adjacent to a creek. Soils in the area are mainly solodized-solonetz with a thin friable surface layer underlain by a dense, dispersed clay layer. (Westin *et al.*, 1959). These sites support a growth of western wheatgrass (*Agropyron Smithii*),² green needlegrass (*Stipa viridula*), sand dropseed (*Sporobolus cryptandrus*), blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*). In disturbed sites where prairie-dog activity was greatest, prickly pear (*Opuntia* spp.), red three-awn (*Aristida longiseta*), tumblegrass (*Schedonnardus paniculatus*), curlycup gumweed (*Grindelia squarrosa*) and woolly plantain (*Plantago Purshii*) were commonly found.

Aerial and ground surveys showed that prairie-dog towns were distributed throughout the western half of Mellette County. In some areas, 11 prairie-dog towns were known to occur per township. Other areas had only one or two towns per township. All ferrets observed during the study were on prairie-dog towns within a radius of ten miles. Prairie-dog towns where ferrets were not observed existed within four miles of towns inhabited by ferrets.

RESULTS AND DISCUSSION

Ferrets were most readily observed at night by use of a spotlight. Their eyes appeared bright green and could often be seen up to 200 yards away. They appeared unalarmed by either a light or vehicle and paid little attention to the observer. During daylight hours ferrets were most readily detected by viewing prairie-dog towns with a spotting scope or binoculars.

Of 21 ferrets observed, 8 were presumed to be adults and 13 were known to be young. The young were in three litters, one of five (litter 1) in 1966 and two of four each (litters 2 and 3) in 1967.

Young in litter 1, when first observed on July 12, appeared three-fourths the size of the adult female, and by late August had attained adult size. Young ferrets closely resembled the adult, but their mask and feet were not as dark. The adult female appeared thin and unkempt.

Young in litter 2, when first observed in early July, appeared one-third the size of the adult female. They also closely resembled the adult except for a lighter mask and feet. Young in litter 3 appeared adult in size when first observed in early August. Little data were gathered from these ferrets as litter 2 was under intensive observation at that time.

External sex organs provided the only reliable means of sex

²Scientific names are according to Fernald (1950).

identification. A dark, ventral line running from behind the back legs to the penis was more pronounced in male ferrets but occurred in females. This line was observed in the field when ferrets stood on their hind legs (Henderson *et al.*, *op. cit.*).

Seasonal and Daily Activity Patterns

Twenty-one ferrets were observed from April through November, 1966 and 1967. None was observed from December through March, but hours of observation were few compared to those spent during the summer. Sign indicative of ferret activity was, however, seen frequently during winter months. Ferrets were most active during early morning and late evening (Table 1 and Figure 1).

Climatic factors did not appear to limit ferret activity. Although ferrets were most active in early morning and late evening, ferrets were observed during mid-day when air temperatures exceeded 100°F. During winter, ferrets were observed when air temperatures were below 0°F (Henderson *et al.*, *op. cit.*). Wind did not appear to affect activity since ferrets were active during 25-30 mile-per-hour winds. Although little time was spent on prairie-dog towns during rainy periods, one ferret was seen during a rain shower.

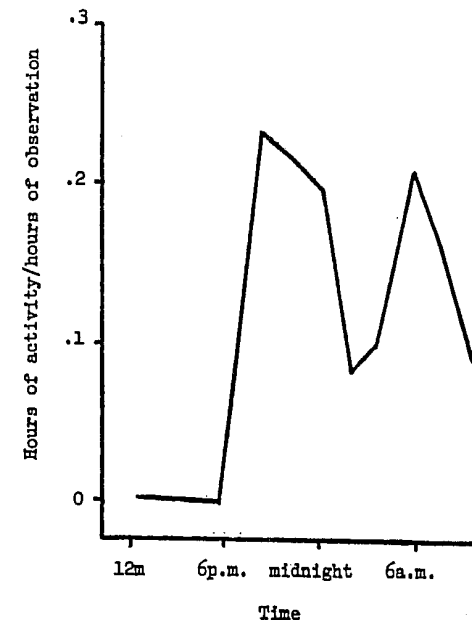


Figure 1. Daily activity of ferrets during summer months.

TABLE 1 FERRET OBSERVATIONS IN MELLETT COUNTY, S.D.

Time	No. of ferret observations	Hours spent observing dog-towns inhabited by ferrets	Hours ferrets were observed
<i>p.m.</i>			
12m-2	2	46	0.3
2-4	1	28	0.5
4-6	—	27	—
6-8	—	42	—
8-10	19	73	16.9
10-12	41	109	23.9
<i>a.m.</i>			
12-2	27	86	17.0
2-4	10	76	6.3
4-6	17	118	11.8
6-8	46	172	35.9
8-10	36	146	22.9
10-12m	14	102	8.8

Behavior of Mother and Young

In early July, young ferrets were never seen until the adult female brought them above ground. She held the young in her mouth by the skin on the back of their neck and backed out of the burrow. She would then carry it to another burrow and return for remaining young. As the young grew older, she no longer carried them but pulled them away one at a time from the burrow entrance and led them in single file over the dog town. When young ferrets were aware of an observer, they were reluctant to leave the burrow entrance. In such an instance, they would join the adult female only after much coaxing.

When first observed, eyes of young in litter 2 were only partially opened and it seemed that they followed the adult female by sound alone. She would descend the burrow occupied by her young and upon reappearing would utter a low, whimpering sound, apparently signaling the young to follow. Sense of hearing seemed very acute at close range. However, ferrets paid little heed to loud noises or the banging of a car door at greater distances.

On one occasion one young was carried by its mother to a burrow ten feet from where I was sitting. She left the young at the burrow entrance and returned to the burrow occupied by the remaining young. As I walked away, the young ferret followed, stopping only when I stopped. The adult returned and I moved so that she was between me and the young ferret. She then picked it up and carried it to another burrow. Returning to within four feet of me, she hissed and snarled in an attempt to drive me away.

Even though young ferrets were inquisitive, they seldom ventured more than a few feet from their burrow. Young ferrets were not particularly wary of humans or livestock and could often be approached within 5 feet before they went down their burrow. They

remained at the entrance and hissed or gave a bark closely resembling that of a prairie dog. When I approached adult ferrets, they remained above ground, descending only when the distance between us was a few feet.

Ferrets seemed to rely on their sense of smell to a large extent and often raised their nose to scent the air. The adult, when carrying her young from one burrow to another, always followed the same zigzag course that she traveled when she moved the first one of the litter. Once, when a vehicle was parked to intercept her travel, she passed under the vehicle when carrying her young to another burrow.

Young often played above ground, running in and out of burrows in pursuit of one another. They bit and pulled at each other, humped their backs, and ran on their toes. They scratched themselves frequently, often turning in circles attempting to bite their tail. Often they were seen chasing flies attracted to their burrow. When approached by the mother, they playfully jumped and bit at her.

No attempt by young to nurse the adult female was observed. Only in early mornings and during some nights was she observed to stay with her young. At other times she occupied different burrows in the vicinity.

Families frequented all portions of prairie-dog towns. Some burrows were utilized more than others, particularly before young were moving about on their own, but none appeared to be a permanent den.

In early July, young ferrets most often occupied one burrow. As the season progressed the mother located them separately throughout the prairie-dog town. At night the mother would go to each burrow occupied by her young and they would follow as she traveled over the town. Most often the ferrets would reappear from the same burrow they had gone down, but on several occasions, where prairie-dog burrows were close together, the ferrets would emerge from a different burrow.

One ferret in litter 1 was considerably larger than the rest. In litter 2, two ferrets appeared larger than the others. These larger individuals, believed to be males, were more active above ground than were the smaller ones. They were more aggressive and readily followed the adult, while the smaller ones were hesitant to leave the burrow. On August 18, 1967, one of the larger young attempted to mount the adult female but was unsuccessful.

Behavior of Individuals

Two different adult ferrets were first observed in a 35-acre prairie-dog town on May 2, 1966. Subsequent observations revealed at least one remained on the town until October. It is believed every observa-

tion after May 4 was of the same animal as distinguishing markings and scars were seen on its head and neck. There was no evidence of a litter in this town.

On August 25, 1966, a light-colored male ferret, probably an adult, was first observed on the prairie-dog town inhabited by litter 1. He was approximately one and one-half times larger than the adult female. On only one occasion were the adult ferrets observed in the near vicinity of one another. Other observations revealed adults in separate areas of the prairie-dog town. Young ferrets were not seen in the town after August 29, and neither adult ferret was seen after September 3, 1966. However, in August 1967, a ferret was observed on this town on one occasion.

Two ferrets inhabiting separate prairie-dog towns were observed in October and November of 1966. These ferrets displayed little activity and remained close to the burrows where they were first observed. Their sex or age could not be determined, and it is not known how long they inhabited the prairie-dog towns prior to initial observation. No ferrets were observed on these prairie-dog towns during summer 1967.

Movement and Dispersion

By late August and early September, the young no longer seemed to be dependent on the adult female. It was assumed the young left the prairie-dog towns at that time as they were never seen there again. Henderson *et al.* (op. cit.) reported that ferret sightings occurred most often in early fall, and that general movements probably occurred at that time.

Infrequent observations of adult animals on a prairie-dog town under intensive surveillance indicated they may have left the prairie-dog town for varying periods of time. During a six-week period from May 25 to July 4, 1966, observations were made on 24 days but ferrets were seen on only two occasions.

Food Habits and Feeding Behavior

Field observations indicated that ferrets fed entirely on prairie dogs, but thirteen-lined ground squirrels (*Citellus tridecemlineatus*), pocket gophers (*Geomys bursarius*), deer mice (*Peromyscus* spp.), and cottontail rabbits (*Sylvilagus floridanus*), as well as upland plovers (*Bartramia longicauda*), horned larks (*Eremophila alpestris*), and western meadowlarks (*Sturnella neglecta*) were potential prey of ferrets. Ferret scats were found infrequently and it is assumed the animals defecate underground. Two scats found were composed of only prairie-dog hair and bones. Ferrets were never

observed to prey on animals other than prairie dogs except those made available for experimental studies.

Young ferrets readily took both live-tethered and dead prairie dogs, thirteen-lined ground squirrels, cottontail rabbits, mice and birds placed near their burrows. Young ferrets approached live-tethered prairie dogs cautiously, sniffed them and then grabbed them quickly on the side of the neck before pulling them down a burrow. If prairie dogs were so securely staked that ferrets were unable to pull them down the burrow, they would not consume any part of the dog until the observer had left the prairie-dog town. Tethered prairie dogs displayed little defiance or fear of the ferrets, and only occasionally moved away when approached.

Adult ferrets were seen to descend burrows, emerge with dead prairie dogs which they had presumably killed and then carry them to another burrow.

During June 1966, the adult ferret inhabiting the 35-acre prairie-dog town was seen twice and both times killed young prairie dogs. On one occasion the ferret lay 20 feet from a burrow which contained a litter of prairie dogs. When an adult prairie dog emerged, the ferret went down and returned within 3 minutes with a young dog, and carried it to another burrow. The ferret eventually took six young dogs in this manner from one burrow.

On July 27, 1966, at 6:40 a.m., a ferret descended a burrow, brought up an adult prairie dog, and carried it 60 feet to a burrow occupied by litter 1. The ferret had difficulty in carrying the dog and dragged it most of the way, occasionally leaving it to inspect a nearby burrow.

On July 10, 1967, at 11:00 p.m., an adult female descended a burrow in which she had been digging and brought up three young prairie dogs. She carried them singly to another burrow after which she rejoined her young (litter 2). The following night she moved her young to the burrow where she had taken the three dead prairie dogs. The young ferrets remained in that burrow for three days.

On June 28, 1967, an adult ferret descended and remained in a burrow for 35 minutes. Upon emerging, it pulled a large, adult, male prairie dog, which was bleeding at the throat, out of the hole and carried it to another burrow 15 feet away. The ferret seemed to have difficulty in carrying this large prairie dog, as it would stop and rest about every 5 feet. Eventually the ferret left the prairie dog near a burrow and did not return. It is not known whether the observer caused the ferret to abandon the dead dog.

Only once was a ferret seen to capture a prairie dog above ground. On September 8, 1967, at 9:15 a.m., an adult female emerged from a burrow and ran towards another burrow where three prairie dogs

were standing near the entrance. As the ferret approached, two dogs quickly ran off, but the ferret grabbed the third by the side of the neck and attempted to pull it down the burrow. As the ferret backed down the burrow, the prairie dog braced its feet against the entrance. The ferret pulled the dog down after a 2-minute struggle. The ferret reappeared 20 minutes later, looked about for 1 minute and then went down the burrow again.

Effects of Predation on Prairie-dog Populations

Effects of ferrets on prairie-dog populations depend on size of the prairie-dog town and number of ferrets inhabiting it. Prairie dogs in towns inhabited by litters of ferrets appeared to decrease in number. Portions of towns often frequented by ferrets were thinly populated with prairie dogs, while portions only occasionally visited by the ferrets had higher densities. Because some of these towns were heavily shot by local ranchers, no quantitative measure of the extent to which ferrets preyed on prairie dogs was available.

In June 1966, the greatest number of prairie dogs observed on a town inhabited by a single adult ferret was 28 adults and 24 young. By November, only 36 dogs remained on that town. No prairie dogs were shot and, because of the town's small size, the counts of dogs are believed accurate. It is not known how long the ferret inhabited this town prior to the initial observation in May 1966. Coyotes (*Canis latrans*), badgers (*Taxidea taxus*), and rattlesnakes (*Crotalus viridis*) are predators which frequented the prairie-dog town, and may have contributed to population decline in prairie dogs.

Behavioral Responses of Prairie Dogs to Ferrets

Observations were made of adult prairie dogs displaying aggressive behavior toward ferrets, particularly when ferrets approached a burrow known to contain young prairie dogs. Prairie dogs would follow ferrets closely, often coming within inches when a ferret stopped at a hole. They often ran in front of ferrets and attempted to change their course of travel.

On one occasion, a ferret which was being followed closely by a large prairie dog, turned and grabbed the prairie dog by the back of its neck and threw it about 3 feet. The prairie dog barked loudly and continued to chase the ferret, which eventually went down a hole occupied by another prairie dog. On another occasion, an adult prairie dog came in direct contact with the ferret and caused it to drop the young dog it was carrying. The ferret chased the offending prairie dog for a short distance, then returned and picked up the dead dog.

Ferrets usually showed little interest in prairie dogs above ground,

even when the dogs approached within inches. Some prairie dogs near a ferret remained alert and watched it intently while others continued feeding and paid little or no attention.

Adult prairie dogs often attempted to cover burrows from which a ferret took young dogs, burrows into which the ferret disappeared with dead dogs, and burrows occupied by ferrets. If there were young prairie dogs in the covered burrow, adult dogs would uncover it later in the day. Ferrets appeared to have no difficulty in uncovering plugged burrows, either from below or above ground.

Ferret Sign

Sign indicative of ferret activity was usually observed before a ferret was seen, but ferrets did not always leave observable sign. A trench-like structure formed by a ferret digging in prairie-dog burrows, as described by Henderson *et al.* (op. cit.), indicated that ferrets were present. These trenches varied somewhat in appearance and were from 2 to 10 feet in length. After descending a burrow, ferrets backed out, pulling dirt away from the entrance with their front feet, and kicking dirt with their hind legs. The trench or depression was formed as the ferret pulled the dirt farther away in the same path each time. Occasionally a trench was not formed, but dirt was scattered in all directions. Except on one occasion ferrets were seen to dig only at night.

Fresh diggings, seen early in the morning before prairie dogs were active, were a reliable indicator of ferret activity. Numerous plugged burrows on a prairie-dog town might also indicate the presence of ferrets. However, Tileston and Lechleitner (1966) reported that black-tailed prairie dogs spent considerable time closing some burrows with plugs of earth, opening previously-plugged entrances and repairing and modifying existing mounds. Thus, the existence of plugged burrows, when no other sign was evident, would not provide a reliable indicator of ferret activity.

In summer, when prairie dogs covered holes occupied or used by a ferret, signs of trenching were usually destroyed the day after they were made. During winter months prairie dogs were less active and the soil was frozen; therefore, trenches persisted for a considerable length of time.

Fresh digging and ferret tracks were often observed in the snow. Distance between tracks was 14 to 17 inches when the animal was bounding and 6 to 8 inches when walking. Mink (*Mustela vison*) have been observed on prairie-dog towns, and since their tracks closely resemble those of ferrets, identification by tracks may not be accurate.

Welfare Factors

Potential predators observed on prairie-dog towns include badgers, coyotes, prairie rattlesnakes, bobcats (*Lynx rufus*), golden eagles (*Aquila chrysaetos*), ferruginous hawks (*Buteo lagopus*) and great horned owls (*Bubo virginianus*). In one instance, a great horned owl swooped at an adult ferret, but the ferret escaped down a burrow. Badgers were seen to dig in burrows previously used but not currently occupied by ferrets. Sperry (1941) found the remains of ferrets in three coyote stomachs. No predation upon ferrets was observed during this study.

Ticks of an unknown species were often observed on the adult ferrets, particularly on their neck, and prairie-dog fleas (*Opisocrostis hirsutus*) were taken from burrows inhabited by ferrets.

Man's activities probably present the greatest threat to ferrets. Henderson *et al.* (op. cit.) reported that of known ferret deaths, automobiles and domestic dogs have been responsible for more than any other form of mortality. Also, ferrets are probably shot when hunters mistake them for prairie dogs.

Control of prairie-dog numbers is a potential threat to ferret survival. Use of sodium monofluoroacetate (Compound 1080), one of the poisons used to control prairie dogs, has possible secondary poisoning effects on ferrets. In an effort to shed light on this subject, 1080-poisoned oats were free-fed to prairie dogs and the poisoned dogs were fed to domestic ferrets (*Mustela putorius*), the closest relative of the black-footed ferret.

Two ferrets were fed eviscerated 1080-poisoned prairie dogs on November 21 and 26, 1967, while two control ferrets were fed eviscerated non-poisoned prairie dogs. Ferrets showed no effects following the first feeding; however, after the second feeding both experimental animals showed abnormal behavior. The ferrets were then fed viscera from the prairie dogs they had consumed previously. One experimental animal died 1½ days later. The other became sick but apparently recovered on the same day. It was again fed viscera and died five hours after eating. Following termination of the experiment, control animals were fed viscera of poisoned dogs. They were fed several times before they died; however, after each feeding both animals exhibited abnormal behavior, which included poor coordination, violent thrashing and muscular spasms.

It has been demonstrated that 1080-poisoned prairie dogs can cause secondary poisoning of domestic ferrets, and when poisoned, ferrets exhibited abnormal behavior which might make them vulnerable to predators. Furthermore, large-scale eradication of prairie dogs un-

doubtedly influences the distribution and status of ferrets by greatly reducing their food supply.

SUMMARY

Twenty-one black-footed ferrets were observed at six different locations in southwest South Dakota between April 1966, and September 1967. All observations were made on black-tailed prairie-dog towns from 15 to 100 acres in size. Due to proximity of towns inhabited by ferrets, it is possible that individual animals were observed in more than one location.

Three litters of ferrets were studied. Young ferrets were most active during early morning and late evening hours. Ferrets remained as a group on prairie-dog towns until early fall when dispersal evidently occurred. Young ferrets accepted live-tethered and dead prairie dogs, mice, cottontails and birds placed near their burrow.

A trench-like structure formed by ferrets digging in prairie-dog burrows is a characteristic sign indicating that ferrets are present. Numerous plugged burrows may also indicate that prairie dogs have covered holes presently or recently occupied by ferrets.

All evidence indicated that prairie dogs were the principal food. Adult ferrets were observed to bring up dead prairie dogs from their burrows and carry them to other burrows. Also, one adult ferret was observed capturing a live prairie dog above ground. A reduction in prairie-dog numbers was noted on towns inhabited by ferrets.

Widespread use of sodium monofluoroacetate (Compound 1080) presents a threat to ferrets. It has been shown that 1080-poisoned prairie dogs can cause secondary poisoning of domestic ferrets. Also, eradication of prairie dogs reduces the ferret's food supply.

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No Evidence of Persistent *Yersinia pestis* Infection at Prairie Dog Colonies in North-Central Montana

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ABSTRACT: Sylvatic plague is a flea-borne zoonotic disease caused by the bacterium *Yersinia pestis*, which can cause extensive mortality among prairie dogs (*Cynomys*) in western North America. It is unclear whether the plague organism persists locally among resistant host species or elsewhere following epizootics. From June to August 2002 and 2003 we collected blood and flea samples from small mammals at prairie dog colonies with a history of plague, at prairie dog colonies with no history of plague, and from off-colony sites where plague history was unknown. Blood was screened for antibody to *Y. pestis* by means of enzyme-linked immunosorbent assay or passive hemagglutination assay and fleas were screened for *Y. pestis* DNA by polymerase chain reaction. All material was negative for *Y. pestis* including 156 blood samples and 553 fleas from colonies with a known history of plague. This and other studies provide evidence that *Y. pestis* may not persist at prairie dog colonies following an epizootic.

Key words: *Cynomys*, fleas, prairie dogs, sylvatic plague, *Yersinia pestis*.

Sylvatic plague is a flea-borne zoonotic disease of mammals caused by the bacterium *Yersinia pestis*. The disease primarily affects wild rodents, although many other groups of wild and commensal mammals can become infected (Gage et al., 1995). *Yersinia pestis* likely evolved in Asia with subsequent introduction onto all continents except Antarctica and Australia. In North America, the presence of *Y. pestis* was first identified in approximately 1900, having arrived in Pacific Coast ports via infected rats (*Rattus* sp.) on ships from Asia (Eskey and Haas, 1940). Today, the range of the disease in North America includes areas west of the 100th meridian (Cully et al., 2000).

The maintenance of *Y. pestis* in the wild depends on a complex set of interactions between host, vector, pathogen, and envi-

ronmental factors that are poorly understood. In general, the sylvatic cycle of infection is characterized by relatively stable periods of enzootic activity where *Y. pestis* circulates at low levels within the “maintenance” host community, followed by explosive epizootics involving one or more species of “amplifying” host that often experience high mortality. In western North America, these epizootic hosts include species of prairie dogs (*Cynomys*) in which plague-associated die-offs can be particularly dramatic, with mortality often approaching 100% within colonies (Rayor, 1985; Menkens and Anderson, 1991).

Prairie dogs often repopulate colonies following epizootics (Menkens and Anderson, 1991; Cully et al., 1997) and these colonies may then persist for many years or experience a plague epizootic again. Barnes (1982) reported a recurrence of plague epizootics within 4 to 5 yr and Cully et al. (1997) reported an epizootic again after 3 yr. Whether these cases in which the same colonies experience plague again represent a continued presence of infection among hosts in that area or a reintroduction of *Y. pestis* from surrounding areas is not known. The objective of this study was to address two competing hypotheses regarding the maintenance of *Y. pestis* between epizootics: 1) following an epizootic, *Y. pestis* persists in an area at low levels within the host community or 2) following an epizootic, *Y. pestis* does not persist in a localized area and recurring plague epizootics result from reintroduction of the organism (i.e., *Y. pestis* is absent during the period of recovery). To test this we collected blood and flea samples from small mammals at prairie dog colonies with a history of

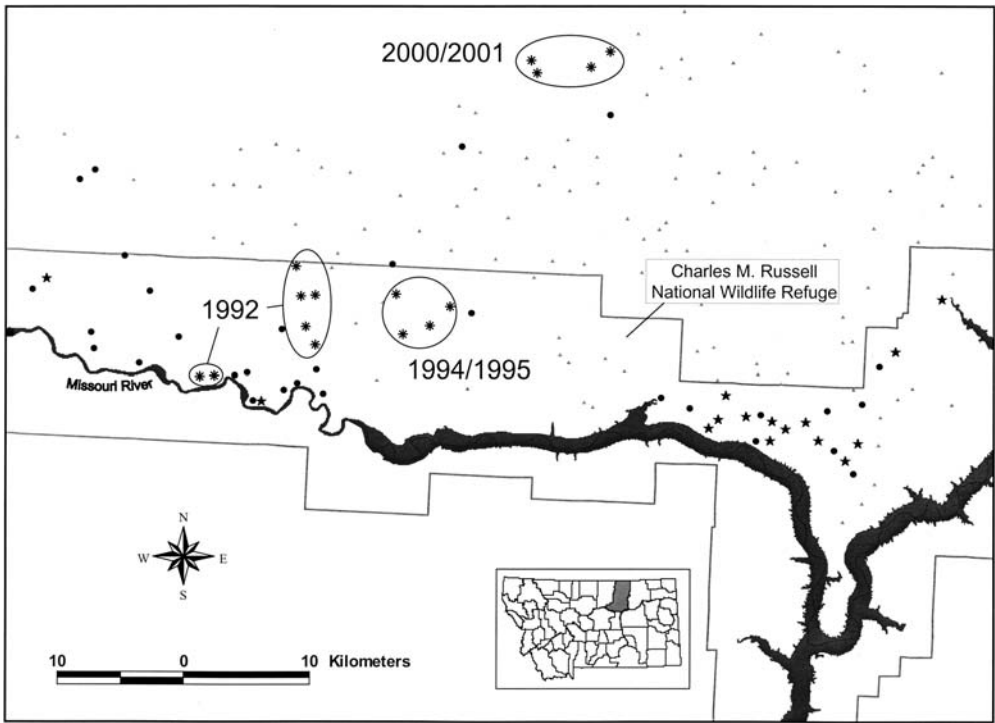


FIGURE 1. Map of southern Phillips County, Montana, showing the location of study sites including prairie dog colonies with a history of plague (asterisks), colonies with no history of plague (stars), and off-colony sites (circles). The year of plague epizootics also is indicated. Grey triangles are point locations of additional prairie dog colonies in the study area, some affected by plague, some not, and many where plague history is uncertain.

sylvatic plague epizootics and screened them for evidence of *Y. pestis*. In addition, we also collected samples from prairie dog colonies with no known history of plague and from off-colony sites where plague history was unknown.

The study took place in southern Phillips County, Montana, USA (47°35' to 47°50'N, 107°45' to 108°45'W) during June through August 2002 and 2003 (Fig. 1). The area is characterized by shrub and grassland habitats typical of the northern Great Plains, with big sagebrush (*Artemisia tridentata*), black greasewood (*Sarcobatus vermiculatus*), western wheatgrass (*Agropyron smithii*), and blue grama (*Bouteloua gracilis*) as common species. In addition, the southern margin of the county borders the Missouri River and consists of forested "breaks" topography with ponderosa pine (*Pinus ponderosa*),

Douglas-fir (*Pseudotsuga menziesii*), and Rocky Mountain juniper (*Juniperus scopulorum*). Elevations of study sites are between 740 and 1,050 m. The area is a mosaic of federal, state, and private land ownership and has supported approximately 300 active black-tailed prairie dog (*C. ludovicianus*) colonies during the past 20 years. The majority of study sites were located on the Charles M. Russell National Wildlife Refuge (CMR) with the remainder located on adjacent Bureau of Land Management (BLM) lands north of the refuge.

We sampled 36 sites in 2002 and 60 sites (36 resampled from 2002 and 24 new) in 2003. In total, 15 sites were prairie dog colonies with a history of plague, 15 were prairie dog colonies with no history of plague, and 30 were off-colony sites. Sites with a history of plague were

identified through regular mapping efforts by CMR and BLM personnel such that the location and year of epizootics among prairie dogs were known. Plague epizootics occurred between 1992 and 2001 at sites included in this study (Fig. 1). We are confident that die-offs attributed to plague were in fact plague epizootics because no other disease has yet been identified that causes such high mortality in prairie dogs (Barnes, 1993) and antibody to *Y. pestis* has been consistently found in coyotes (*Canis latrans*) and badgers (*Taxidea taxus*) in the study area (Matchett, 1999). Off-colony sites occurred in a variety of habitats and were located >400 m from the nearest prairie dog colony. Plague history at these sites was unknown because prairie dogs were the sentinel species used to indicate the presence or absence of plague epizootics and off-colony sites had no prairie dogs present for at least the past 20 years.

Each study site consisted of a 10 by 10 grid of 100 Sherman live-traps (H. B. Sherman, Tallahassee, Florida, USA) with 10-m spacing and 20 Tomahawk live-traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) placed at prairie dog burrows on colony sites and systematically throughout the grid at off-colony sites. We anesthetized captured animals with isoflurane ("IsoFlo" Abbot Laboratories, North Chicago, Illinois, USA or "IsoSol" Halocarbon Laboratories, River Edge, New Jersey, USA) before blood and flea sampling. Fleas were collected from animals by using a conventional flea comb as well as from prairie dog burrows by using a previously described swabbing technique (Holmes, 2003). Fleas were stored in vials containing 2% NaCl solution with a small amount (<0.01%) of Tween 80, identified to species, and then frozen. We collected blood samples of approximately 200 μ l from the retro-orbital sinus of small rodents by using micro-hematocrit tubes (Chase Scientific, Rockwood, Tennessee, USA) and for larger animals such as prairie dogs and cottontails (*Sylvilagus*

audubonii) we collected blood by clipping a hindfoot toenail to induce bleeding. In 2002, whole-blood samples were stored in a conventional (-20°C) freezer upon return from the field. In 2003, most blood samples were centrifuged the day of collection to separate serum, which was then stored as above. The remaining samples were collected onto individual Nobuto filter papers (Advantec MFS, Pleasanton, California, USA) which were air-dried, placed in paper envelopes, and stored at room temperature.

Laboratory diagnostics were performed at the Centers for Disease Control and Prevention, Division of Vector-Borne Infectious Diseases, Plague Section, Fort Collins, Colorado, USA. Serologic analyses followed protocols described by Chu (2000). Serum and blood samples were screened for the presence of antibody against *Y. pestis*-specific Fraction 1 antigen by using either a competitive enzyme-linked immunosorbent assay (cELISA) or a passive hemagglutination assay (PHA); all Nobuto strips were screened using PHA. Flea pools of one to 10 individuals (corresponding to the same species, host, date, and site of capture) were screened for the presence of *Y. pestis* with a multiplex polymerase chain reaction (PCR) assay described by Stevenson et al. (2003).

The number and source of samples screened for evidence of *Y. pestis* by serologic and PCR analysis is given in Tables 1 and 2, respectively. All 156 blood samples and 553 fleas from small mammals trapped at prairie dog colonies with a history of plague over two summers were negative for antibodies to and DNA from *Y. pestis*. Likewise, all materials from prairie dog colonies with no history of plague (369 blood, 1,894 fleas) and from off-colony sites (439 blood, 603 fleas) were negative for antibodies to and DNA from *Y. pestis*. Although we sampled an equal number of prairie dog colonies with and without a history of plague in each year of the study, the number of diagnostic samples collected at colonies with no

TABLE 1. Number and source of serum and blood samples collected in Phillips County, Montana, during June through August 2002 and 2003. Samples are from prairie dog colonies with a history of plague (Plague), prairie dog colonies with no history of plague (No Plague), and off-colony sites (Off).

Host	2002			2003		
	Plague	No Plague	Off	Plague	No Plague	Off
<i>Cynomys ludovicianus</i>	22	36	—	17	32	—
<i>Microtus ochrogaster</i>	—	—	—	1	—	20
<i>Neotoma cinerea</i>	—	—	—	—	—	4
<i>Onychomys leucogaster</i>	1	1	1	12	6	3
<i>Peromyscus maniculatus</i>	45	84	98	53	205	302
<i>Reithrodontomys megalotis</i>	—	—	—	—	—	4
<i>Sylvilagus audubonii</i>	3	1	—	2	4	4
<i>Tamias minimus</i>	—	—	—	—	—	3
Total	71	122	99	85	247	340

history of plague was greater because capture rates were consistently higher at those sites than at colonies with a history of plague.

Two previous studies (Lechleitner et al., 1968; Cully et al., 1997) followed the progression of plague epizootics among prairie dogs and demonstrated that, in general, *Y. pestis* positive fleas from

prairie dogs, their burrows, and associated mammals are most likely to be collected during an epizootic. These studies also illustrated that one year following an epizootic, some *Y. pestis* positive fleas may still be present in prairie dog burrows, but after two years, there is little or no evidence of *Y. pestis* in the vector community. Serologic results from these

TABLE 2. Number and source of fleas collected for plague testing in Phillips County, Montana, during June through August 2002 and 2003. Samples are from prairie dog colonies with a history of plague (Plague), prairie dog colonies with no history of plague (No Plague), and off-colony sites (Off). The flea species and total number tested are given for each host.

Host	2002			2003		
	Plague	No Plague	Off	Plague	No Plague	Off
<i>Cynomys ludovicianus</i> ^a	67	683	—	83	310	—
<i>Microtus ochrogaster</i> ^b	—	—	—	4	—	44
<i>Neotoma cinerea</i> ^c	—	—	—	—	—	86
<i>Onychomys leucogaster</i> ^d	3	11	—	22	8	6
<i>Peromyscus maniculatus</i> ^e	125	233	119	129	402	328
<i>Reithrodontomys megalotis</i> ^f	—	—	—	—	—	3
<i>Sylvilagus audubonii</i> ^g	1	—	—	2	6	17
Prairie dog burrow ^h	48	145	—	69	96	—
Total	244	1,072	119	309	822	484

^a *Oropsylla hirsuta* (n=208), *Oropsylla tuberculata* (n=68), *Pulex simulans* (n=867).

^b *Aetheca wagneri* (n=4), *Malareus telchinus* (n=2), *Peromyscopsylla hesperomys* (n=2), *Orchopeas leucopus* (n=40).

^c *Aetheca wagneri* (n=9), *Eumolpianus eumolpi* (n=1), *Orchopeas agilis* (n=76).

^d *Aetheca wagneri* (n=22), *Foxella ignota* (n=5), *Malareus telchinus* (n=3), *Peromyscopsylla hesperomys* (n=20).

^e *Aetheca wagneri* (n=1,145), *Callistopsyllus terinus* (n=4), *Epitedia wenmanni* (n=1), *Eumolpianus eumolpi* (n=1), *Foxella ignota* (n=1), *Malareus telchinus* (n=82), *Orchopeas leucopus* (n=11), *Peromyscopsylla hesperomys* (n=91).

^f *Aetheca wagneri* (n=3).

^g *Aetheca wagneri* (n=2), *Cediopsylla inaequalis* (n=24).

^h *Aetheca wagneri* (n=11), *Oropsylla hirsuta* (n=147), *Oropsylla tuberculata* (n=40), *Peromyscopsylla hesperomys* (n=1), *Pulex simulans* (n=159).

two studies also failed to document evidence of persistent infection in the host community at affected colonies. Lechleitner et al. (1968) found antibodies to *Y. pestis* in only one of 108 deer mice (*Peromyscus maniculatus*) (the one seropositive animal was sampled during the active epizootic) and Cully et al. (1997) only found antibodies in prairie dogs. In both studies, the epizootic appeared to diminish over the course of about a year. Davis et al. (2004) also found evidence of a one to two year "fade-out" period following plague epizootics among populations of the great gerbil (*Rhombomys opimus*) in Asia when evidence of *Y. pestis* was still detectable but after which the populations were apparently plague-free.

We found no evidence that *Y. pestis* persists at black-tailed prairie dog colonies with a history of plague, at least in the host and vector species that we sampled. The most conservative interpretation of these negative data is that *Y. pestis* infection was not widespread among small mammals in southern Phillips County. However, if infection occurred in isolated pockets or was present in only a small proportion of the small mammal community we may not have been able to detect it with our sampling effort. What these data also suggest is that prairie dog colonies per se are not ideal focal areas for the long-term maintenance of *Y. pestis* in our study area.

The mechanism by which *Y. pestis* persists is still unclear. One potential scenario is that the disease continually moves across the landscape, driven by new infection of susceptible hosts. However, the patchy distribution of plague-affected prairie dog colonies in Phillips County does not appear to support this hypothesis, although several colonies in close proximity to one another were often affected at once. Another possibility is that *Y. pestis* persists in discrete enzootic foci that maintain appropriate conditions for long-term persistence, and these are a source of bacteria for epizootics among highly susceptible species such as prairie dogs. In

Phillips County, this may occur off of prairie dog colonies where the diversity of potential enzootic hosts is higher (Holmes, 2003). Maintenance of *Y. pestis* is thought to be dependent on this continued circulation among competent hosts (Barnes, 1993) and several authors (Olsen, 1981; Gage et al., 1995; Biggins and Kosoy, 2001) have proposed that the factors most likely to support permanent plague foci include several host species co-occurring in areas of diverse or patchy habitats. If so, areas where such diverse habitats occur in proximity to prairie dog colonies—that is, where both the proposed enzootic and epizootic components of the plague system coexist—may prove important in supporting permanent plague foci and perpetuating epizootics.

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that these may not be difficult to obtain, if a sensitive assay for detection of antibody in hybridoma supernatants is available. For example, Legrain *et al.* (11) obtained in BALB/c mice 17 monoclonal antibodies against a single BALB/c idio-type, and in every case the idiotype-anti-idiotype reaction was specifically inhibited by antigen. Similar observations have been made by others (12, 13). It should be pointed out that the two monoclonal antibodies do not have to be raised in a single strain of mice. Instead, monoclonal antibody 2 could originate in mice of a different allotype, or even in another animal species, for example, in rats.

Some of the attractive features of the 4i-assay are shared with those of IRMA performed with monoclonal antibodies. For example, the antigen does not have to be purified or labeled, and most labeled antibodies have a long shelf life. Also, because the antibodies are products of hybridomas, they are homogeneous and can be obtained in unlimited amounts. However, most variants of commonly used immunoradiometric methods, such as the sandwich or two-site IRMA (14, 15), require a minimum of two separate epitopes, whereas the 4i-assay requires only a single epitope.

This unique characteristic may be particularly attractive when the antigen is a small polypeptide, or weakly immunogenic, or when one is attempting to identify a portion of an antigen associated with an epitope. For example, the epitope of Pb44 recognized by 3D11 seems to be involved in the interaction of sporozoites with their target cell (16), and in protective immunity against malaria (1, 2). The isolation of a fragment of Pb44 bearing this epitope could be important for the development of a malaria vaccine. This and similar undertakings may be greatly facilitated by the availability of a sensitive and epitope-oriented assay, such as the one described here.

From the point of view of those interested in malaria and other vector-transmitted diseases, the present results indicate that the 4i-assay is sensitive enough to detect a relatively small number of sporozoites in crude extracts of mosquitoes, and might therefore be used in epidemiological surveys.

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Prairie Dogs Avoid Extreme Inbreeding

Abstract. *Black-tailed prairie dogs (Rodentia: Sciuridae: Cynomys ludovicianus) live in colonies composed of contiguous but separate family groups called coteries. During the 6 years that individuals in a colony were observed, they almost never mated with close genetic relatives. Inbreeding is avoided in four ways: (i) a young male usually leaves his natal coterie before breeding, but his female relatives remain; (ii) an adult male usually leaves his breeding coterie before his daughters mature; (iii) a young female is less likely to come into estrus if her father is in her coterie; and (iv) an estrous female behaviorally avoids mating with a father, son, or brother in her coterie.*

Although inbreeding may sometimes be advantageous (1, 2), biologists generally assume that most organisms outbreed (3). The reasons, extent, and mechanisms of outbreeding, however, are rarely understood (4). Particularly in social species, the details of how and to what extent inbreeding is avoided may provide insights into significant biological and social questions (5). To acquire extensive knowledge of exact genetic relationships among social individuals requires long-term field studies. From a 6-year study of 200 marked individuals under natural conditions, I report four mechanisms of outbreeding in a highly social species, the black-tailed prairie dog (*Sciuridae: Cynomys ludovicianus*).

Black-tails are large, diurnal rodents. At Wind Cave National Park, Hot Springs, South Dakota, where I study them, they mate in February and March, and weaned juveniles first emerge from their natal burrows in May and June. The area of my study colony is about 500 m by 130 m (6.6 hectares) and in late spring of each year contains 142.9 ± 33.6 (mean $\pm$ standard deviation) yearlings and adults (≥ 2 years) and 72.4 ± 36.9 juveniles arranged into 24.2 ± 1.47 family groups called coteries. A coterie typically contains one adult male, three to

four adult females, and several yearlings and juveniles of both sexes. Males and females first breed as 2 year olds, although females occasionally breed as yearlings. Individuals remain within well-defined contiguous territories and are usually amicable toward members of their own coterie and hostile toward members of other coteries (6).

From 1975 through 1980, all young were marked with ear tags and fur dye before they mixed with young from other litters (7), so that exact genetic relationships through common female ancestors and probable genetic relationships through common male ancestors are now known for more than 90 percent of all colony residents (8). With three to six field assistants in February and March 1978, 1979, and 1980, I observed the colony with binoculars from three towers (5 m) for most (≥ 99 percent) of the daylight hours when prairie dogs were aboveground; we observed 94 periods of estrus, involving 74 different females.

Black-tail copulations usually occur underground during daylight hours, and only estrous females enter a burrow with adult males. Because there are specific behaviors associated with what we term an underground consortship (9), we are often able to pinpoint when a copulation

has occurred (10). Two independent lines of evidence support the assumption that underground consortships represent copulations. First, the date of weaning varied directly with the mother's date of estrus and underground consortship in 1978, 1979, and 1980 ($P < .001$ for each year; Kendall rank correlation test) (10). Second, paternities determined from an electrophoretic analysis of blood proteins agree closely with those inferred from behavioral observations (8, 10).

Black-tails, like other sciurid rodents (11), separate by sex before the age of first breeding (Fig. 1). Females usually remain in the natal coterie for life, but males usually depart 12 to 14 months after weaning. One result is that adult females have little opportunity to breed with sons, nephews, or cousins.

A young black-tail male attempts to acquire a breeding coterie, and, if successful, remains there until he dies, is evicted by an invading male, or departs, apparently, on his own initiative. Since males regularly live to be 4 to 5 years old (12), an older male may sometimes live in the same coterie with his 2-year-old daughter. If the avoidance of extreme inbreeding is important, then an adult male should not remain in the same breeding coterie for more than two consecutive years. In 87 of 92 (94.6 percent) observed residencies, an adult male remained in the same coterie for only 1 or 2 years, precluding father-daughter inbreeding. Of the nine adult males that changed coteries after the second breeding year (13), seven would have been in the same coterie with breeding daughters in the third year if they had not transferred to another coterie in the colony. By contrast, of the five adult males (5.4

Table 1. Dispersal of older black-tail males versus the possibility of father-daughter inbreeding. Differences shown are significant at $P = .060$ (one-tailed Fisher exact probability test).

Adult male in same breeding coterie	Father-daughter inbreeding in third year	
	Possible	Not possible
Only 2 years	7	2
3 years	1	4

Table 2. The effect of the father's presence in the natal coterie on the probability of copulation by yearling females. Differences shown are statistically significant at $P = .021$ (one-tailed chi-square test, $\chi^2 = 4.11$, d.f. = 1).

Copulation by yearling female	Father's status in coterie	
	Present	Departed
Does	2	13
Does not	26	37

percent) that remained in the same breeding coterie for three consecutive years (Table 1), four did not have any breeding daughters at home in the third year; the fifth male had two 2-year-old daughters in his coterie in the third year, but father-daughter inbreeding was behaviorally avoided. The findings of Table 1 suggest that the dispersal of older males may be an evolutionary response to the possibility of father-daughter inbreeding.

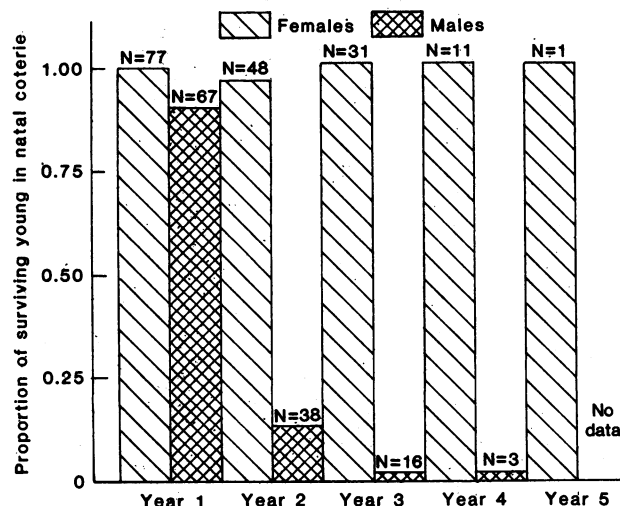
A black-tail female sometimes first breeds as a yearling. If the avoidance of extreme inbreeding is important, then a yearling female should only breed if her father is no longer in her natal coterie.

Yearling females whose fathers were not in the natal coterie were more likely to come into estrus and copulate than were yearling females whose fathers were still in the natal coterie (Table 2) (14). This difference was evidently unrelated to weight: yearling females that copulated were neither lighter nor heavier than were yearling females that did not [$P > .100$, Mann-Whitney U tests: 1978, $U(6, 4) = 16$; 1979, $U(12, 1) = 1.5$; and 1980, $U(6, 7) = 29$].

In 9 of 94 cases (9.6 percent) of observed estrus, breeding close genetic relatives of the opposite sex were not separated by male dispersal. In cases one and two, the female copulated with her male relative but also with at least one other male from a different coterie who invaded the female's home coterie on her day of estrus; in one of these cases a yearling female copulated with her father (≥ 4 years), and the other involved a 4-year-old female and her 2-year-old half brother from the same mother (15). In cases three, four, and five, the home coterie contained two adult males (6), and the estrous female avoided her male relative and copulated exclusively with the unrelated male; these cases involved a 3-year-old female and her yearling nephew (16), a 5-year-old female and her 2-year-old son, and a yearling female and her 3-year-old father. In case six, a 2-year-old female avoided copulating with her father (≥ 4 years) by leaving her home coterie on the afternoon of her estrus and copulating exclusively with a male in an adjacent coterie before returning home (17). In case seven, a 3-year-old male died or dispersed the day before his mother (≥ 6 years) came into estrus, and he was never seen again; none of the other 88 adult males in 1978 through 1980 disappeared during the breeding season. In case eight, a female (≥ 5 years) whose 2-year-old son was the only adult male in her coterie (18) failed to come into estrus. She was only the second of 69 adult females observed in 1979 and 1980 that showed no estrus (19, 20); the other was a female (≥ 6 years) in poor physical condition during the breeding season who disappeared and presumably died shortly thereafter (21). In case nine, a 2-year-old female was in a coterie in 1979 where the only male was her 2-year-old brother or half brother (22); this female copulated in both 1978 and 1980 but, even though she showed several signs of estrus (9, 10) in 1979, she was the only one of 94 estrous females that evidently did not copulate.

Black-tails thus avoid extreme inbreeding in the four specific ways described above, and these can be reduced

Fig. 1. Dispersal patterns of male and female black-tails. From 1975 through 1979, all 298 young (146 males, 152 females) from 107 litters were marked and their movements were followed. Numbers above each bar indicate the number of known survivors at the end of the indicated year. At the end of year 1, an individual had been weaned for 12 months; at the end of year 2, an individual had been weaned for 24 months; and so on. During the study period, a total of five females and ten males immigrated into the study colony and produced weaned offspring; all other females and males originated at the study colony. For each of the first 4 years, the sexual difference in dispersal was significant ($P \leq .008$, one-tailed chi-square test or one-tailed Fisher exact probability test).



to two general mechanisms: male dispersal and reluctance of females to copulate with male relatives. Existence of these mechanisms is easily understood if, as is the case with many plants and animals (23), inbreeding commonly leads to genetically inferior offspring. I have few data bearing on this issue. Of the two females that copulated with a male relative, one probably never gave birth and offspring of the other were found dead aboveground shortly after weaning. These two cases are inconclusive, since mortality is also high among young of outbred litters (6).

If prairie dogs avoid extreme inbreeding, then the frequency of heterozygotes at polymorphic loci should be higher than that expected under conditions of Hardy-Weinberg equilibrium (24). At the four polymorphic loci examined, Foltz and I found (25) that, as predicted, there was a consistent excess of heterozygotes in 1978, 1979, and 1980.

Behavioral and physiological avoidance of copulation with male relatives in the home coterie (a kind of female choice) is probably an evolved mechanism of outbreeding. Male dispersal patterns may also have evolved primarily to promote outbreeding. However, it is also possible that male dispersal patterns are secondary consequences of female choice (26): why should a male remain in a coterie if his female relatives there are unlikely to mate with him?

Numerous investigators have demonstrated one or two mechanisms by which individuals avoid inbreeding (4), but single mechanisms of outbreeding usually have alternative explanations (1, 2). Alternative explanations become less parsimonious when several different mechanisms all suggest the same conclusion. Four mechanisms are described for prairie dogs; except possibly for humans (5), so many mechanisms have not previously been implicated in the maintenance of outbreeding.

Even when individuals avoid mating with close genetic relatives such as parents, offspring, and siblings, inbreeding coefficients can be high if populations are small and isolated or if individuals regularly mate with more distant relatives such as nieces, nephews, and first cousins (1, 27). Black-tail colonies are usually large and there is regular immigration of males (6, 25) (Fig. 1). Whether individuals avoid mating with their more distant genetic relatives is not yet known.

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- In 1978, for example, 16 of 25 (64.0 percent) adult males of known age at the study colony were ≥ 4 years old; in 1979, 5 of 28 (17.9 percent) adult males of known age were ≥ 5 years old.
- Adult males that disappeared after 2 years in the same breeding coterie may have died rather than dispersed; therefore, I did not use data from these males in Table 1.
- Since the adult male sires most of the offspring born into his coterie during his residency (6, 8, 10), I assumed that the adult male in a female's natal coterie in her year of birth was her father; for all 15 of the 28 cases in Table 2 for which the critical blood samples were available, the samples supported this assumption.
- Of the other 92 estrous females, 20 (21.7 percent) copulated with a second adult male from a different coterie.
- This nephew was the only male at the study colony known to breed as a yearling.
- In cases one through six, the unrelated male chosen by the estrous female was not consistently either older or heavier than the available male relative.
- The male in case eight moved to an adjacent coterie in his first year and then returned to his natal coterie as a 2 year old; no other male returned to his natal coterie after dispersing as a yearling.
- Although the female in case eight weaned litters in the two previous years, she showed no sign of pregnancy (6, 10) when her 2-year-old son was back in her coterie, indicating that we did not simply fail to detect a subtle estrus.
- Field assistants and I failed to detect several estrous periods in 1978, our first year of breeding observations; therefore, 1978 data are not included here.
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- This male is the same described in case eight (18).
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Inner Ear: Dye Injection Reveals

Peripheral Origins of Specific Sensitivities

Abstract. In the American bullfrog (*Rana catesbeiana*) tracing of functionally identified, dye-filled fibers of the eighth cranial nerve to their peripheral origins has provided the first precise functional overlays for the microstructural maps of inner-ear sensory surfaces.

The inner ear of the frog comprises eight sensory surfaces and the various structures accompanying each of them (1). Certain features of those structures suggest the general class of sensitivity associated with each surface: the semi-circular canal accompanying each of the three cristae implies sensitivity to rotational motion about a particular axis; the calciferous mass accompanying each of the three maculae implies sensitivity to gravity or to linear motion; and the intimate connections between the chambers of the basilar and amphibian papillae and

the sound-conducting apparatus of the middle ear imply auditory sensitivity. These implications have been supported by electrophysiological and behavioral experiments of earlier investigators (Table 1).

None of the eight sensory surfaces is topographically uniform. For example, each macula (utricle, saccule, and lagena) comprises two fields (a central field surrounded by a peripheral field) with distinctly different receptor cells (hair cells) (2). On the utricle and lagena maculae, the central fields are thin

own offspring, but the offspring of female kin as well—the same offspring they tried to kill only a few weeks earlier! Levels of inbreeding among prairie dogs are also unusual. They avoid copulating with close kin, but regularly copulate with more distant kin such as half nieces, half nephews, and full first cousins.

Even though prairie dogs are so colonial and social, the rules of prairie dog society are often surprisingly simple. For example, females evidently do not adjust the sex ratios of their litters in response to environmental, physiological, or social cues. Unlike other ground-dwelling squirrels that have distinct antipredator calls for avian and terrestrial predators, prairie dogs use only one call for both. And the kin recognition that is so striking among prairie dogs seems to depend entirely on direct social learning within the home coterie territory.

Coloniality is the obvious and most important theme of this book. Another theme is that important trends in behavioral ecology sometimes do not emerge without longterm research. For example, I did not even suspect infanticide among prairie dogs until 1980, after I had been studying them for 7 years. And I never imagined that females would kill the juvenile offspring of their daughters and sisters.

A third theme is that even longterm research does not always produce clear answers about the behavioral ecology of animals as social and complicated as prairie dogs. Although I have witnessed 770 sexual consortships, for example, I still do not understand why male prairie dogs give a unique mating call after insemination.

A fourth and final theme is that animals do not always evolve a mechanism for doing something that human observers might regard as adaptive (Davies 1992; Williams 1992). For example, cuckolded prairie dog males evidently do not discriminate between their own and another male's offspring. Further, prairie dog mothers do not seem to discriminate between close and more distant kin during behavioral interactions or when committing infanticide. In situations such as these, perhaps behavioral ecologists expect too much of natural selection. More likely is that our imperfect understanding of an animal's ecology and natural history sometimes precludes realistic predictions and accurate interpretation of results.

2 Taxonomy and Natural History

Chapter 1 summarizes the lives of prairie dogs as social animals. Here I provide additional background information on prairie dogs that is important for a proper understanding of issues in later chapters.

Taxonomy

Prairie dogs are diurnal, colonial, burrowing rodents of the squirrel family (Sciuridae), and are akin to marmots, tree squirrels, flying squirrels, chipmunks, and ground squirrels (table 2.1). Prairie dogs differ anatomically from their closest relatives, the ground squirrels, by having a larger body size, larger teeth with higher crowns, and broader skulls (Hollister 1916; Drearden 1953; Clark 1973; Hall 1981; Hafner 1984). The paleontological record indicates that prairie dogs diverged from ground squirrels about 2 or 3 million years ago (Wood 1933; Hibbard 1942, 1956; Bryant 1945; Green 1960, 1963; Black 1963; Clark, Hoffmann, and Nadler 1971; Pizzimenti 1975).

Table 2.1. Taxonomy of North American Squirrels

Order Rodentia
Suborder Protrogomorpha
Family Sciuridae
Subfamily Petauristinae
<i>Glaucomys</i> (flying squirrels)
Subfamily Sciurinae
Tribe Tamiini
<i>Tamias</i> , <i>Eutamias</i> (chipmunks)
Tribe Sciurini
<i>Sciurus</i> , <i>Tamiasciurus</i> (tree squirrels)
Tribe Marmotini
Subtribe Marmotina
<i>Marmota</i> (marmots)
Subtribe Spermophilina
<i>Spermophilus</i> , <i>Ammospermophilus</i> , <i>Cynomys</i> (ground squirrels and prairie dogs)

Source: Modified from Hafner 1984.

So why do we call them prairie dogs? The first part of the common name, of course, refers to their grassland habitat (Hollister 1916; Clark 1977). The second part refers to the antipredator call of the black-tailed prairie dog, which reminded early settlers of a domestic dog's bark (Smith et al. 1977; Clark 1979). Other names for the prairie dog include petit chien, wishtonwish, Louisiana marmot, Louisiana prairie dog, barking squirrel, barking ground squirrel, barking marmot, prairie marmot, prairie squirrel, prairie barker, Missouri barking squirrel, Missouri prairie dog, mound yapper, yaprat, yek-yek, tousa, tillkeha, pispiza, ping-spingsa, and sod poodle (Coues and Allen 1877; Hollister 1916; Seton 1929; Costello 1970; Halloran 1972; Chace 1976; Smith 1979).

Taxonomists currently recognize five living species of prairie dogs, all in North America: white-tailed prairie dogs, Utah prairie dogs, Gunnison's prairie dogs, Mexican prairie dogs, and black-tailed prairie dogs (Hollister 1916; MacClintock 1970; Clark, Hoffmann, and Nadler 1971; Hall 1981; Pizzimenti 1975) (table 2.2; appendix A). In morphology and appearance, the species are remarkably similar (fig. 2.1). Excluding the tail, adults of all species are 25 to 40 centimeters long. Color of the fur ranges from yellowish to reddish to dark brown (Coues and Allen 1877; Hollister 1916), except for the rare white pelage of certain black-tailed prairie dog mutants (Tate 1947; Costello 1970). Standing adults are distinctly pear-shaped, and adult body mass varies from 300–900 grams in spring to 500–1,500 grams in late summer and early fall (Hollister 1916; Bakko and Brown 1967; Pizzimenti 1975; chap. 16). Prairie dogs thus resemble either small marmots or portly ground squirrels.

Mammalogists currently assign all five of the prairie dog species to the genus *Cynomys* (Pizzimenti 1975). Prior to Hollister's (1916) careful taxonomic revision, different biologists had assigned prairie dogs to the following genera: *Arctomys*, *Monax*, *Cynomis*, *Cynomomus*, *Mamcynomiscus*, and *Spermophilus* (Coues and Allen 1877; Hollister 1916). Mammalogists have divided the genus *Cynomys* into two subgenera (Hollister 1916; Pizzimenti 1975): *Leucocrossuromys* (consisting of white-tails, gunnisons, and utahs) and *Cynomys* (consisting of mexicans and black-tails). White-tails, utahs, and gunnisons all have short tails—30 to 65 millimeters and less than 20% of the total body length—with a variable amount of white or gray hair. They hibernate for several months of each year, and live in mid- or high-grass meadows at altitudes of 1,700 to 3,000 meters. Mexicans and black-tails have longer tails—60 to 110 millimeters and more than 20% of the total body length—with a distinct black tip, do not hibernate, and live in low-grass prairies at altitudes of 700 to 1,700 meters. The classification of utahs and mexicans as separate species, rather than as relict populations of white-tails and black-tails respectively, is somewhat arbitrary (Hollister 1916; Pizzimenti 1975).

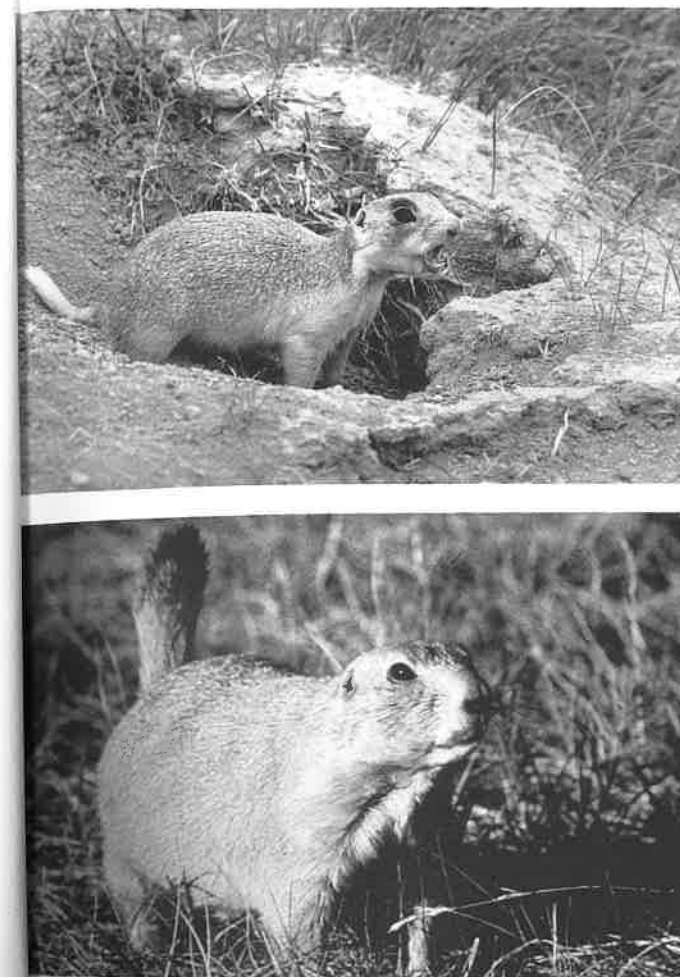


Fig. 2.1. Two species of prairie dogs. (a) White-tailed prairie dog. Note the short, white tail and the black line over the eye. Utah prairie dogs look almost exactly the same. Gunnison's prairie dogs are similar, but without the black line over the eye. (Photo by John L. Hoogland.) (b) Black-tailed prairie dog. Note the long, black-tipped tail and the absence of the black line over the eye. Mexican prairie dogs look almost identical, but the tail is slightly longer. (Photo courtesy of Wind Cave National Park.)

Especially for black-tailed prairie dogs, vegetation differentiates colonies from surrounding areas in two ways. First and more conspicuous, the height of vegetation is markedly lower within black-tail colonies (King 1955; Koford 1958; Tileston and Lechleitner 1966; chap. 5). Second, the composition of the plant community is radically different within colonies (Koford 1958; Klatt and Hein 1978; Agnew, Uresk, and Hansen 1986; Whicker and Detling 1988). Indeed, certain plants—such as scarlet globemallow, black nightshade, pigweed, and the appropriately named prairie dog weed—almost never grow outside black-tail colonies (King 1955).

Table 2.2. Descriptions of the Five Species of Prairie Dogs

	Black-tailed prairie dog	Mexican prairie dog	Gunnison's prairie dog	White-tailed prairie dog	Utah prairie dog
Range	Narrow belt from southern Canada to northern Mexico	Central Mexico	Arizona, Colorado, New Mexico, Utah	Colorado, Montana, Utah, Wyoming	Utah
Habitat	Low-grass prairie	Low-grass prairie	High-grass prairie	High-grass prairie	High-grass prairie
Altitude (meters)	700-1,700	700-1,700	1,700-3,000	1,700-3,000	1,700-3,000
Sexual dimorphism	About 15%	About 15%	>20%	>20%	>20%
(adult male body mass/ adult female body mass)					
Length of tail (mm)	60-100	90-110	30-65	30-65	30-65
Number of teats	8	8	10	10	10
Tail with black tip	Yes	Yes	No	No	No
Black spot above eye	No	No	No	Yes	Yes
Fleas	Common	Common	Common	Common	Common
Lice	Common	?	Rare	Common	Rare
Ticks	Rare	Rare	Rare	Rare	Rare
Typical colony size (adults and yearlings)	>1,000	?	<500	<500	<500
Typical colony density (adults and yearlings per hectare)	>10	<7?	<7	<7	<7

Number of different vocalizations	12	?	9	7	7?
Burrows with "rim craters"	Yes	Yes	No	No	No
Burrow mounds with ≥2 entrances	Rare	Rare	Common	Common	Common
Hibernation	No	No	Yes	Yes	Yes
Number of chromosomes (2n)	50	50	40	50	50
Usual place of copulation	Underground	?	Underground	Aboveground	?
Gestation (days)	34 or 35	?	29 or 30	?	?
Lactation (days)	37 to 51	41 to 50?	35 to 44	?	?
Social system	Matrilocal with harem-polygyny	Matrilocal with harem-polygyny	Matrilocal with harem-polygyny	Matrilocal with harem-polygyny	Matrilocal with harem-polygyny
Usual age (years) of first copulation	2	1?	1	1	1
Infanticide	Common	Rare	Rare	Rare	Rare
Status of species	Rare	Endangered	Rare	Rare	Threatened

Sources: Merriam 1892, 1902; Hollister 1916; Burnett and McCampbell 1926; Stockard 1929, 1930, 1934, 1936; Scheffer 1937, 1945; Soper 1938; Longhurst 1944; Dalquest 1953; Wilcomb 1954; King 1955, 1959; Koford 1958; Tilston and Lechleitner 1966; Bakko and Brown 1967; Smith 1967; Erpino 1968; Tipton and Mendez 1968; Tyler 1968, 1970; Lechleitner 1969; Costello 1970; Waring 1970; Clark, Hoffmann, and Nadler 1971; Collier and Spillett 1972a,b, 1973, 1975; Kerwin 1972; Pizzimenti and Nadler 1972; Clark 1973, 1977, 1979; Pizzimenti and Hoffmann 1973; Smith et al. 1973, 1976, 1977; Fitzgerald and Lechleitner 1974; Pizzimenti and McCleneghan 1974; Collier 1975; Pizzimenti 1975; Pizzimenti and Collier 1975; Crocker-Bedford and Spillett 1977, 1981; Hoogland 1977, 1981a,b, 1985, 1986, unpublished data; Wright-Smith 1978; Flath 1979; Slobodchikoff and Coast 1980; Hall 1981; Player and Urness 1982; Slobodchikoff 1984; Ceballos and Wilson 1985; Rayor 1985a,b, 1988; Slobodchikoff, Fischer, and Shapiro 1986; Grossman 1987; Loughry 1987a,b, pers. comm.; Rayor, Brody, and Gilbert 1987; Garrett and Franklin 1988; Shalaway and Slobodchikoff 1988; Slobodchikoff and Schulz 1988; Cully 1989; Robinson and Slobodchikoff 1990; Trevino-Villarreal 1990; Slobodchikoff et al. 1991; Ceballos, Mellink, and Hanebury 1993; Mellink and Madrigal 1993.

Despite the physical similarities of the various species of prairie dogs, mammalogists can discriminate among specimens. Useful characters for this task include length and color of tail, karyotype, serum proteins, and skeletal measurements (Hollister 1916; Lechleitner 1969; Clark 1973; Pizzimenti and Hoffmann 1973; Pizzimenti and Collier 1975; Pizzimenti 1975).

Can the amateur behavioral ecologist identify prairie dogs living under natural conditions? Yes, fortunately. Because the species' ranges do not overlap (fig. 2.2), locality alone is diagnostic. Prairie dogs living in Kansas, for example, are obviously black-tails, and prairie dogs in western Wyoming must be white-tails. To a lesser degree, vocalizations are also useful to behavioral ecologists. Specifically, antipredator and territorial calls define three distinct groups: (1) gunnisons, (2) white-tails and utahs, and (3) black-tails and mexicans (Tileston and Lechleitner 1966; Waring 1970; Smith et al. 1977; Wright-Smith 1978).

Of the five species, the black-tailed prairie dog is the most common, the most conspicuous, and the one most likely to be found in zoos. When either scientists or nonscientists use the term "prairie dog," they almost invariably mean black-tails. Similarly, I am referring only to black-tails when I use the abbreviated term "prairie dog" in this book.

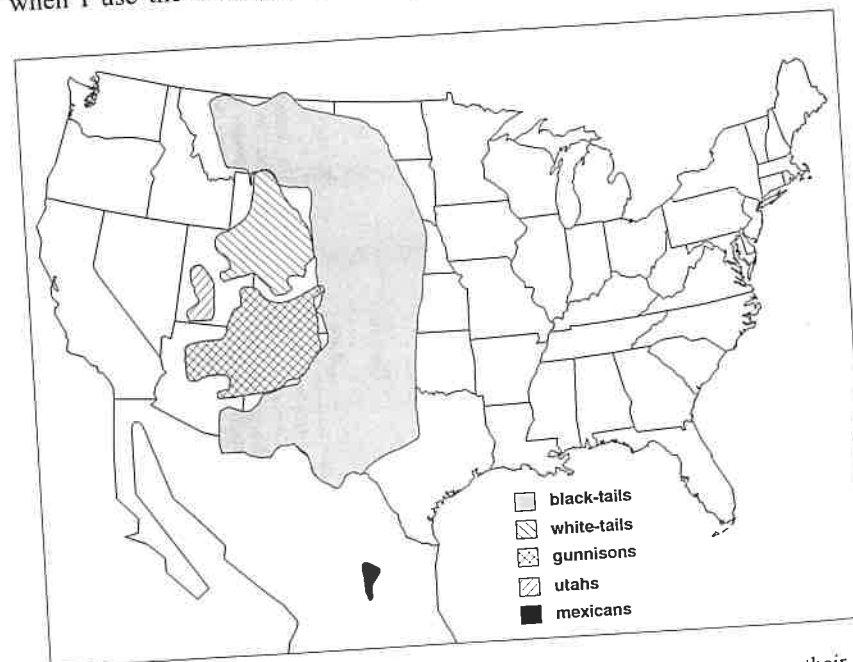


Fig. 2.2. Geographic distribution of the five species of prairie dogs. Because their ranges do not overlap, biologists can determine the species of prairie dog from locality alone.

Natural History

Diurnality

Like most sciurids except northern and southern flying squirrels (Muul 1968, 1969; Dolan and Carter 1977; Sonenshine et al. 1979; Wells-Gosling 1985; Stapp and Mautz 1991), prairie dogs of all species are diurnal and come aboveground only during daylight hours. Consistent with the plethora of cones and paucity of rods in their retinas (Walls 1941, 1942; King 1955; Jacobs and Yolton 1972; Green and Dowling 1975; West and Dowling 1975), individuals released from traps shortly after sunset (i.e., before total darkness) sometimes seem totally disoriented (King 1955; but see chap. 11). In warm weather, individuals first emerge from their burrows at about sunrise and remain aboveground until about sunset (King 1955; Fitzgerald and Lechleitner 1974; Clark 1977). Thus, prairie dogs of all species are radically different from other burrowing rodents such as moles (Hall 1981; Yates and Pedersen 1982), pocket gophers (Williams and Baker 1976; Chase, Howard, and Roseberry 1982), and naked mole rats (Jarvis and Bennett 1991) that spend almost their entire lives underground. Except when hibernating, individuals usually spend more than 95% of their time aboveground in good weather during daylight hours. When temperatures rise above 27°C or so, however, individuals frequently submerge into their burrows, presumably to cool off (Bakko, Porter, and Wunder 1988). Black-tails in South Dakota usually remain underground for only 15 to 20 minutes at a time in hot weather (King 1955; my own unpublished data). White-tails, gunnisons, and mexicans, however, sometimes remain underground for several hours on a hot day before resurfacing in the coolness of late afternoon (Fitzgerald and Lechleitner 1974; Clark 1977; Rayor 1988; Trevino-Villarreal 1990; my own unpublished data).

Even though they spend so much time aboveground during daylight hours, prairie dogs of all species have the exasperating habit of submerging for certain critical behaviors. Black-tailed and Gunnison's prairie dogs, for example, go underground to copulate (chap. 11) and to nurse their own and others' offspring (chap. 9), and black-tails also go underground to kill others' offspring (chap. 7).

Colonies, Wards, and Coteries

Prairie dogs live in aggregations called *colonies*, *towns*, or *villages* (Coues and Allen 1877; King 1955; Costello 1970). When unsuitable habitat such as a hill, tall vegetation, or a stream divides a prairie dog colony, the resulting subcolonies are called *wards* (King 1955). When such subcolonies are not evident within a colony, I consider that colony to have a single ward; thus, each colony has at least one ward. Residents of one ward can usually see and hear residents of an adjacent ward, but movements and communications between wards are uncommon.

Colonies of black-tailed prairie dogs contain harem-polygynous, territorial family groups called *coterie*s (chaps. 1 and 6). Social units similar to *coterie*s also occur within colonies of mexicans (Trevino-Villarreal 1990; W. J. Loughry, pers. comm.) and gunnisons (Fitzgerald and Lechleitner 1974; Rayer 1988; my own unpublished data), and probably also within colonies of white-tails and utahs (Clark 1977; Wright-Smith 1978; my own unpublished data).

The Prairie Dog Diet

Prairie dogs of all species are herbivorous, as shown by observations of foraging individuals and by analyses of feces and stomach contents (Stockard 1930; Kelso 1939; Bonham and Lerwick 1976; Fagerstone 1982; Shalaway and Slobodchikoff 1988; Uresk, Schenbeck, and Cefkin 1988). Exceptions to herbivory include an occasional meal of insects such as cutworms, ground beetles, and short-horned grasshoppers (Whitehead 1927; Kelso 1939; Costello 1970; O'Meilia, Knopf, and Lewis 1982).

Black-tailed prairie dogs are selectively herbivorous, with their preferences at one time of the year differing from preferences at other times (King 1955; Koford 1958; Costello 1970; Rogers-Wydeven and Dahlgren 1982; see table 2.3). Favorite foods in the summer include wheatgrass, grama, buffalo grass, scarlet globemallow, and rabbitbrush (Summers and Linder 1978). Favorites in the winter include prickly pear cactus and thistle; eating of underground roots is also more common in winter (King 1955; Costello 1970; Summers and Linder 1978). Common plants within colonies that prairie dogs usually avoid include sagebrush, threeawn, prairie dog weed, and horseweed (King 1955; Costello 1970; Summers and Linder 1978). Curiously, black-tailed prairie dogs sometimes eat fresh or old American bison scats, which are common within colony sites at Wind Cave National Park.

I did not investigate the diet in detail, but I did discover one important deviation from herbivory for black-tailed prairie dogs: cannibalism. Cannibalism occurs mainly after lactating females kill the unweaned juveniles of other females (chap. 7). I also observed cannibalism in four cases after an adult or yearling died aboveground.

Predators

Numerous animals prey on the various species of prairie dogs (Sperry 1934; Scheffer 1945; Halloran 1972; Olendorff 1976; Campbell et al. 1987; chap. 5). Major mammalian predators include American badgers, bobcats, coyotes, long-tailed weasels, black-footed ferrets, and humans (fig. 2.3); other mammals that occasionally prey on prairie dogs include red foxes, common gray foxes, grizzly bears, and mountain lions. In addition, snakes, especially bull snakes and rattlesnakes, sometimes prey on prairie dogs (Scheffer 1945; Owings and Owings 1979; Halpin 1983; Owings and

Loughry 1985; Loughry 1987a,b). Avian predators include golden eagles, northern harriers, peregrine falcons, prairie falcons, Cooper's hawks, red-tailed hawks, and several other species of *buteo* and *accipiter* hawks (fig. 2.4).

Contrary to popular opinion (e.g., Swenk 1915; Hollister 1916; Allen 1967; Costello 1970), burrowing owls usually do not attack prairie dog adults or young. These small, diurnal owls usually live in burrows abandoned by prairie dogs (Scheffer 1937, 1945), and are especially common in prairie dog colonies whose populations have recently crashed—after poisoning or an outbreak of bubonic plague, for example. I have never observed burrowing owls at Wind Cave National Park.

Predators on prairie dogs are more common and important in some areas than in others. The only exception is the black-footed ferret, which is rare everywhere—probably extinct in most prairie dog habitats—and which might be the rarest mammal in all North America (Casey, DuWaldt, and Clark 1986; Richardson 1986; Biggins and Schroeder 1988; Clark 1989; Seal et al. 1989; Oldemeyer et al. 1993).

With so many avian, mammalian, and reptilian enemies, is it any wonder that prairie dogs spend as much as 40% to 50% of their time scanning for predators (chap. 5)?

Molting

At least twice each year, prairie dogs of all species molt the entire pelage (King 1955; Smith 1967). Inexplicably, and incorrectly, Hollister (1916, 9; see also Costello 1970) asserted that prairie dogs molt the fur on the tail only once each year. In the switch from long, thick winter fur to shorter, sparser summer fur, molting starts on the underside and moves to the dorsal side, where it starts near the eyes and progresses posteriorly (fig. 2.5). In the switch from summer fur to winter fur, the progression reverses: from tail to eyes to underside. I could not easily track the ventral fur, but the disappearance of dye markings (chap. 4) indicates that complete molting and replacement of dorsal fur requires about 7 to 14 days for black-tailed prairie dogs.

The initiation and duration of molting vary with latitude, altitude, and other climatic factors (Hollister 1916). At the study colony in South Dakota, black-tail adults and yearlings molt the winter pelage as early as mid-April or as late as June or July. Molting of the summer pelage occurs in August or September. For fast-growing juveniles in their first summer, molting seems to occur almost continuously (Hollister 1916; M. G. Garrett, pers. comm.; W. J. Loughry, pers. comm.).

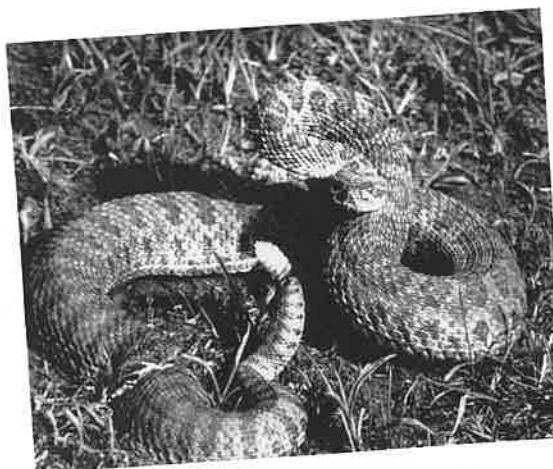
Molting correlates positively, albeit roughly, with individual condition (Hollister 1916). At my black-tail study colony in South Dakota, for example, the first individuals to molt the winter pelage in mid-April are usually nonbreeding male and female yearlings, which gain body mass



Fig. 2.3. Some mammals that prey on prairie dogs. (a) Coyote, which quickly charges into colonies. (Photo courtesy of Wind Cave National Park.) (b) American badger, which sometimes enlarges prairie dog burrows in search of prey. (Photo courtesy of Wind Cave National Park.) (c) Bobcat, which slowly stalks before pouncing. (Photo by Leonard Rue Enterprises.) (d) Black-footed ferret, a slender nocturnal specialist that can easily fit into prairie dog burrows. (Photo courtesy of Wind Cave National Park.)



Fig. 2.4. Some reptiles and birds that prey on prairie dogs. (a) rattlesnake; (b) golden eagle; (c) prairie falcon. (Photos courtesy of Wind Cave National Park.)



rapidly in early spring (chap. 16). Next in early to mid-May come the nonbreeding adults of both sexes, which gain body mass less rapidly. Then in mid- to late May come the breeding males, which gain body mass still less rapidly. And finally in late May—or even June or July—come the lactating females, which frequently *lose* body mass in early spring (chap. 16).

Hibernation

White-tails, gunnisons, and utahs hibernate for several months of each year, whereas black-tails and mexicans do not hibernate. Specifically, individual white-tails, gunnisons, and utahs disappear underground for several consecutive months during late autumn and winter (Fitzgerald and



Fig. 2.5. Initiation of molting. In the spring, dorsal molting begins around the eyes and progresses toward the tail. Before the initiation of molting, this marked prairie dog's head was entirely black. (Photo by John L. Hoogland.)

Lechleitner 1974; Pizzimenti 1975; Clark 1977; Wright-Smith 1978). Black-tails and mexicans, however, come aboveground during all months of the year (King 1955; Pizzimenti and McCleneghan 1974; Harlow and Menkens 1986; Bakko, Porter, and Wunder 1988; Trevino-Villarreal 1990). Among black-tails I have observed two deviations from this pattern (see also Jillson 1871; Anthony 1955; Koford 1958; Thomas and Riedesel 1975; Hamilton and Pfeiffer 1977; Harlow and Menkens 1986). First, during prolonged stretches of severe weather in late autumn and winter, no prairie dogs, or only a small number (fewer than 1% of the colony residents) appear aboveground for several consecutive days. While the brevity of this sort of dormancy precludes the use of the term "hibernation," the resemblance is clear. Second, some individuals remain underground for several weeks in late winter. In 1979, for example, when I began daily behavioral observations on 14 February, six marked yearlings living in one burrow did not first appear aboveground until 12 March. In 1985, when I began daily observations on 16 February, one marked adult male and six marked yearlings living in one burrow did not first appear aboveground until 16 March. And in 1988, when I began daily observations on 21 February, two adult females living in one burrow and one yearling female living in another burrow did not first appear aboveground until 26 March. These sixteen late-emerging individuals, all small and in poor condition, had probably been constantly underground—thus giving the impression of hibernation—since November or December of the previous year.

Population Status

As recently as 100 years ago, western North America was teeming with prairie dogs. The total population was probably over 5 billion, and a single black-tail colony in Texas contained an estimated 400 million residents (Merriam 1902; Clark 1979; Grossman 1987)! However, shooting, poisoning, and destruction of habitat have changed all that (see below). When I started my study of prairie dogs in 1974, four of the five species were on the list of endangered species, with only white-tails exempt. Populations of gunnisons, utahs, and black-tails have all increased in the last 20 years, and only mexicans are still on the list of endangered species; utahs are on the list of threatened species (see table 2.2).

Prairie Dogs and People

Why Do Ranchers Dislike Prairie Dogs?

Ranchers disdain prairie dogs for two reasons (Costello 1970; Jameson 1973; Chace 1976; Petzal 1993). First, they worry that horses and cows will fall into prairie dog burrows and break a leg. Second, they believe that prairie dogs compete with livestock for food. In addition, ranchers complain that prairie dogs are prolific breeders from which they are not safe until every single pest is gone. In response to these complaints, as many as 125,000 people per year sometimes have worked to eliminate prairie dogs via poisoning, drowning, or shooting (Merriam 1902; Swenk 1915; Randall 1976a,b; Clark 1979; Garrett and Franklin 1983)—even though the financial costs of eradication usually exceed the possible benefits (O'Meilia, Knopf, and Lewis 1982; Collins, Workman, and Uresk 1984; Uresk 1985; Knowles 1986a; Radcliffe 1992). In combination with loss of habitat, eradication had brought all the prairie dog species except white-tails to the brink of extinction by the early 1970s (see above).

The ranchers' antagonism toward prairie dogs has secondarily increased their antagonism toward certain predators as well. By eliminating prairie dog populations, for example, ranchers have simultaneously reduced the food supply of coyotes and bobcats. As a result, these deprived predators are more likely to attack cattle and sheep.

None of my research directly concerns the effect of prairie dogs on the raising of livestock. A few comments are nonetheless in order. Consider the possibility of broken legs caused by prairie dog burrows, for which published frequencies do not exist. Over the years I have chatted with more than a hundred ranchers in Wyoming, Colorado, and South Dakota and have asked them about leg fractures. All these ranchers worry about broken legs, but only one could pinpoint a possible case. Upon cross-examination, this rancher could only verify that a cow that sometimes foraged in a field with prairie dogs somehow sustained a broken leg. The

usual response to my questioning goes something like this: "Well . . . er . . . uh . . . none of my cows has actually broken a leg in a prairie dog burrow. But check with Rancher Jones down the road. Several of his cattle have fallen into prairie dog burrows." A check with Rancher Jones always yields a similar negative response.

Contrary to ranchers' assertions, prairie dogs are not prolific breeders. Both sexes usually defer breeding until the second year, only about 50% of the adult females rear emergent juveniles each year, and litter size is usually only three or four (chap. 16). Further, the physical area occupied by a colony does not automatically increase over time (chaps. 4 and 5). Finally, under natural conditions population crashes commonly follow colony expansions (chaps. 5 and 16).

Mysteriously, Merriam (1902, 258; see also Bailey 1905; Bell 1920; Taylor and Loftfield 1924) somehow calculated that "32 prairie dogs consume as much grass as 1 sheep, and 256 prairie dogs as much as 1 cow." If these calculations are true, then ranchers should indeed detest prairie dogs! *But they are not true*, for at least four reasons. First, despite some overlap and hence competition, prairie dogs avoid numerous plants that livestock prefer and prefer numerous plants that livestock avoid (Coppock, Detling, et al. 1983; Coppock, Ellis, et al. 1983; O'Meilia, Knopf, and Lewis 1982; Uresk 1984). Second, the presence of prairie dogs improves the quality of certain plants, so that American bison, pronghorn antelope, and livestock commonly *prefer* to forage within colonies (Koford 1958; O'Meilia, Knopf, and Lewis 1982; Coppock, Detling, et al. 1983; Coppock, Ellis, et al. 1983; Knowles 1986b; Krueger 1986). Third, prairie dogs are especially likely to colonize areas *that livestock have already overgrazed* (Bond 1945; Osborn and Allan 1949; Koford 1958; Clark 1968, 1977, 1979; Costello 1970; Snell 1985; Knowles 1986b). Following arrival of the rodents, ranchers grumble: "Look at those prairie dogs. They've eaten all my grass." In reality the prairie dogs are usually the *effect*, rather than the cause, of overgrazing. Finally, consider the scene 200 years ago when millions of American bison lived sympatrically with billions of prairie dogs. Because the habits and dietary requirements of cattle and American bison are so similar, large numbers of cattle and prairie dogs probably should be able to co-exist in the same areas.

I am not arguing here or elsewhere that prairie dogs are always harmless to the livestock rancher. They do sometimes cause financial loss. However, prairie dogs are not the villains that the ranchers allege. Broken legs of livestock caused by prairie dog burrows are rare, competition between livestock and prairie dogs is probably minimal, and sound grazing practices deter colonization by prairie dogs. The inescapable conclusion is that recent attempts to eradicate prairie dogs have been misguided and inappropriate.

Prairie Dogs and the Ecosystem

By their foraging and clipping of tall vegetation, prairie dogs radically alter the plant communities of western North America. Because their colonies attract predators and so many other animals, prairie dogs also have a major impact on wildlife ranging from mites and harvester ants to black-footed ferrets and American bison (table 2.3). For these and other reasons, the extinction of prairie dogs would be a tragedy (Costello 1970; McNulty 1971; Chace 1976; Scott 1977).

Table 2.3. Partial Listing of Plants Eaten or Clipped Down by Prairie Dogs and Animals Attracted to Prairie Dog Colonies

Plants eaten or clipped by prairie dogs	
Aster, biscuitroot, black nightshade, brome, buffalo grass, cocklebur, cryptantha, cutleaf nightshade, deathcamus, dropseed, false pennyroyal, fescue, fluffweed, foxtail, glorybind, grama, horsetweed, inland saltgrass, knotweed, lambsquarters, mat sandbur, milkvetch, mullein, needle-and-thread, pepperweed, phlox, pigweed, plaitain, prairie dog weed, prickly pear cactus, rabbitbrush, ragweed, ricegrass, Russian thistle, sagebrush, saltbrush, scarlet globemallow, scurfpea, sedge, skeleton weed, snowberry, sorrel, spiny buffalobur, nightshade, spurge, stickseed, summer cypress, thistle, threeawn or wire grass, tumblegrass, verbena, wheatgrass, wild onion, winterfat	
Animals attracted to prairie dog colonies	
Internal parasites	Protozoa, roundworm, spiny-headed worm, tapeworm
Arachnids	Black widow spider, mite, pseudoscorpion, tick
Insects	Bluebottle fly, bombardier beetle, cave cricket, cutworm, darkling beetle, dung beetle, flea, ground beetle, harvester ant, louse, robber fly, short-horned grasshopper
Amphibians	Tiger salamander, toad
Reptiles	Bull snake, lesser earless lizard, lined snake, rattlesnake, Texas horned lizard, western box turtle, western hognose snake
Birds	American robin, black-billed magpie, burrowing owl, Cooper's hawk, ferruginous hawk, golden eagle, goshawk, horned lark, Lapland longspur, lark bunting, McCown's longspur, mountain bluebird, mountain plover, mourning dove, northern harrier, prairie falcon, red-tailed hawk, rough-legged hawk, sharp-shinned hawk, sharp-tailed grouse, Sprague's pipit, Swainson's hawk, western meadowlark
Mammals	American badger, American bison, black-footed ferret, bobcat, coyote, deer mouse, desert cottontail, long-tailed weasel, mule deer, northern grasshopper mouse, pocket mouse, prairie vole, pronghorn antelope, swift fox, thirteen-lined ground squirrel, wapiti, white-tailed jackrabbit

Sources: Scheffer 1937; King 1955; Koford 1958; Vetterling 1962; Tileston and Lechleitner 1966; Smith 1967; Tyler 1968, 1970; Costello 1970; Buscher and Tyler 1975; Tyler and Buscher 1975; Bonham and Lerwick 1976; Summers and Linder 1978; Fagerstone, Tietjen, and Williams 1981; Uresk 1985; Wilcomb 1954.

Note: Scientific names for organisms listed in this table are in appendix A.

Prairie Dogs as Human Food Items

When they were omnipresent long ago, prairie dogs were important food items for certain Indian tribes and white explorers and settlers (Wedel 1961; Costello 1970). One explorer described the meat as "excellent," another as "well flavoured . . . [resembling] that of the woodchuck" (Scheffer 1945; see also Gorman 1974). More recently, Nordyke and Nordyke (1964, 202) argue that the meat is "tasty" and "superior to wild rabbit or squirrel."

Because they do not hibernate, black-tailed prairie dogs were probably especially valuable to Indians as food during the winter. Perhaps because they are so rare, human consumption of prairie dogs is now trivial.

Prairie Dogs and Medicine

Black-tailed prairie dogs frequently develop gallstones under laboratory conditions. This curiosity has led to a better understanding of gallstones and gall bladder disease among humans (Brenneman et al. 1972; Holzbach et al. 1976; Gurll and DenBesten 1978; Broughton et al. 1991; Roslyn et al. 1991). White-tailed and black-tailed prairie dogs have also been useful in studies of metabolism and hibernation (Bakko 1977; Pfeiffer, Reinking, and Hamilton 1979; Harlow and Menkens 1986; Harlow and Buskirk 1991).

Prairie Dogs as Pets

If captured when young, prairie dogs make excellent, engaging pets (Jillson 1871; Squire 1925; Cates 1927; Dale 1947; Ferrara 1985) (fig. 2.6)—

Fig. 2.6. Prairie dogs as pets. If captured at first juvenile emergence or earlier, prairie dogs make excellent pets. This juvenile pet stays warm in its owner's pocket. (Photo by John L. Hoogland.)



probably because, like young mallards shortly after hatching (Hess 1964, 1973; Lorenz 1970), they seem to "imprint" to their human owners. Prairie dog pets are easily house-trained, and respond with a jump-yip call when the owner returns after a short absence. They like to be groomed by their owners, and try to groom back in return. When a strange human approaches, however, prairie dog pets chatter their teeth and flare their tails—but they almost never bite.

Prairie dogs make good pets only if captured as, or before, they first appear aboveground when about 6 weeks old. Older animals do not tame down enough to make good pets.

If prairie dogs are so charming, then why don't more people have them as pets? One problem is that prairie dogs like to chew on furniture. Another problem is the disagreeable odor sometimes emitted from the perianal scent glands. The most serious problem, however, is that prairie dogs do not breed readily in laboratories or in pet shops. The only way to get more than a few pets, therefore, is to catch them in the wild as they first appear aboveground. This method is difficult and time-consuming, and consequently deters most pet store owners.

Summary

1. Despite their misleading common name, prairie dogs (genus *Cynomys*) are medium-sized (400 to 1,500 grams) rodents of the squirrel family (Sciuridae).
2. Taxonomists currently recognize five species of prairie dogs. White-tailed, Gunnison's, and Utah prairie dogs belong to the subgenus *Leucocrossuromys*. Black-tailed and Mexican prairie dogs belong to the subgenus *Cynomys*.
3. Characters useful for discriminating among specimens of the different prairie dog species include length and color of tail, karyotype, serum proteins, and skeletal measurements. For wild prairie dogs, locality and vocalizations are diagnostic.
4. In good weather prairie dogs first emerge from their burrows at about sunrise, and remain aboveground until about sunset.
5. Physical barriers such as hills or tall vegetation sometimes divide prairie dog colonies into subcolonies called wards. Within colonies, prairie dogs live in territorial, harem-polygynous family groups called coteries.
6. Prairie dogs are herbivorous. Occasional exceptions to herbivory include insectivory and cannibalism.
7. Major predators on prairie dogs include American badgers, bobcats, coyotes, black-footed ferrets, golden eagles, northern harriers, prairie falcons, numerous species of buteo and accipiter hawks, bull snakes, and rattlesnakes.

8. At least twice each year, prairie dogs molt the entire pelage.
9. Although most black-tailed prairie dogs come aboveground during all months of the year, individuals in poor condition sometimes remain underground for several consecutive months and appear to hibernate.
10. Leg fractures due to prairie dog burrows are rare among livestock, and ranchers sometimes misunderstand and exaggerate the competition between prairie dogs and livestock. Further, prairie dogs are more likely to colonize areas that livestock have already overgrazed. Thus, ranchers commonly exterminate prairie dogs for the wrong reasons.

5 Costs and Benefits of Coloniality

Why Do Animals Live in Colonies?

Some animals might live in colonies because of an extreme shortage of suitable habitat, others to obtain more food, and still others to avoid predators (Alexander 1974; Bertram 1978; Wittenberger and Hunt 1985). The first of these possibilities is equivalent to "forced coloniality," in which individuals do not gain from the proximity of conspecifics as they do in the other two types of coloniality (Alexander 1974). Forced coloniality is rare, perhaps being important for animals such as barn swallows, certain seabirds, and northern elephant seals (Bartholomew 1952; Lack 1968; Snapp 1976). However, some colonies where habitat seems to be limiting result because individuals seek out remote places safe from enemies, and thus depend ultimately on attempts to escape predation (Lack 1968; Alexander 1974; Robinson 1985; Wittenberger and Hunt 1985).

Coloniality dependent on the social facilitation of foraging can occur in two ways. The first involves cooperation among conspecifics to capture large or elusive prey that is inaccessible to solitary foragers. Such cooperation probably occurs for predators such as Harris's hawks, killer whales, African wild dogs, and spotted hyenas (Martinez and Klinghammer 1970; Lawick and Lawick-Goodall 1971; Kruuk 1972; Bednarz 1988; Fanshawe and Fitzgibbon 1993). This route to coloniality is uncommon, partly because predators are relatively rare (compared with herbivores, for example) and partly because the teamwork necessary for cooperative hunting does not evolve easily (Alexander 1974).

Coloniality dependent on the social facilitation of foraging also might result when large food supplies—swarming insects, for example—are so ephemeral or unpredictable that solitary foragers can only rarely find them. If so, then communication—whether deliberate or accidental—about the location and quality of food can occur at the colony site, which serves as an "information center" (Ward 1965; Ward and Zahavi 1973; Hoogland and Sherman 1976). Colonies that serve as "information centers" are

probably uncommon (Alexander 1974), but perhaps occur for common terns, cliff swallows, ospreys, and evening bats (Erwin 1978, 1979; Waltz 1982, 1987; Brown 1986; Greene 1987; Wilkinson 1992b).

Coloniality is ubiquitous among animals of all taxonomic groups, from protozoans through primates. If coloniality resulting from either shortage of suitable habitat or social foraging is rare, the inescapable conclusion is that coloniality most commonly evolves to reduce predation. Why is this so? One reason is that most animals have one or more predatory species that they must avoid in order to survive and reproduce. By contrast, few animals either experience a severe shortage of suitable habitat or would gain by social foraging.

Coloniality dependent on avoiding predators is common for another reason. Suppose that parents of a solitary avian species always try to chase predators away from the home nest, and that such chasing deters 50% of all attackers. By merely nesting close to another conspecific pair, parents of avian species such as kittiwakes and common, black-headed, and Franklin's gulls instantly increase the probability of successful deterrence of predators because additional parents are now available for cooperative attack ("mobbing") (Kruuk 1964; Burger 1974; Andersson 1976; Gotmark and Andersson 1984). Such increased protection of the home nest need not involve intricate teamwork, but instead results simply because two sets of parents benefit from deterring a predator from the same general area.

Two other benefits are also readily available to prey individuals who initially nest closer than usual for some reason. First, via "protection by dilution" (Hamilton 1971; Bertram 1978; McKaye 1981), the probability that any particular individual will be the predator's victim varies inversely with colony size for animals such as monarch butterflies, common eiders, and black-headed gulls (Patterson 1965; Munro and Bedard 1977; Calvert et al. 1979). Second, via "selfish herd effects" (Hamilton 1971; Vine 1971; Alexander 1974), individuals within groups of animals such as starlings, queleas, and red deer have the opportunity to manipulate other group members into being more conspicuous and vulnerable (Darling 1937; Tinbergen 1951; Crook 1960).

Because of cooperative attack against predators, "protection by dilution," and "selfish herd effects," the initial step toward coloniality is often easy when the ultimate causation is avoidance of predation. However, the initial step is more difficult when coloniality depends on social facilitation of foraging. Reduced predation is thus more likely than social facilitation of foraging to be the founding advantage of coloniality (Alexander 1974; Bayer 1982).

Like coloniality dependent on social facilitation of foraging, coloniality dependent on reduced predation can result from more than one mechanism. I have just discussed the possibilities of cooperative attack, "protection by dilution," and "selfish herd effects," for example. Increased awareness of

predators offers another such mechanism. When stalking a solitary individual, a predator must elude only that individual's detection system. When stalking an individual within a colony, however, the predator must elude numerous individuals' detection systems (Bertram 1980; Pulliam and Caraco 1984; Fitzgibbon 1990). If individuals give either an intentional or an unintentional signal after spotting a predator, then colonial animals such as laughing doves, bank swallows, and cliff swallows detect predators more quickly and thus have more time to flee than do solitary individuals (Siegfried and Underhill 1975; Hoogland and Sherman 1976; Brown and Brown 1987).

In colonies that serve as "information centers" (Ward 1965; Ward and Zahavi 1973; Brown 1986), individuals must live close enough so that they can monitor the foraging activities of conspecifics, with or without specific food-finding signals (Alexander 1974; Hoogland and Sherman 1976). Such monitoring does not require dense packing of individuals, and the costs of coloniality will encourage individuals to *minimize* density so long as they can still monitor their conspecifics. In coloniality dependent on reducing predation, however, benefits resulting from "protection by dilution" and "selfish herd effects" are sometimes maximal at the highest possible densities (Hamilton 1971; Alexander 1974; Bertram 1978); an extreme shortage of suitable habitat also might promote high density within colonies. In some extreme cases, nests almost or actually touch, as in colonies of sandwich terns, Adélie penguins, common murrelets, and northern and Peruvian gannets (Cullen 1960; Tenaza 1971; Birkhead 1977, 1978; Nelson 1978). In other extreme cases, individuals are constantly crawling over or bumping into conspecifics, as in colonies of Mexican free-tailed bats and northern and southern elephant seals (Davis, Herreid, and Short 1962; Le Boeuf 1974, 1981; McCann 1981; McCracken 1984). Colony density thus might help ecologists to distinguish between coloniality dependent on "information centers" and coloniality dependent on either reduced predation or a shortage of suitable habitat.

Regardless of ultimate causation, coloniality is never without certain costs, some of which are automatic and unavoidable (Alexander 1974; Hoogland and Sherman 1976). For example, frequent contacts within colonies inevitably promote the transmission of diseases, ectoparasites, and endoparasites (Schoening, Schwartz, and Lindquist 1956; Simms 1956; Rothschild and Clay 1957; Davis, Herreid, and Short 1962; Kennedy 1975)—sometimes with catastrophic results for animals such as purple martins, sooty terns, brown pelicans, cliff swallows, and harbor and Baikal seals (Camin and Moss 1970; Feare 1976; King, Blankinship, and Paul 1977; Brown and Brown 1986; Harwood and Hall 1990). Bubonic plague commonly eliminates entire colonies of white-tailed, black-tailed, Gunnison's, and Utah prairie dogs (Lechleitner, Tileston, and Kartman 1962; Lechleitner et al. 1968; Barnes, Ogden, and Campos 1972; Collier and Spillett 1975;

Clark 1977; Rayor 1985a; Cully 1989; Fitzgerald 1970, 1993). Infanticide is a major source of mortality for colonial animals such as northern elephant seals, hanuman langurs, and African lions (Hrdy 1974; Bertram 1975; Le Boeuf and Briggs 1977), and is *the* major source of juvenile mortality for Belding's ground squirrels (Sherman 1981b) and prairie dogs (chap. 7).

Colonies also inexorably foster competition for critical resources such as food and mates. Further, the visual and vocal conspicuousness of colonies of animals such as sandwich terns, black-headed gulls, and shelducks commonly attracts the attention of predators (Cullen 1960; Kruuk 1964; Pienkowski and Evans 1982). Finally, even though their usual function is to reduce predation, colonies sometimes offer unique opportunities for certain predatory specialists. Prairie dog coloniality, for example, has probably evolved against diurnal predators such as coyotes, bobcats, golden eagles, and prairie falcons, but has secondarily left prairie dogs exceedingly vulnerable to nocturnal black-footed ferrets (see below).

Both costs and benefits usually increase directly with colony size, but not necessarily in linear fashion. For example, the relationship between ectoparasitism per individual and colony size might be positive only up to a certain asymptotic point—perhaps because an individual can harbor only a finite number of fleas and lice. If the benefits consistently increase more sharply than the costs with colony size, then the upper colony size that is still adaptive might be unlimited. If the costs consistently increase more sharply with colony size, however, then only smaller colony sizes might be adaptive, with one size perhaps being "optimal." Another, albeit remote, possibility is that the ratio of benefits to costs remains constant with colony size; under these "ideal free conditions" (Fretwell and Lucas 1970; Parker and Sutherland 1986), colony size does not affect reproductive success (Pulliam and Caraco 1984; Brown 1985, 1988; Jones 1987).

On the other hand, "optimal" colony size might vary for different individuals (Pulliam and Caraco 1984; Brown, Stutchbury, and Walsh 1990). Individuals that are especially adept at avoiding or removing fleas and lice, for example, can more easily incur the cost of increased ectoparasitism in large colonies—so that "optimal" colony size will be higher for these individuals than for other individuals. Conversely, fast, wary individuals that easily evade predators gain little from the increased vigilance of large colonies—and therefore will have a lower "optimal" colony size than other individuals.

"Optimal" colony size might vary for the same individual over time. When wary, fast, and in good condition, for example, young adults might seek out small colonies and thereby avoid the higher costs of larger colonies. As eyesight and swiftness decline with age, however, individuals probably will be more likely to tolerate the greater costs of larger colonies in order to be safer from predators.

In this chapter I document the increased competition and increased ectoparasitism that result from prairie dog coloniality. I then show that the only offsetting benefit of prairie dog coloniality is probably increased safety from predators. Finally, I assess comparative data from white-tailed prairie dogs.

The Costs of Prairie Dog Coloniality

Increased Aggression

Ecologists measure the intensity of competition in many ways (Tilman 1982). One obvious way is to quantify aggression, with the assumption that aggression results ultimately from competition. I predicted that aggression among prairie dogs would increase directly with ward (subcolony) size (fig. 5.1). But a mere documentation of more fights, chases, runaways, and territorial disputes in larger wards would be trivial. The real issue is whether more aggressive interactions *per individual* occur in larger groups, as they do for animals such as bank swallows and yellow-bellied marmots (Barash 1973; Armitage 1975, 1977; Hoogland and Sherman 1976). Figure 5.2 shows the predicted per individual trends for prairie dogs.

Prairie dogs within an isolated coterie territory—and thus a small ward—obviously cannot interact with prairie dogs from other coterie territories. However, individuals living in a coterie territory surrounded by other territories—i.e., a larger ward—can have both intra- and intercoterie interactions. The positive trends in figure 5.2 probably result primarily from increased intercoterie aggression in the larger wards. However, the prairie dogs in the three wards that I observed were unmarked, so I could not investigate this hypothesis.



Fig. 5.1. Fight involving two prairie dogs. Male-0 is about to attack the unidentified prairie dog on the right. (Photo courtesy of Monte G. Garrett.)

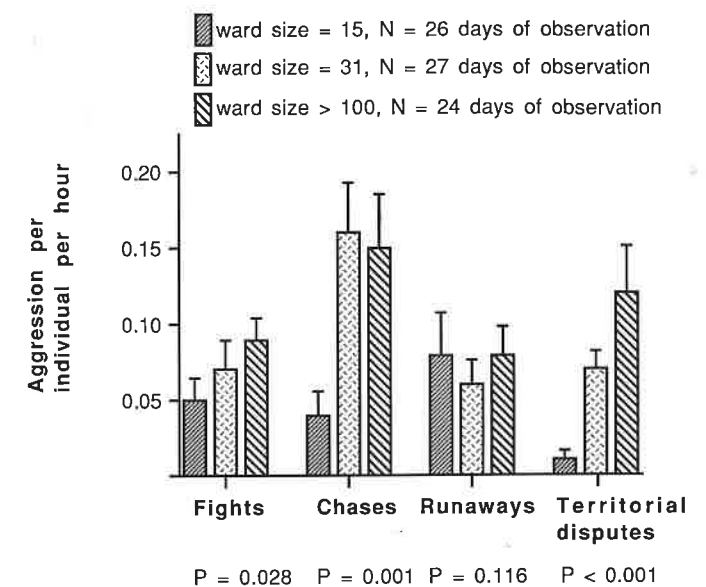


Fig. 5.2. Aggression versus ward size. Two field assistants and I quantified aggression, usually simultaneously, from 1100 hours until 1300 hours, at three wards of different sizes, from 17 February through 25 March 1975. *P*-values are from the Kendall rank correlation test.

Is aggression *costly* to prairie dogs? Three lines of evidence indicate an affirmative answer. First, aggressive interactions among prairie dogs inevitably involve losses of time and energy, as they also do for animals such as acorn woodpeckers, spotted hyenas, and red deer (Kruuk 1972; Koenig 1981b; Clutton-Brock, Guinness, and Albon 1982). The mean $\pm$ SD duration of territorial disputes among prairie dogs in February and March of 1978, for example, was 4.76 ± 6.00 minutes ($N = 694$) (fig. 5.3). Two pregnant females in 1980 set the record by having a dispute that began as soon as they first emerged on a cold winter morning and continued until one submerged for the night—over 6 hours with no foraging! Second, winners of aggressive interactions sometimes temporarily or permanently chase losers away from colony sites. Away from burrows and other prairie dogs, evicted losers are easy prey (chap. 16; see also King 1955; Garrett and Franklin 1988). Finally, like other animals in general (Geist 1971; Kruuk 1972; Schaller 1972; Miller 1975; Wilkinson and Shank 1976) and squirrels in particular (Smith 1968; Steiner 1972; Holmes 1977; Sherman and Morton 1984; Michener and Locklear 1990), prairie dogs commonly incur injuries from fights (fig. 5.4). For example, adult males and females have few facial injuries and scars before the frequent, vicious fighting that occurs during the breeding season of February and March (see chap. 11).

By the end of the breeding season, however, facial injuries and scars among breeding individuals are common (fig. 5.5). Further, facial scars are more common among breeding males, who fight more than breeding females and who sometimes incur facial wounds inflicted by their mates during copulation (chap. 11). Injuries include loss of fur and blood, and leg injuries sometimes hobble individuals for several weeks. Two extreme fights led to the loser's death (fig. 5.4b).

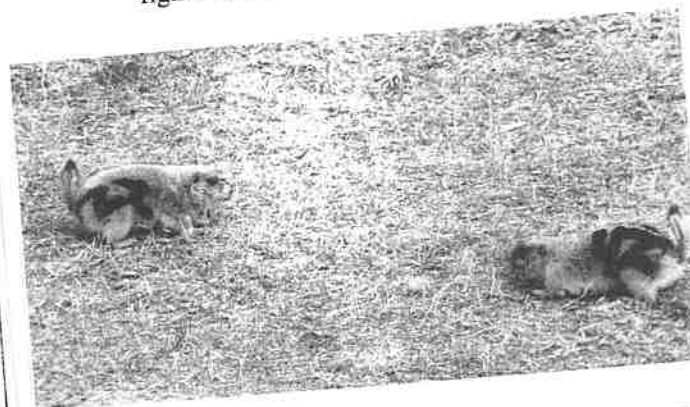


Fig. 5.3. Different orientations during a territorial dispute. (a) Face-to-face, involving male-22 and male-42. (b) Face-to-rear, involving female-75 and female-RS (racing stripe). (c) Rear-to-rear, involving male-33 and male-24. Territorial disputes commonly persist for more than 15 minutes, and sometimes involve fights as well. Notice the flared tails of disputing individuals. (Photos by John L. Hoogland.)



Fig. 5.4. Costly outcomes of aggression among prairie dogs. (a) Male-24's head is so scarred that he hardly has any hair left. (b) After killing male-00 in a vicious series of fights, male-47 cannibalizes him at burrow entrance-R. (Photos by John L. Hoogland.)

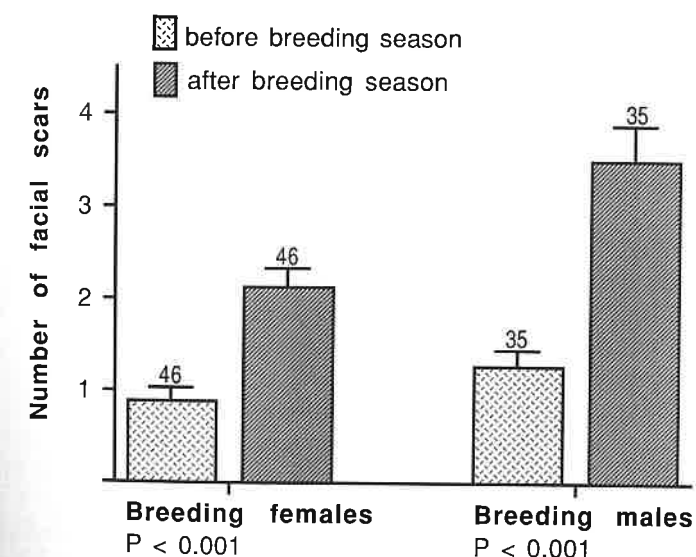


Fig. 5.5. Facial scars before and after the breeding season. In 1984 and 1985, I examined adult prairie dogs for facial scars in February, just before the onset of breeding. I then examined the same individuals for scars in April, shortly after the breeding season was over. The number above each SE line indicates the number of breeding individuals examined. P -values are from the Wilcoxon matched-pairs signed-ranks test. Breeding individuals of both sexes have more scars after the breeding season. Further, breeding males have more facial scars than breeding females both before ($P = .044$, Mann-Whitney U test) and after ($P = .008$, Mann-Whitney U test) the breeding season.

Increased Transmission of Diseases and Ectoparasites

Individuals of colonial species probably contract diseases and ectoparasites more often than individuals of closely related solitary species. Further, diseases and ectoparasites probably are more troublesome in large than in smaller colonies (Alexander 1974; Freeland 1976, 1979; Duffy 1983; Brown and Brown 1986). At least two reasons underlie these predictions. First, diseases and ectoparasites spread best during periods of proximity or actual physical contact (Stefferd 1956; Rothschild and Clay 1957; Kennedy 1975). Second, some ectoparasites require repeated contacts with different host individuals for maximal reproductive output (Cheng 1974).

The most devastating disease for prairie dogs is bubonic plague, also called sylvatic plague or wild rodent plague (Eskey and Haas 1940; Miles, Wilcomb, and Irons 1952; Pollitzer and Meyer 1961; Barnes 1982, 1993). Bubonic plague first arrived unnaturally in North America only a few hundred years ago via fleas on animals unloaded from European ships (Pollitzer 1951; Olsen 1981; Barnes 1982, 1993). Fleas are the major vectors, but lice and ticks also might transmit bubonic plague (Hirst 1953; Pollitzer 1952; Barnes 1982, 1993). Entire colonies of prairie dogs quickly disappear after the initial introduction of bubonic plague (Barnes, Ogden, and Campos 1972; Barnes, 1993).

Although bubonic plague devastates other sciurid populations as well, prairie dogs seem to be especially susceptible (Eskey and Haas 1940; Pollitzer and Meyer 1961; Olsen 1981). The logical reason for this difference is that prairie dogs are more densely colonial than other squirrels (Armitage 1981; Hall 1981; Michener 1983). However, their extreme vulnerability might be an artifact that results because prairie dogs are easier to census and track than other, less colonial squirrels (Lechleitner et al. 1968; Miles, Wilcomb, and Irons 1952).

I cannot easily study the transmission of bubonic plague or other prairie dog diseases. I can, however, count ectoparasites, which indirectly influence the transmission of disease. My prediction is that ectoparasitism should increase directly with colony size, as it does for animals such as cliff and barn swallows, Townsend's big-eared bats, and common vampire bats (Kunz 1976; Wilkinson 1985; Brown and Brown 1986; Shields and Crook 1987). Figure 5.6 supports this prediction for flea counts at burrow entrances made in August 1975, June 1977, and April 1978 (fig. 5.7; see chap. 4). However, the variation in fig. 5.6 demonstrates that factors other than colony size also must affect flea infestation of prairie dog burrow entrances.

Do ectoparasites depress individual fitness for prairie dogs, as they do for other colonial animals such as purple martins and cliff swallows (Camin and Moss 1970; Brown and Brown 1986), and for other squirrels such as

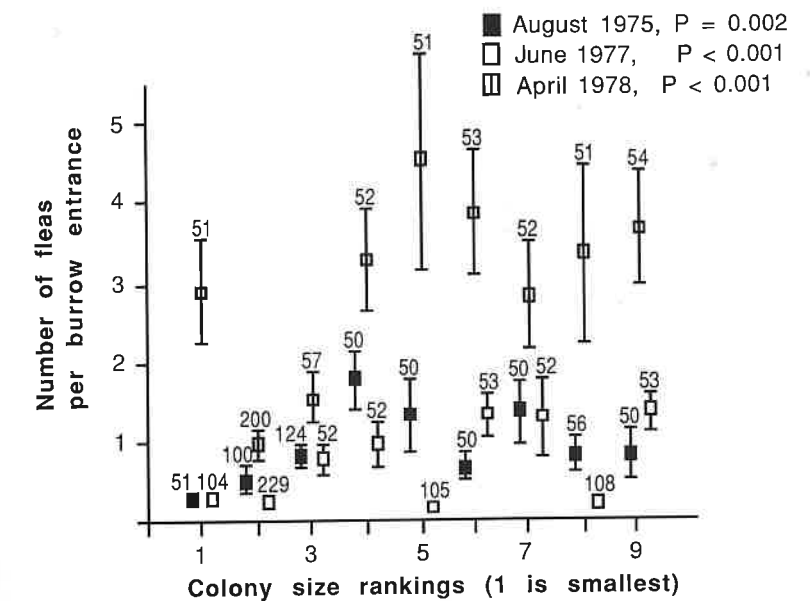


Fig. 5.6. Number of fleas per burrow entrance versus colony size. The number above each SE line indicates the number of burrow entrances sampled. *P*-values are from the Kendall rank correlation test. I could not accurately count all residents at each colony, but could rank colonies by size as shown here.

eastern chipmunks and woodchucks (McKinney and Christian 1970; Ko 1972a,b; Bennett 1973)? Three lines of evidence indicate an affirmative answer. First, although I did not directly observe such transmission, ectoparasites can transmit debilitating or fatal diseases such as bubonic plague (see above). Second, ectoparasites frequently remove blood. Third, their bites, especially those of ticks, sometimes damage the integument and thereby promote infections.

Autogrooming and allogrooming remove ectoparasites for animals such as house mice, common vampire bats, Thomson's and Grant's gazelles, and mantled howler monkeys (Murray 1961, 1987; Bell and Clifford 1964; Wilkinson 1986; Dudley and Milton 1990; Hart 1990). The same is probably true for prairie dogs. If so, then auto- and allogrooming should be more common in large wards, which contain more fleas than smaller wards. These behaviors are costly, not only because they involve time and energy, but also because they reduce individual wariness (Hart et al. 1992; Maestripiere 1993). Curiously, rates of autogrooming and allogrooming in small and large prairie dog wards are almost identical (fig. 5.8).



Fig. 5.7. Two ways to measure ectoparasitism among prairie dogs. (a) To measure ectoparasitism at burrow entrances, a researcher counts fleas that jump onto a piece of white flannel that has been submerged 2 meters for 30 seconds. This method only rarely detects lice and ticks. (Photo by John L. Hoogland.) (b) To measure ectoparasitism on the prairie dogs, I comb the back and each side 10 times with a fine-toothed comb and then count the fleas, lice, and ticks that fall below. I also count all ectoparasites that I see on the fur or skin. (Photo by Judy G. Hoogland.)

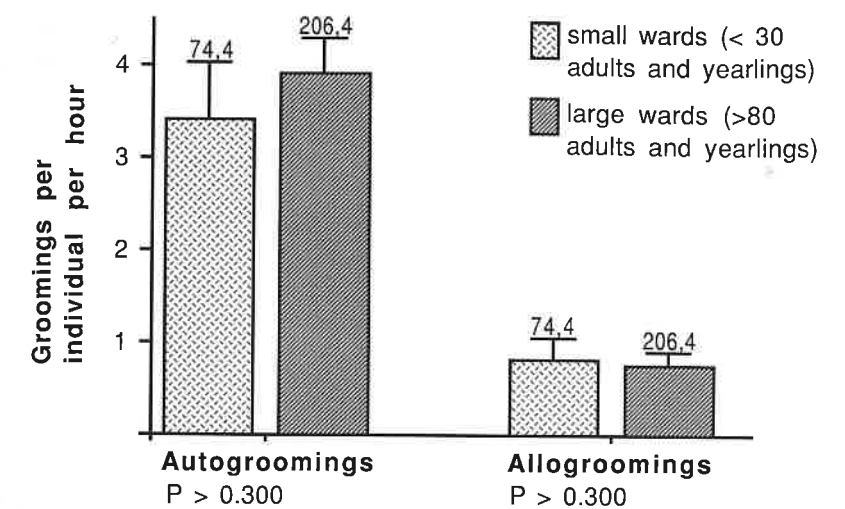


Fig. 5.8. Autogroomings and allogroomings versus ward size. I record groomings during 30-minute periods when I also record individual alertness (see fig. 5.15). The numbers above each SE line indicate the number of 30-minute observation periods and the number of different wards observed. *P*-values are from the Mann-Whitney *U* test.

Increased Probability of Misdirected Parental Care

Parents of solitary animals only rarely mistake another nest for their own, encounter unrelated offspring at the home nest, or have their own offspring wander into strange nests. But these are common problems within colonial animals such as royal and crested terns, common and thick-billed murres, northern elephant seals, and Mexican free-tailed bats (Davies and Carrick 1962; Buckley and Buckley 1972; Le Boeuf, Whiting, and Gantt 1972; McCracken 1984, 1993; Gaston, De Forest, and Noble 1993). One possible consequence is that parents of colonial animals will lose their offspring in a crowd. Another is that parents will accidentally rear others' offspring. Is misdirected parental care another cost of prairie dog coloniality?

Following first juvenile emergences from the natal burrow, quick mixing of young from different litters is ubiquitous for ground squirrels and marmots (McCarley 1966; Michener 1973; Slade and Balph 1974; Leger and Owings 1978; Barash 1989). The same is true for prairie dogs: juveniles from different litters within the home coterie territory begin to interact aboveground within days after first emergence from the natal burrow (fig. 5.9; see also King 1955; Costello 1970). First mixings result primarily from the wanderings of the juveniles themselves. However, first mixings also result when a mother transfers her emergent young from the home nursery burrow to a burrow containing another mother's young. For the latter, the

mother uses her mouth to grab her offspring one at a time by the nape of the neck, the belly, or one of the legs (fig. 5.10). Sometimes mothers transfer by slowly "leading" offspring from one burrow entrance to another. Soon after first mixing, juveniles from different litters begin to spend the night together with one or more mothers in the same burrow, where communal nursing occurs (chap. 9). The difficulty of live-trapping entire litters at more than one colony has precluded an investigation of the effect of colony size on juvenile mixing.

When the possibility of misdirected parental care becomes serious, then natural selection sometimes favors either parents that can discriminate between their own and others' offspring, or juveniles that can discriminate between their own and others' parents. Such parent-offspring recognition helps to redirect parental effort, and occurs for colonial animals such as bank and cliff swallows, Mexican free-tailed bats, Galápagos fur seals, and Galápagos sea lions (Trillmich 1981; Beecher, Stoddard, and Loesche 1985; Beecher et al. 1986; Balcombe 1990; Balcombe and McCracken 1992). Curiously, prairie dog mothers do not reject juveniles from other litters of the home coterie territory that wander near the home nursery burrow and mix with their own offspring—even when the invading juveniles have been aboveground for several weeks. Further, emergent juveniles seem unable to discriminate between their own and others' mothers.

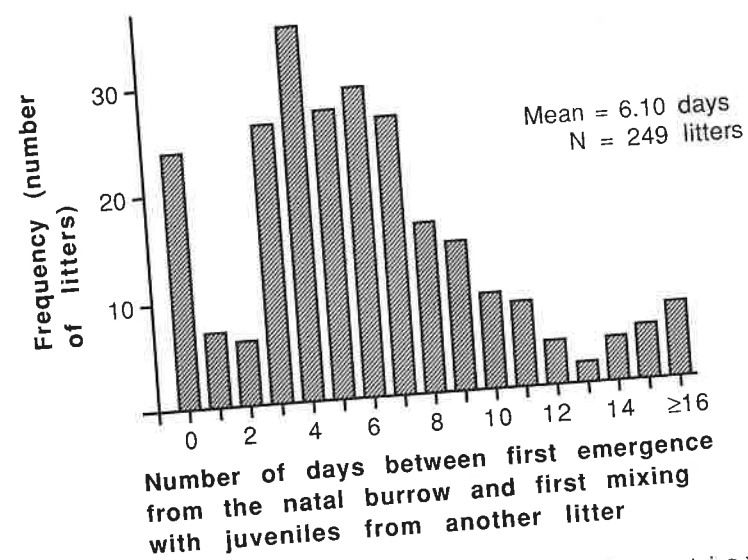


Fig. 5.9. Number of days between first juvenile emergence and first mixing with young from a different litter. I record mixing when two juveniles interact aboveground or when they appear on the same burrow mound.



Fig. 5.10. Prairie dog mother-H3 transferring juvenile-H3X from the natal burrow to a different burrow. Mothers usually transfer by grabbing the juvenile by one of the legs, as seen here, or by the neck or belly. Sometimes mothers transfer their juveniles to a burrow containing juveniles from another litter. (Photo by John L. Hoogland.)

Evidently the mixing of emergent young from the same coterie territory is not seriously costly to prairie dog mothers, even though communal nursing of foster juveniles is a common result (see also chaps. 9 and 10).

Increased Conspicuousness and Increased Attractiveness to Predators

A colony of animals must almost always be more conspicuous and attractive to predators than is a single animal (Cullen 1960; Sillén-Tullberg 1990; Cooper and Vitt 1991). Increased exposure to predators is therefore a possible cost of coloniality.

A predator might detect a prairie dog colony by seeing mounds at burrow entrances, by seeing the prairie dogs themselves, or by hearing their vocalizations. All three of these potential cues increase directly with ward size ($P < .001$, Kendall rank correlation test; see fig. 5.11 and Hoogland 1979a).

If increased vocal conspicuousness within large wards is costly, then natural selection might favor individuals who are unusually quiet. If so, then territorial (or jump-yip; see chap. 8) calls *per individual* per hour might vary inversely with ward size even though territorial calls per hour vary directly with ward size (fig. 5.11). Contrary to this prediction, the

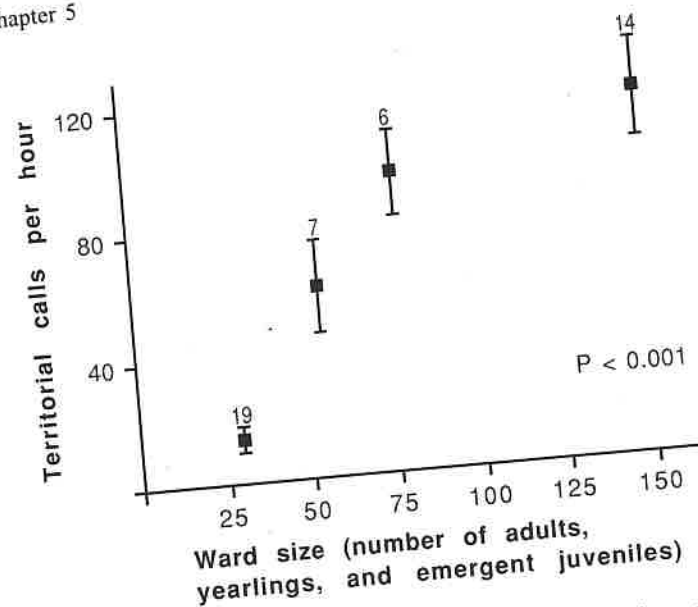


Fig. 5.11. Territorial calls per hour versus ward size. The number above each SE line indicates the number of days on which I counted territorial calls for 30 minutes. The P -value is from the Kendall rank correlation test. Ward size for this graph includes emergent juveniles, which sometimes give territorial calls.

number of territorial calls per individual per hour varies directly with ward size ($P < .001$, Kendall rank correlation test; data taken from fig. 5.11, then transformed). Evidently, either increased vocal conspicuousness of colonies to predators is not seriously deleterious, or the importance of territorial calls in aggression outweighs any associated costs. Similarly, prairie dogs evidently do not attempt to reduce the visibility of either themselves or their burrow mounds. Indeed, several of their activities—such as the construction of ostentatious rim craters (chap. 3) and the regular clipping of tall vegetation (chap. 2 and below)—clearly increase the visual conspicuousness of colonies.

Miscellaneous Costs

Besides the four costs discussed above, other costs of prairie dog coloniality also might exist. Likely possibilities include increased probability of deterioration of burrows and their mounds, loss of nest materials to pilfering conspecifics, interference with copulations, misdirected parental care resulting from either intraspecific brood parasitism or cuckoldry, and loss of offspring to marauding conspecifics (Hoogland and Sherman 1976). Because of their rarity (e.g., stealing of nest materials; see below) or difficulty of observation (e.g., infanticide; see chap. 7), I did not compare

these miscellaneous costs with prairie dog colony size. Here I will only comment briefly on some of the more interesting miscellaneous costs.

Like Belding's ground squirrels and hoary and Olympic marmots (Sherman and Morton 1979; Barash 1989), prairie dogs—especially pregnant and lactating females—frequently collect nest material for burrows where they spend the night (chap. 3; see also King 1955 and fig. 11.17). I therefore expected regular stealing of nest material similar to what occurs within colonies of birds such as kittiwakes, Adélie penguins, and cattle egrets (Cullen 1957; Tenaza 1971; Siegfried 1972). Incredibly, I observed stealing by only one prairie dog. Female-WA in 1986 repeatedly stole nest material from the burrow where the resident breeding male regularly spent the night and took it into the nursery burrow containing her unweaned offspring.

Interference with copulation—when a male tries to separate a copulatory pair—commonly occurs in colonial animals such as dunlocks, Belding's ground squirrels, yellow-toothed caviars, wild guinea pigs, and stump-tailed macaques (Rood 1972; Hanken and Sherman 1981; Davies 1985; Bruce and Estep 1992). Interference with copulation also occurs among prairie dogs (chaps. 11 and 12).

Intraspecific brood parasitism, common among birds but rare among mammals, occurs when a parent transfers its offspring into another parent's nest for rearing (Yom-Tov 1980; Andersson 1984a; Rohwer and Freeman 1989; Petrie and Møller 1991). Does such parasitism occur within prairie dog colonies? Specifically, do females ever give birth in the nursery burrows of other females? Evidently not. I have never seen a female enter another female's nursery burrow on the same day that the trespassing female also gave birth. Nor have I ever seen a female carry one of her own offspring into another female's nursery burrow, except just before or just after first juvenile emergence (see above and chap. 9).

Misdirected male parental care resulting from cuckoldry is omnipresent among avian species (Wrege and Emlen 1987; Brown and Brown 1988a; Sherman and Morton 1988; Brooker et al. 1990; Møller and Birkhead 1993). The minimal frequency of misdirected paternal care among prairie dogs resulting from cuckoldry is 8% (chap. 12).

The most serious cost of prairie dog coloniality is the increased incidence of infanticide. Because it is so common (affecting 39% of litters born) and so varied (four distinct types), I have devoted an entire chapter to infanticide among prairie dogs (see chap. 7).

Possible Reasons for Prairie Dog Coloniality

Shortage of Suitable Habitat?

Unused Habitat Within or Near Colonies. Emigration to, and colonization of, new colony sites probably is expensive and dangerous for prairie dogs (chaps. 3 and 16). However, expansion of already existing colonies

should be easier and safer. If habitat is limiting, then unused suitable habitat near established colonies should be rare.

Unfortunately, unless prairie dogs are actually living in a particular area, verification of its suitability is practically impossible. With this reservation in mind, I have qualitatively examined nine prairie dog colonies at Wind Cave National Park for evidence of adjacent surplus habitat. Every colony has unused, level prairie habitat adjacent to it that appears suitable for expansion. In other words, prairie dogs seem to be more clumped than necessary.

Evidently in response to adjacent suitable habitat, King's (1955) "ward A" increased from 2.10 hectares in 1948 and 1949 to 2.95 hectares in 1950. Such increases are the rule rather than the exception for prairie dog colonies tracked for more than a year (Lovaas 1973; Knowles 1985; Halpin 1987; Garrett and Franklin 1988). The implication is that prairie dogs typically have unused suitable habitat at their disposal.

Frequency of Isolated Prairie Dogs. If coloniality results mainly from a shortage of suitable habitat, then prairie dogs should avoid the costs of coloniality by isolating themselves whenever possible. Such isolation could occur either when patches of habitat are large enough for only one individual or when patches are too large to be saturated by the local population. Costello (1970) once found a lone prairie dog living near Nunn, Colorado. Though I have looked, I have never detected an isolated prairie dog. Perhaps this dearth results because isolates are so vulnerable to predation (see below).

Social Facilitation of Foraging?

The usual factors that promote social facilitation of foraging do not apply to prairie dogs. For example, individuals are herbivorous and do not hunt in groups (chap. 2). Further, food supplies are neither large nor unpredictable; rather, individuals feed on herbaceous tidbits growing within the home coterie territory (chap. 6).

One type of social facilitation of foraging might conceivably apply to prairie dogs. Individuals commonly expose subsoil during the excavation and maintenance of burrows. This subsoil promotes the growth of certain plant species uncommon elsewhere (King 1955; Koford 1958). Further, as in human "fallow farming," prairie dogs sometimes avoid foraging in certain areas with undesirable plant species until new, preferred species establish themselves there (King 1955). Finally, individuals sometimes clip down certain undesirable plant species without consuming them, thereby promoting the invasion of new, preferred species (King 1955; Whicker and Detling 1988). Could these fascinating "agricultural" activities—a form of social facilitation of foraging here termed *farming*—be an important benefit of coloniality? Probably not. Prairie dogs restrict all farming and foraging

to the home coterie territory. Farming in one coterie territory might affect the growth of plants in adjacent territories, but such incidental effects are probably trivial. Thus, even though farming might theoretically explain the evolution of coterie territories, it cannot easily explain the clumping of coterie territories into colonies. Only if prairie dogs fed and farmed throughout the entire area of a colony could the farming hypothesis be relevant to the evolution of large colonies. More likely is that the benefits of farming are secondary consequences of coloniality that has evolved in some other context.

Coloniality might sometimes evolve because groups are better than solitary individuals at defending an important feeding site (Brown and Orians 1970). The conspicuous defense of the home coterie territory by all coterie members suggests that group defense of foraging grounds might be important for prairie dogs. However, recall once again that individuals forage in and defend *only the home coterie territory*, rather than all sections of the home colony. Thus, for reasons that parallel those just presented for farming, group defense of foraging grounds might explain the evolution of coterie territories, but cannot easily explain the grouping of coterie territories into colonies (see also chap. 6). Grouping of coterie territories probably leads to *greater* difficulty in defending a feeding area from conspecifics.

Reduced Predation?

Increased Awareness of Predators. If coloniality ultimately results from predation pressure, then the rate of predation should vary inversely with colony size, and survivorship and reproductive success should vary directly with colony size. Colonial animals that reap these benefits include black-headed gulls, tricolored and red-winged blackbirds, common eiders, and southern sea lions (Patterson 1965; Payne 1969; Robertson 1973; Munro and Bedard 1977; Campagna et al. 1992).

For prairie dogs, my original hope was to compare predation rates and reproductive success directly with colony size. But two problems quickly surfaced. First, monitoring predation and reproductive success at more than one colony is practically impossible. Second, even though I see numerous apparent attempts by just about all known predators except black-footed ferrets (table 5.1), the prairie dog defense system is consistently successful (see also King 1955; Tileston and Lechleitner 1966; Garrett and Franklin 1988). Incredibly, field assistants and I have observed only 26 predations, 22 of them at the study colony (table 5.2). So few observations might suggest that predation has not been important in the evolution of prairie dog coloniality. Contrarily, so few predations in the face of so many attempts probably result because natural selection has molded an incredibly effective defense against a potentially devastating problem.

My original plan dashed, I have attempted to compare antipredatory defense versus colony size indirectly. Specifically, I perform experiments with a stuffed specimen of an American badger mounted on a plastic sled

Table 5.1. Predators Seen at the Study Colony in 1987 (26 January through 13 June)

Species	Number of sightings
Bald eagle	3
Golden eagle	87
Prairie falcon	12
Northern harrier	6
Cooper's hawk	8
American kestrel	6
Northern goshawk	5
Red-tailed hawk	9
Sharp-shinned hawk	6
Ferruginous hawk	2
Hawk, species unknown	25
Coyote	2
Bobcat	7
American badger	1
Prairie rattlesnake	1
Total	180

Note: I score all sightings, but do not always know whether the predator is actually hunting prairie dogs. These data are from 1987 only, but similar sightings occur at roughly the same frequencies every year.

Table 5.2. Predations Observed at the Study Colony or the Pringle Colony

Colony	Date	Type of predator	Victim	Age of victim	Sex of victim
Pringle	18 May 1979	Prairie falcon	UnX	Weanling	Unknown
Pringle	Apr 1982	Golden eagle	Un	Unknown	Unknown
Pringle	Apr 1983	Golden eagle	Un	Unknown	Unknown
Pringle	07 Apr 1984	Golden eagle	21	1 year	Male
Study colony	11 Jun 1976	Prairie falcon	WAX	Weanling	Male
Study colony	21 Jun 1978	Prairie falcon	WAOX	Weanling	Male
Study colony	06 Jun 1979	Cooper's (?) hawk	HOX	Weanling	Unknown
Study colony	10 Jun 1979	Prairie falcon	HX	Weanling	Female
Study colony	23 Apr 1980	Bobcat	74	3 years	Female
Study colony	21 May 1980	Prairie falcon	WAX	Weanling	Female
Study colony	02 Mar 1981	Bobcat	71	≥ 7 years	Female
Study colony	01 Apr 1981	Bobcat	R81	1 year	Female
Study colony	22 May 1981	Cooper's (?) hawk	TSX	Weanling	Unknown
Study colony	08 Jun 1981	Coyote	RR3	4 years	Female
Study colony	30 Oct 1981	American badger	CR	2.5 years	Female
Study colony	21 Mar 1982	Prairie falcon	RR7	6 years	Female
Study colony	06 May 1984	Coyote	2RS	4 years	Female
Study colony	23 Oct 1984	Coyote	R17	0.5 years	Male
Study colony	26 Oct 1984	Bobcat	R51	0.5 years	Female
Study colony	12 Jun 1985	Coyote	92	3 years	Female
Study colony	21 Mar 1986	Bobcat	WARS	6 years	Female
Study colony	01 May 1986	Bobcat	Un	0.5 years	Male
Study colony	02 Jun 1986	Bobcat	84	4 years	Female
Study colony	13 Jun 1986	Bobcat	WA4	3 years	Female
Study colony	10 Jun 1987	Bobcat	R76	1 year	Female
Study colony	29 Jul 1989	Bobcat	= 4X	Weanling	Male



Fig. 5.12. Three stuffed American badgers on Plexiglas sleds. I used these badgers in more than 1,000 experimental runs to study how quickly prairie dogs detect a predator, and to determine which individuals give antipredator calls. (Photo by John L. Hoogland.)

(fig. 5.12; see chap. 4). My prediction is that individuals in large colonies should detect predators more quickly than individuals in smaller colonies (Galton 1883; Pulliam 1973; Dimond and Lazarus 1974; Treisman 1975a,b).

A prairie dog warns conspecifics of danger in two ways. Sometimes it gives a *visual alarm* by running to a burrow mound or by freezing in one of several alert postures (Clark 1977). Visual alarms are probably secondary consequences of individual efforts to see the predator better, decrease individual conspicuousness, or get closer to an escape burrow. After giving a visual alarm, a prairie dog sometimes gives a *vocal alarm*, or *antipredator call* (chap. 8). Other individuals usually join the first caller, leading to a chorus of antipredator calls during a predatory attack. Antipredator calls probably function primarily, rather than merely secondarily, to warn conspecifics. Perhaps because an alerted prairie dog is practically impossible to capture, both terrestrial and avian predators usually stop hunting following a flurry of visual and vocal alarms. Perhaps the sound of the antipredator call itself also helps to deter predators.

As predicted, prairie dogs detect the American badger and give visual and vocal alarms more quickly in large wards than in smaller wards (fig. 5.13). Earlier alarms in larger wards are probably important for at least two reasons. First, an early signal occurs when the predator is still far enough away so that its success from continued hunting is unlikely. Second

and more important, an early alarm gives conspecifics more time to reach safety. The increased ability to detect predators is probably the major benefit of prairie dog coloniality.

The number of visual alarmers during experiments with the stuffed American badger increases directly with ward size (fig. 5.14). The same is probably true for antipredator callers, but I could not investigate this possibility because callers are so numerous and difficult to identify. More visual and vocal alarms in large colonies presumably increase the probability of seeing or hearing an alarm for uninformed individuals. This higher probability might be important under conditions of poor visibility (as on foggy mornings) or poor audibility (as on windy days). Further, the probability of deterring certain predators might vary directly with the number of confusing, distracting, or obnoxious visual and vocal alarm signals.

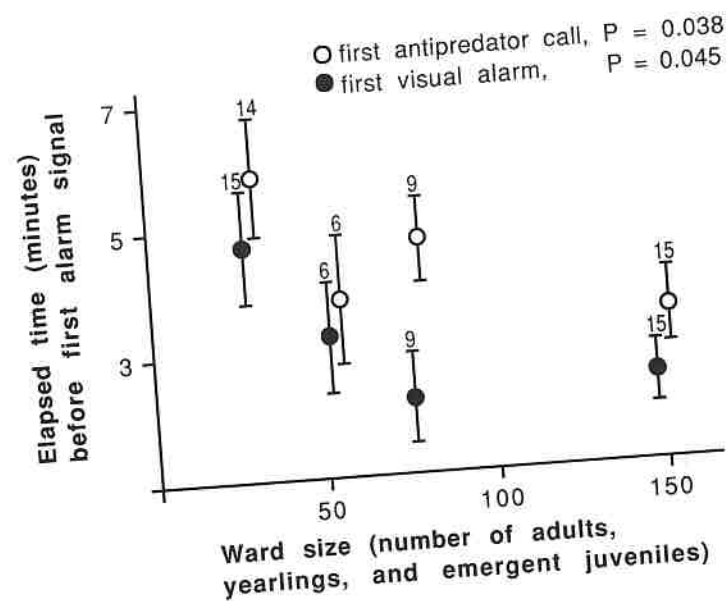


Fig. 5.13. Detection of the stuffed badger versus ward size. The number above each SE line indicates the number of experimental runs with the stuffed American badger. P -values are from the Kendall rank correlation test. Ward size for this graph includes emergent juveniles. The vertical axis here shows the elapsed time in minutes, and might suggest that the prairie dogs are slow to respond. However, the badger is 30 meters from an outermost peripheral burrow entrance at the start of each experimental run, and sometimes is more than 50 meters from foraging prairie dogs. Further, the field assistant pulls the badger slowly—at a rate of only 11 centimeters per second—so that I can accurately record the first visual alarm and the first antipredator call. For experiments to determine the identity of callers (chap. 8), the field assistant pulls the badger at a faster rate.

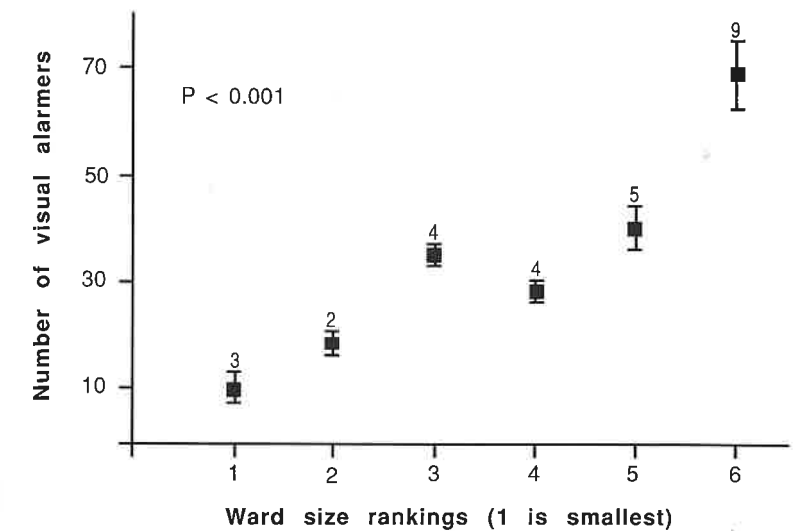


Fig. 5.14. Number of visual alarmers versus ward size. The number above each SE line indicates the number of experimental runs with the stuffed American badger. The P -value is from the Kendall rank correlation test. I could not accurately count all residents of each ward, but could rank wards by size, as shown here. A visual alarmer is a prairie dog that stands on or near a burrow mound. Visual alarmers often give antipredator calls as well.

When the potential for detecting predators varies directly with group size, individuals in large groups should be able to scan less often for predators—and thus have more time for feeding (Clark and Mangel 1986; Watts 1985; Elgar 1989; Scheel 1993). Like ostriches (Bertram 1980), several species of geese (Lazarus 1978; Drent and Swierstra 1977; Lazarus and Inglis 1978; Black et al. 1992), white-nosed coatis (Burger and Gochfield 1992), and yellow-bellied and Olympic marmots (Armitage 1962; Barash 1973; Svendsen 1974; Carey and Moore 1986) in larger groups, prairie dogs in large wards spend less time scanning for predators than do prairie dogs in smaller wards (fig. 5.15; see also Kildaw 1991). Such scanning occurs from every imaginable posture (fig. 5.16).

For animals such as Florida scrub jays, Arabian and black-lored babblers, vervet monkeys, dwarf mongooses, and meerkats (Moran 1984; Wickler 1985; Rasa 1986; McGowan and Woolfenden 1989; Baldellou and Henzi 1993), individuals coordinate their vigilance, with certain individuals ("sentinels") scanning for predators more often than others. Prairie dogs do not systematically coordinate their vigilance, but reproductive males do scan for predators slightly more often than females and nonreproductive males (Loughry 1993a,b).

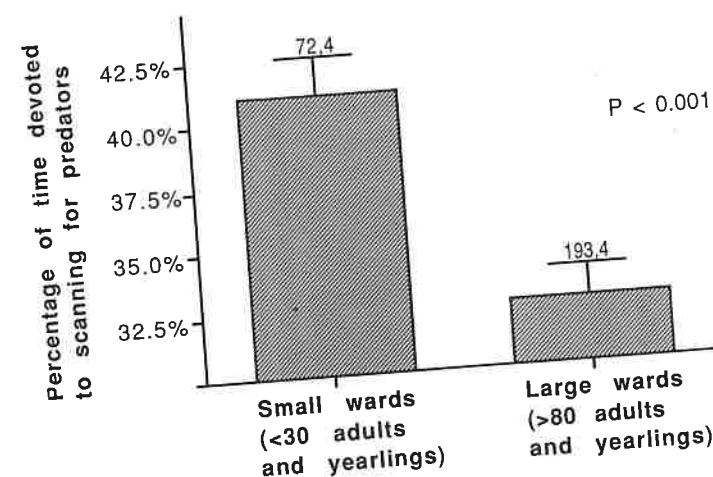


Fig. 5.15. Percentage of time that individual prairie dogs spend scanning for predators (individual alertness) versus ward size. I watch each prairie dog for 30 minutes, and record the number of minutes during which the individual looks around, presumably for predators. The numbers above each SE line indicate the number of 30-minute observation periods and the number of wards observed. The P -value is from the Mann-Whitney U test.

Increased Ability to Deter Predators. Prairie dogs do not mob large predators such as coyotes, American badgers, bobcats, or golden eagles. However, like dwarf and banded mongooses (Rood 1975; Rasa 1977), prairie dogs do sometimes physically "mob" certain small predators, as the following examples attest. First, Stromberg (1974) observed two individuals ram into a grounded red-tailed hawk that had just killed a member of the rammers' home coterie. Second, on two occasions I observed three or more prairie dogs cooperatively chasing a long-tailed weasel that had entered the home coterie territory (see also Hillman and Linder 1973). Hillman (1968) observed similar chasing in response to black-footed ferrets, and also observed prairie dogs cooperatively closing burrow entrances entered by black-footed ferrets (chap. 3). Finally, mobbing and harassing by prairie dogs—sometimes accompanied by biting and interment—sometimes occur in response to snakes (King 1955; Owings and Owings 1979; Halpin 1983; Owings and Loughry 1985; Loughry 1987a,b, 1988; see also chaps. 3 and 8). In all these circumstances, prairie dogs ignore small predators in other coterie territories and only attack when the predator enters the home coterie territory.

Adult and yearling prairie dogs are usually too large for predation by long-tailed weasels, snakes, and small aerial predators such as Cooper's and red-tailed hawks. Within only a few weeks after first emergence,



Fig. 5.16. Different levels of individual alertness among prairie dogs. (a) Prairie dog stands tall on two legs while scanning for predators from a burrow mound. (Photo by Wendy Shattil/Bob Rozinski, copyright 1992.) (b) One prairie dog scans on all fours from a burrow mound, and the other scans while sitting on its rump and rear legs. (Photo by Judy G. Hoogland.) (c) Two prairie dogs scan while continuing to feed. (Photo courtesy of J. Perley Fitzgerald.) (d) Because its eyes are so high on the head, a prairie dog can scan from a burrow entrance with only the top of its head protruding. During an attack, prairie dogs usually do not completely submerge unless a predator approaches within 5 meters or so. (Photo courtesy of Wind Cave National Park.)

juveniles are also too large. Mortality from small predators is therefore rare, and mobbing of small predators is probably a secondary consequence of the coloniality that has evolved primarily to reduce mortality from larger predators.

Increased "Selfish Herd Effects." The study colony is small relative to most prairie dog colonies (chap. 4). Most coterie territories about the colony's edge, so that center-edge comparisons with reproductive success are difficult. I have, however, compared center-edge differences in individual alertness at other, larger colonies. Like peripheral wood pigeons, cliff swallows, and yellow-bellied marmots (Murton 1968; Armitage 1962; Brown and Brown 1987), prairie dogs at colony peripheries spend more time scanning for predators than do more central individuals in 76% of comparisons (16/21; $P = .005$, Wilcoxon matched-pairs signed-ranks test using 21 pairs, each watched for 30 minutes, from 10 wards).

I predicted that prairie dogs would synchronize reproduction within colonies, in order to better capitalize on "selfish herd effects" (Hamilton 1971; Ims 1990a,b). I further predicted that reproductive success would be higher for synchronous breeders than for asynchronous breeders (Patterson 1965; Brown and Brown 1987). Data in chapter 13 support the first prediction, but not the second.

Increased Number and Density of Burrows. Prairie dogs ultimately depend on their burrows for safety from weather and predators (chap. 3). Suppose that a single prairie dog can excavate and maintain five burrows. Because sharing of burrows occurs (chap. 3), each prairie dog in a colony of two would have access to ten burrows, each prairie dog in a colony of three would have access to fifteen burrows, and so on. Could access to more burrows—and perhaps also a higher density of burrows—explain prairie dog coloniality? If so, then the number and density of burrows should vary directly with colony size. Counting burrow entrances and estimating the density of burrow entrances are easy, but accurate estimates of colony size require livetrapping and therefore are more elusive. Sufficient data to compare prairie dog colony size with the number and density of burrows and burrow entrances are presently unavailable (Hoogland 1981a).

Comparative Data from White-Tailed Prairie Dogs

Costs and Benefits of White-Tail Coloniality

White-tailed prairie dogs also live in colonies. Not surprisingly, white-tails incur many of the same costs of coloniality as do black-tails. For example, aggression, flea infestation, and visual and vocal conspicuousness to predators all vary directly with white-tail colony size (Hoogland 1979a).

Probably in response to the greater ectoparasitism there, white-tails in large wards autogroom more often than white-tails in smaller wards ($P < .010$, Mann-Whitney U test). White-tails also reap many of the same benefits of coloniality as do black-tails. For example, white-tails in large wards detect predators more quickly, see more visual alarms and hear more antipredator calls during a predatory attack, and spend less time scanning for predators than white-tails in smaller wards (Hoogland 1981a).

Black-tail colonies are generally larger and more densely populated than white-tail colonies (fig. 5.17). Consequently, the costs of coloniality should be more extreme for black-tails than for white-tails. Interspecific comparisons support this prediction. For example, competition is probably more extreme among black-tails, as is visual and vocal conspicuousness to predators (Hoogland 1979a). Further, counts from the animals and from their burrow entrances both indicate that black-tails harbor more fleas than white-tails (Hoogland 1979a); as a probable consequence, black-tails auto- and allogroom more than white-tails do ($P < .050$ for both, Mann-Whitney U test).

Interspecific comparisons of benefits also yield the predicted results. Even though they devote less time to individual alertness (35% versus 43%), black-tails detect predators more quickly than white-tails do (Hoogland 1981a). Black-tails also have access to more visual alarms during a predatory attack (Hoogland 1981a). Finally, antipredator calls are louder and more numerous in black-tail colonies (Waring 1970; chap. 8 and unpublished data).

Why Are Black-Tails More Colonial than White-Tails?

Surely no simple reason explains why white-tails live in small, sparsely populated colonies while black-tails live in large, densely populated colonies. Here I will briefly speculate on two likely possibilities (see also Hoogland 1977, 1981a).

Interspecific Differences in Predation. Increased predation might lead to larger, more dense colonies (Alexander 1974; Heard 1992). Specifically, black-tails might be more colonial than white-tails because of higher predation rates over evolutionary time. This possibility seems unlikely in qualitative terms, because known or suspected predators on black-tails and white-tails are identical (Tileston and Lechleitner 1966; Clark 1973, 1977; Campbell and Clark 1981; Hoogland 1981a). In quantitative terms, comparing rates of predation on black-tails and white-tails throughout their ranges would be practically impossible.

But wait, what about black-footed ferrets? Powell (1982) has argued that black-footed ferrets occur only in black-tail habitats. If so, then black-footed ferrets might ultimately explain why black-tails form larger, more

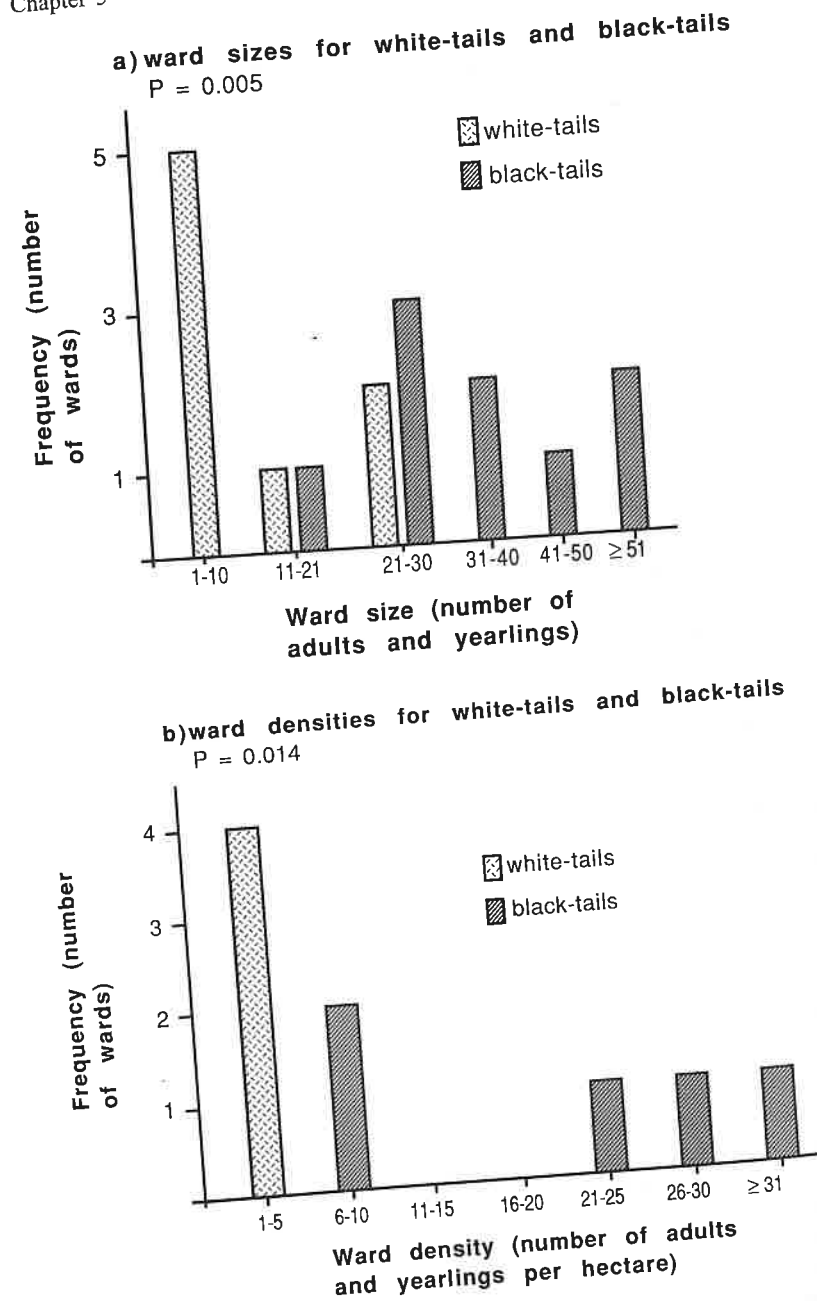


Fig. 5.17. Interspecific comparison of (a) ward size and (b) ward density for white-tailed and black-tailed prairie dogs. Data are only from wards in which the researcher color-marked every adult and yearling (King 1955; Tileston and Lechleitner 1966; Clark 1977; Garrett and Franklin 1988; Halpin 1987; this study). P -values for both graphs are from the Mann-Whitney U test.

densely populated colonies than white-tails. However, Powell's argument stems from the black-footed ferret's range map depicted in Hall (1981), which does not include recent findings of live black-footed ferrets and black-footed ferret skulls in white-tail colonies located several hundred kilometers from the nearest black-tail colonies (Martin and Schroeder 1978, 1980; Anderson and Inkley 1985; Clark, Forrest, et al. 1986; Clark, Richardson, et al. 1986; Biggins and Schroeder 1988; Seal et al. 1989). Further, black-footed ferrets are usually active only at night (Hillman 1968; Campbell et al. 1987; Paunovich and Forrest 1987; Richardson et al. 1987; Schroeder 1987). How could nocturnal predation affect the coloniality of animals as diurnal as prairie dogs (chap. 2)? "Selfish herd" effects (Hamilton 1971) offer one possible solution to this problem. More likely, however, is that coloniality of white-tails and black-tails has evolved primarily in response to more diurnal predators such as coyotes, bobcats, and raptors—with the secondary consequence that individuals are especially vulnerable to nocturnal, burrow-entering black-footed ferrets.

Interspecific Differences in Protective Cover. Some animals depend on hiding from predators to avoid predation, while others depend on detecting predators soon enough to allow time for escape. Despite some marvelous exceptions (e.g., see Wickler 1968; Owen 1980), hiding from predators is usually feasible only for single individuals and small groups that live in habitats with extensive protective cover. Conversely, the potential to detect predators is best for animals that live in large groups and in open habitats, as do various species of ungulates, kangaroos, and primates (Jarman 1974; Kaufmann 1974; Clutton-Brock and Harvey 1977a,b; Alexander et al. 1979). Might interspecific differences in protective cover explain why black-tails are more colonial than white-tails?

Black-tails typically colonize overgrazed habitats with little protective cover (King 1955; Tileston and Lechleitner 1966; Hoogland 1977, 1981a; Coppock, Detling, et al. 1983; Coppock, Ellis, et al. 1983). Black-tails further increase visibility by razing tall plants (fig. 5.18). White-tails, on the other hand, colonize habitats with more, taller plants, which they do not remove or shorten (Tileston and Lechleitner 1966; Clark 1977; Hoogland 1981a). Interspecific differences in protective cover thus might ultimately explain why black-tails form large, densely populated colonies—to maximize quick detection of predators. By contrast, white-tails form small, sparsely populated colonies—to compromise between the benefits of hiding and of quick detection of predators.



Fig. 5.18. Clipping of tall vegetation. (a) On 07 June 1976 at 1800 hours, I transplanted tall grasses to an area near the center of a coterie territory. (b) By 0900 hours on the following day, prairie dogs had clipped down all the tall vegetation. In 93% of such transplants (13/14) into fourteen different coterie territories of six different wards, prairie dogs removed more than 50% of the tall grasses within a few days. By contrast, all five "control" transplants placed outside ward boundaries were intact after 15 days. (Photos by Judy G. Hoogland.)

Summary

1. Aggressive interactions among prairie dogs that increase directly with ward size include fights, chases, runaways, and territorial disputes. Costs of aggression include lost time and energy, temporary or permanent eviction from the home coterie territory, and bodily injuries.
2. Ectoparasites on prairie dogs include fleas, lice, and ticks. The number of fleas at burrow entrances increases directly with colony size. Costs of ectoparasitism include increased transmission of diseases, loss of blood, and open wounds.
3. Prairie dog juveniles from different litters within the home coterie territory mingle soon after their first emergences from the natal

burrow. Consequently, parents might lose time and energy while trying to locate their own offspring, and mothers sometimes suckle foster offspring. Curiously, parents do not seem to discriminate between their own and others' offspring during the first month that juveniles are aboveground.

4. Miscellaneous costs of prairie dog coloniality include an increased probability of infanticide and of misdirected paternal care resulting from cuckoldry.
5. The availability of seemingly suitable habitat at colony edges and the absence of isolated prairie dogs both suggest that prairie dog coloniality does not result merely from a shortage of habitat.
6. Because individuals are herbivorous and their food supplies are evenly distributed, social facilitation of foraging probably has not been important in the evolution of prairie dog coloniality.
7. Even though they spend less time scanning for predators, prairie dogs in large wards detect predators more quickly than prairie dogs in smaller wards. Reduced predation is probably the primary benefit of prairie dog coloniality.
8. White-tailed prairie dogs live in smaller, less densely populated colonies than do black-tails. Consistent with this interspecific difference, white-tails fight less frequently, are less conspicuous to predators, have fewer ectoparasites, auto- and allogroom less often, and detect predators less quickly than black-tails—even though white-tails spend more time scanning for predators.
9. Unlike white-tail colonies, black-tail colonies contain little protective cover. This interspecific difference might ultimately explain why black-tails form large, densely populated colonies—to maximize quick detection of predators. By contrast, white-tails form small, sparsely populated colonies—to compromise between the benefits of hiding and of quick detection of predators.

Toxicological Studies of Zinc Phosphide^{*,†}

By HENRY DOUGLAS JOHNSON[‡] and ELBERT VOSS[§]

An investigation has been made to determine some of the acute and chronic effects of zinc phosphide, a rodenticide. Sublethal administration of this compound to domesticated albino rats produces damage to liver and lungs without visible effects on other organs. Evidence is presented to support the assumption that the acute and chronic symptoms of zinc phosphide intoxication are due to phosphine released by gastric acid. Dogs and cats seemed, in general, less susceptible to zinc phosphide than rats, rabbits, and fowls.

FOR a number of years zinc phosphide (Zn_3P_2) has been used as a poison in rodent control and has proved to be an effective and convenient agent for this purpose. In view of its increasing use, this work was undertaken.

The effects of chronic exposure to zinc phosphide have been studied in albino rats in respect to weight gain, histopathological changes, and fertility. Acute effects in dogs, cats, and rabbits have been noted and a possible mechanism of action for acute and chronic poisoning by zinc phosphide is postulated.

CHRONIC EXPERIMENTS

A preliminary survey indicated that zinc phosphide could be incorporated into a rat's diet at 0.02% and 0.03% levels without undue mortality rates. Some deaths do occur at the higher level.

Exposure.—Rats were individually caged and given water and poisoned bait *ad libitum*. The bait was prepared by grinding the regular ration ("Friskies" brand dry dog pellets), thoroughly incorporating the appropriate percentage of zinc phosphide, and finally, moistening the mixture, shaping into pellets, and air-drying. Rats seemed to waste less food when it is offered in pellet form than when it is offered as a powder.

Series I.—Groups of six albino rats weighing from 70 to 100 Gm. were exposed to baits containing 0.02% and 0.03% zinc phosphide. A control group of like size was kept.

Weight Gains.—Rats were weighed daily, and statistical analyses of weight gains were made after one-week and one-month periods. Rats receiving the 0.03% bait were compared after the one-week period only; these animals failed to gain weight and several soon died. The initial weights of the three groups did not differ significantly. After exposure, however, both experimental groups showed significantly lower gains in weight than the control group. This was true after both the one-week and one-month periods.

Statistical Analysis of Weight Gains.—All rats survived the first week of exposure. After this, however, the 0.03% dosage level proved to be too

toxic, and the rats in that group died. Two rats in the 0.02%-level group died, but the remainder survived the experimental period.

Table I presents the initial weights and the weight gains of the control group and of experimental Group I which received 0.03% zinc phosphide. Statistical comparison of the mean initial weights of the two groups shows that the initial groups did not differ significantly ($t = 0.1$). However, the weight gains during one week of exposure were significantly lower in the experimental group ($t = 8.3$).

Table II presents similar data and treatment for experimental Group II which received 0.02% zinc phosphide. In addition to a comparison of the weight gains after one week, another comparison is made after one month. As in Group I, the mean initial weight of experimental Group II did not differ significantly from that of the control group ($t = 0.1$). After one week of exposure, the mean weight gain of the experimental Group II differs significantly from that of the controls ($t = 3.9$).

TABLE I.—COMPARISON OF EXPERIMENTAL GROUP I OF RATS RECEIVING 0.03% ZINC PHOSPHIDE IN DIET WITH CONTROL GROUP

	Rat No.	Initial Weights, Gm.	Gain during One-week Exposure, Gm.
Control Group	C-1	88	25
	C-2	111	35
	C-3	70	26
	C-4	105	26
	C-5	82	28
	C-6	79	24
	Mean:	89.2	26.7
Experimental Group I	Standard Deviation of Mean:	±15.7	±4.5
	E-1	81	8
	E-2	76	8
	E-3	109	3
	E-4	93	2
	E-5	85	11
	E-6	86	-1
Mean Difference between Control and Experimental Group I:	Mean:	88.3	5.2
	Standard Deviation of Mean:	±11.6	±4.5
	Standard Deviation of Difference of Two Means:	±8.0	±2.6
Ratio to Standard Error:		0.1	8.3 ^a

^a Significant.

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The difference in mean weight gains remains significant after one month of exposure in the experimental group ($t = 3.0$).

Histopathology.—After exposure periods varying from thirteen to thirty-one days in the group receiving 0.03% zinc phosphide and from thirty-nine to fifty-eight days in the group receiving 0.02%, rats were sacrificed by severing the jugular veins. No gross pathology was observed. The following tissues were taken for study: liver, lung, kidney, adrenal gland, intestine, pancreas, spleen, heart, ovary, and testis. Tissue sections were prepared by usual methods using hemotoxylin and eosin stain.

In the liver, several zones of injury were evident, especially about the central and peripheral lobular areas which exhibited injury sufficient to kill the parenchyma cells. For variable distances extending from these areas, the parenchyma cells were disintegrated or in the process of disintegration as manifested by failure of the cell nuclei to stain while the cytoplasm was coagulated and deeply stained with eosin. A great increase in numbers of fibroblastic nuclei was observed within and around the portal canal areas in sections taken from rats receiving more intensive exposure.

The alveolar capillaries of the lung were congested with blood, numerous areas evincing indication of hemorrhage or serous exudation into the alveolar spaces. Considerable mononuclear infiltration was observable around the smaller bronchi and bronchioles of some sections.

No infallible signs of damage were observed in sections of spleen, pancreas, intestine, adrenal, heart, kidney, ovary, or testis.

Series II, Breeding Experiment.—Ten adult male and ten adult female albino rats were exposed to 0.03% zinc phosphide in their diet for twenty-two days. During this period four females and one male died. After removal from the poisoned diet, all animals were bred to normal animals. Each poi-

soned male was caged with a normal female, and each two poisoned females were caged with one normal male. All poisoned rats proved to be fertile.

ACUTE EXPERIMENTS

Since it has been observed that zinc phosphide seemed nontoxic to animals eating poisoned rats (1), attention was directed to a study of acute effects of zinc phosphide on dogs, cats, and rabbits, as well as rats. Lethal doses of 7–17 mg./Kg. for fowls have been reported, indicating that fowls are quite susceptible to zinc phosphide (2). The oral LD₅₀ for rats has been placed at 40.5 ± 2.9 mg./Kg. (3) and its acceptability to them as a poison established (4).

The effects of oral zinc phosphide on blood pressure and respiration were studied in animals anesthetized with sodium pentobarbital I. V. Doses of zinc phosphide were given by stomach tube after recording, on a kymograph, control periods of respiration (via tracheal cannula and tambour) and blood pressure (via carotid cannula and mercury manometer).

Dogs.—The results of these experiments with fasting dogs are tabulated in Table III, Part A. They indicate that zinc phosphide alone is not immediately toxic in fasting dogs, even at rather high dosage. It was postulated, however, that this apparent species resistance might be due to a difference in the digestive processes on the poison. A known reaction of zinc phosphide is its release of phosphine (PH₃) in the presence of acids (5). A lack of gastric hydrochloric acid could explain relative immunity to zinc phosphide if the mechanism of its action involved such a release of phosphine. To test this hypothesis, 0.5% hydrochloric acid was given along with zinc phosphide, the results of which are listed in Part B of Table III. Obviously, hydrochloric acid given with zinc phosphide increases the toxicity of the latter in dogs.

TABLE II.—COMPARISON OF EXPERIMENTAL GROUP II OF RATS RECEIVING 0.02% ZINC PHOSPHIDE IN DIET WITH CONTROL GROUP

	Rat No.	Initial Weights, Gm.	Gain during One-week Exposure, Gm.	Gain during One-month Exposure, Gm.
Control Group	C-1	88	25	88
	C-2	111	35	146
	C-3	70	26	122
	C-4	105	22	84
	C-5	82	28	88
	C-6	79	24	88
	Mean:	89.2	26.7	102.7
Experimental Group II	Standard Deviation of Mean:	± 15.7	± 4.5	± 25.5
	E-7	105	3	Died
	E-8	72	6	Died
	E-9	101	22	67
	E-10	98	18	65
	E-11	84	18	64
	E-12	82	7	62
Mean Difference between Control and Experimental Group II:	Mean:	90.3	12.3	64.5
	Standard Deviation of Mean:	± 12.9	± 7.9	± 2.1
	Ratio to Standard Error:	0.1	3.9 ^a	3.0 ^a
Standard Deviation of Difference of Two Means:		± 8.3	± 3.7	± 12.8
Ratio to Standard Error:		0.1	3.9 ^a	3.0 ^a

^a Significant.

All dogs previously used were fasted. If hydrochloric acid were the necessary factor, then the normal gastric secretion following stimulation by food should make zinc phosphide toxic to dogs.

Therefore, 200 mg./Kg. of zinc phosphide was administered in capsules to a fasting intact dog followed by the dog's regular meal. The result is listed in Table III, Part C. Death occurred after

TABLE III.—EFFECTS OF ZINC PHOSPHIDE ON DOGS

Dog No.	Weight, Kg.	Dose Zn_3P_2 , Mg./Kg.	Dose 0.5% HCl, Cc.	Time	Observations
Part A: Anesthetized Dogs					
1 (Female)	12.5	30	..	0:00	No effect
		50	..	3:30	No effect
				5:30	Sacrificed
2 (Female)	11.0	300	..	0:00	No effect
		1,000	..	2:00	No effect
				3:30	Sacrificed
Part B: Anesthetized Dogs					
3 (Female)	12.0	1,000	75	0:00	Dog vomited, losing part of
				0:45	dose. Blood pressure fell.
4 (Female)	7.5	200	40	0:00	Respiration stimulated,
					then depressed. Death.
					Blood pressure depressed;
					respiration stimulated,
				1:00	then depressed.
					Death
Part C: Unanesthetized Dogs					
5		200		0:00	Food given along with dose
		(Food also		0:43	Vomiting
		given)		3:13	Death

TABLE IV.—EFFECTS OF ZINC PHOSPHIDE ON RABBITS

Part A: Anesthetized Rabbits (with $NaHCO_3$, as indicated)					
Rabbit No.	Weight, Kg.	Dose Zn_3P_2 , Mg./Kg.	Dose $NaHCO_3$, Gm./Kg.	Time	Observation
3 (Male)	2.4	35	..	0:00	No effect
				2:00	Sacrificed
5 (Male)	2.3	35	...	0:00	No effect
				3:00	Sacrificed
1 (Female)	2.75	40	...	0:00	Respiration stimulated, then depressed. (Blood pressure not recorded)
				0:40	Death
6 (Male)	2.8	45	...	0:00	Irregular blood pressure
				2:30	Sacrificed
2 (Female)	2.5	50	...	0:00	Depressed blood pressure
				1:25	Respiration stimulated, then depressed
					Death
Part B: Anesthetized Rabbits (with $NaHCO_3$, as indicated)					
7 (Male)	2.0	100	0.6	0:00	Irregular blood pressure
				3:30	Sacrificed
Control: 8 (Male)	1.5	100	...	0:00	Falling blood pressure and respiration
				1:10	Death
Part C: Unanesthetized Rabbits (with $NaHCO_3$, as indicated)					
9 (Female)	1.7	200	0.6	0:00	
				1:00	Death
10 (Male)	2.1	...	0.6	0:00	
		100	...	0:30	Lived over three hours; died during night
11 (Female)	1.3	...	0.6	0:00	
		100	...	0:30	
		...	0.6	1:55	
				5:00	Death
Control: 12 (Female)	1.2	100	...	0:00	
				0:55	Death

three hours and thirteen minutes, showing that normally stimulated gastric hydrochloric acid is sufficient to release toxic amounts of phosphine.

Rabbits.—Effects of zinc phosphide in anesthetized rabbits were obtained in a similar manner. Part A of Table IV contains data for the administration of zinc phosphide alone. It is seen that the toxicity of zinc phosphide to the rabbit is of the same order as to the rat.

In accordance with the hypothesis that stomach acid is an essential factor in the acute effects of zinc phosphide, it was decided to give sodium bicarbonate, along with zinc phosphide, to rabbits in order to ascertain the effect of reduced stomach acid. Part B of Table IV contains the result. Sodium bicarbonate prevented death from a toxic dose of zinc phosphide during the experimental period. To determine the possible value of sodium bicarbonate as an antidote, it was given along with zinc phosphide by stomach tube to intact rabbits. A tabulation is in Table IV, Part C. Concurrent administration of sodium bicarbonate along with zinc phosphide was to no great extent effective in delaying zinc phosphide death. However, administration of sodium bicarbonate thirty minutes ahead of the poison, giving the bicarbonate time to neutralize all acid, delayed death several hours. A repeated dosage with sodium bicarbonate did not save the rabbit's life. This may have been due to ineffective control of stomach acid, or to other toxic mechanisms of zinc phosphide.

Cats.—A similar study was made on cats. Doses of zinc phosphide below 160 mg./Kg. were not effective during the experimental period. Doses from 200 to 300 mg./Kg. gave variable results, death not always following administration. No additional cats were available. However, the data would seem to indicate that cats are less susceptible to zinc phosphide than rats, rabbits, and fowls. Data are presented in Table V.

TABLE V.—EFFECTS OF ZINC PHOSPHIDE ON CATS

Cat No.	Weight, Kg.	Dose Zn ₃ P ₂ , Mg./Kg.	Time	Observation
1 (Male)	3.5	50	0:00	No effects
			3:00	Sacrificed
3 (Male)	4.0	120	0:00	No effect
			4:00	Sacrificed
5 (Female)	2.0	160	0:00	No effect
			3:00	Sacrificed
4 (Male)	1.8	200	0:00	Depressed blood pressure
			3:30	Sacrificed
2 (Female)	2.0	250	0:00	Blood pressure depressed
				Death
6 (Female)	2.3	300	0:00	No effect
			3:00	Sacrificed

Rats.—If, as assumed, the toxicity of zinc phosphide is in part due to the release of phosphine by stomach acid, then poisoned animals should excrete this gas on their breath. This was tested in rats. Two rats (one control, one experimental) were anesthetized with sodium pentobarbital, their tracheas cannulated and connected to one-way valves which forced all exhaled air through vials containing filter paper soaked in 2% silver nitrate solution. Silver

nitrate reacts with phosphine to produce a brown-to-black precipitate of elemental silver (5). The experimental rat was given a toxic dose of zinc phosphide via stomach tube. Brown stains first appeared in the vial after fifteen minutes and continued to form until the rat died after one hour and ten minutes. No stains whatsoever appeared on the silver nitrate paper connected with the control rat.

The fact that phosphine is at least partially blown off in the lungs may explain the appearance of pathology in the liver and lungs only in chronically poisoned rats. Phosphine would be absorbed in the intestines, carried to the liver via the portal circulation, then to the lungs via the right heart and pulmonary arteries, and in part blown off. Since in chronically poisoned rats the concentration of zinc phosphide is low, and that of phosphine proportionate, the lungs might effectively remove the phosphine so that organs other than liver and lungs would not be acutely harmed.

The toxicity of phosphine is well established (5). However, for immediate evidence, phosphine was generated by adding hydrochloric acid to zinc phosphide, and the resulting gas led to a bell jar containing a mouse. Death occurred after thirty-five minutes.

DISCUSSION

The release of phosphine by stomach acid as a mechanism for zinc phosphide toxicity is supported by these facts:

(1) One-half per cent hydrochloric acid along with zinc phosphide given orally causes quick death in fasting dogs. Zinc phosphide alone does not cause death during the experimental period even at high dosages.

(2) Similarly, gastric secretion induced by food makes zinc phosphide toxic to dogs.

(3) Sodium bicarbonate delays zinc phosphide death in rabbits.

(4) Poisoned rats excrete phosphine on their breath.

Other facts easily explained by and tending to support this theory are:

(1) Pathology from chronic poisoning is confined to liver and lungs, a fact easily explained by the phosphine release theory.

(2) The relative susceptibility of the rat and the relative immunity of the dog could be explained by the fact that, in the rat, acid secretion is continuous, requiring no stimulus (6). In the dog, secretion is a complex mechanism requiring stimuli and would not be active in a fasting dog.

(3) In fowls it was shown that most of the zinc from zinc phosphide was excreted in the feces and that none was stored in the body (2). This would be quite plausible if phosphine were the toxic agent.

With regard to practical use of zinc phosphide as a rodenticide, the following suggestions may be made concerning danger to animals other than rats: animals likely to eat the carcasses of poisoned rats (dogs and cats) are, in general, more resistant to zinc phosphide than rats. This, plus the fact that they are larger than rats, probably would insure that they would not be fatally poisoned by eating the dead rats. Animals likely to eat the bait itself (rabbits and fowls) are equally or more susceptible to zinc phosphide, and precautions should be taken to pre-

vent their access to the poison. Further investigation of the susceptibility of larger animals to zinc phosphide is indicated.

CONCLUSIONS

(1) Sublethal administration of zinc phosphide to domesticated albino rats produces disintegration of parenchyma cells of the liver accompanied by proliferation of fibroblastic nuclei. Hemorrhagic congestion followed by mononuclear infiltration about the smaller bronchi and bronchioles occurs in the lungs.

(2) Sublethal administration of zinc phosphide has no apparent effect on the spleen, pancreas, heart, intestine, kidney, adrenal, ovary, or testis of the albino rat.

(3) Dogs and cats are, in general, less susceptible to zinc phosphide than are rats, rabbits, and fowls.

(4) Evidence is presented to support the theory that the acute symptoms of zinc phosphide poisoning are due to phosphine released by gastric acid.

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Fungistatic Activity of Antihistamines*

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A number of antihistamines and related compounds have been tested against several fungi. The fungistatic potency does not depend upon their antihistaminic activity. The effect of variations in chemical structure is discussed.

SEVERAL REPORTS have recently appeared (1-4) indicating that antihistamines displayed significant fungistatic activity *in vitro*. Since all of the antihistaminic drugs tested displayed this property, their effectiveness has naturally been attributed to a common ability to antagonize histamine. However, this group of compounds also possesses, in varying degrees, other pharmacological properties (local anesthetic, anticholinergic, antiemetic, etc.). It was of interest, therefore, to test whether a parallelism actually exists between a compound's antihistaminic and fungistatic potencies. In addition, this study affords an opportunity to evaluate the fungistatic action of the antihistaminics now commercially available. Finally, it was hoped that some information might be obtained relating chemical structure to activity.

EXPERIMENTAL

The compounds tested and the manufacturers who made them available to us are listed in Table I. All compounds except Thephorin were dissolved in 70% alcohol and made up to 0.10 *M* solution. Thephorin, because of alcohol insolubility, was dissolved in water and prepared in the same concentration. The test cultures employed were *Tricophyton mentagrophytes*, *Tricophyton* species (Klein), *Microsporum canis*, *Microsporum gypseum*, *Monosporium apiospermum*, *Phialophora verrucosa*, *Sporotrichum Schenkii*, and *Candida albicans*.¹ The method of testing for fungistatic activity was as follows: Sabouraud agar plate surfaces were inoculated with a culture of the test organism. A sterile, cotton-tipped swab was dipped into a broth culture of the test fungus and then was used to inoculate the surface of an agar plate. This procedure was repeated, using the same swab, for inoculating each of the test plates with a specific fungus. Filter paper disks² impregnated with various concentrations of a test compound were then placed on these inoculated plates. All compounds were prepared so as to have the following solutions for each: 0.10, 0.05, 0.025, 0.01, 0.005, 0.0025, 0.0010, and 0.0005 *M* concentrations. Sufficient disks for each dilution of each

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¹ All fungus cultures were obtained from the Fourth Army Area Laboratory, Brooke Army Medical Center, Fort Sam Houston, Tex., with the exception of the *Tricophyton* species (Klein) which was isolated in this laboratory.

² Carl Schleicher & Schuell Company, No. 740-E, "Disks for Assay of Penicillin and Other Antibiotics."



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Charadrius montanus: Montane, Grassland, or Bare-Ground Plover?

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***Charadrius montanus*—Montane, Grassland, or Bare-ground Plover?**

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The Mountain Plover (*Charadrius montanus*) is an aridland member of the Charadriidae. This plover is generally considered an associate of the North American shortgrass prairie, which is dominated by blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*; Graul 1975). The species breeds at many locations across the western Great Plains plus at isolated locales in western Colorado, Wyoming, and New Mexico (Leachman and Osmundson 1990) and recently in eastern Utah (K. S. Day pers. comm.). Continental populations of the Mountain Plover declined 63% from 1966 to 1991 (Knopf 1994), with the historic and current breeding stronghold being the Pawnee National Grassland in Weld County, Colorado (Graul and Webster 1976). Currently, a second major breeding population of Mountain Plovers is on the Charles M. Russell National Wildlife Refuge, Phillips County, Montana. Unlike when found on the grassland landscape of Weld County, Mountain Plovers in Phillips County selectively nest in prairie dog (*Cynomys* spp.) towns (Knowles et al. 1982, Olson and Edge 1985) in vegetative settings that include prickly pear (*Opuntia polyacantha*), fringed sagewort (*Artemisia frigida*), big sagebrush (*A. tridentata*), western wheatgrass (*Agropyron smithii*), and blue grama. Collectively, Weld and Phillips counties provide nesting habitat for approximately one-half of the continental population of Mountain Plovers.

Despite the differences in vegetation associations at the two major nesting locales, both Graul (1975) and Olson and Edge (1985) have described the tendency of plovers to place nests in areas of low herbaceous vegetation, reduced shrub cover, and near prominent objects such as cow-manure piles or similar-sized rocks. However, plover nests on Montana prairie dog towns also occur in areas of approximately 27% bare ground, a descriptor not mentioned by Graul (1975). The bare-ground variable may have some significance in light of recent findings of plovers sometimes nesting on plowed fields (Shackford 1991, pers. comm.) and descriptions of wintering habitats of plovers that mention use of freshly plowed ground in the San Joaquin and Imperial valleys of California (Grinnell and Miller 1944). We used a methodology similar to that employed in the Montana studies to ascertain if nest sites of Mountain Plovers also include a component of bare ground in native habitats on the

relatively prairie-dog-free Pawnee National Grassland of Colorado.

The Pawnee National Grassland encompasses 78,130 ha of shortgrass prairie on loamy, clayey, and sandy soils. Historically, the area supported uncountable numbers of bison (*Bison bison*; Frémont 1845, Voorhees 1920, and many accounts in Mattes 1988); hundreds of wallows remain clearly visible and mostly unvegetated. Besides the shortgrasses, common woody plants include prickly pear, yucca (*Yucca* spp.), and rabbitbrush (*Chrysothamnus* spp.).

We located 43 Mountain Plover nests on the Grassland during the 1991 and 1992 breeding seasons. A half-meter (1.0 × 0.5 m) rectangular frame was centered over each nest in a northwest-to-southeast orientation, after which the site was photographed. Comparison sites (also 0.5 m², referred to as "control" sites hereafter) were located by stretching a fiberglass tape oriented to the north for the 1992 nests ($n = 18$), and placing the half-meter frame on the ground in a northwest-to-southeast orientation at marked intervals of 10, 25, and 50 m from the nest. Control sites also were photographed.

During analysis of vegetative cover, a clear dot grid was overlaid on each photograph to estimate the percentage of area in shortgrass vegetation or bare ground. We also recorded frequency of cow-manure piles and prickly-pear plants within each plot.

A Kruskal-Wallis test with a correction factor for tied ranks and chi-square tests (Zar 1984) indicated no differences in percentages of vegetation cover and prickly-pear presence among the 10-, 25-, and 50-m control sites. A chi-square test comparing cow-manure piles in the three groups could not be employed because more than 20% of the expected frequencies were less than 5.0% (observed values in the three groups were 3, 2, and 2, respectively).

Data from control plots ($n = 54$) were combined for comparison with those from nest sites (Table 1). Shortgrass vegetation averaged $86 \pm$ SD of 11% of the area within those plots, 13% had dried cow-manure piles, and 28% contained prickly pear. Comparing nest sites to the pooled control sites, percentage of vegetative cover was significantly lower ($U = 1931.5$, $df = 42$ and 53 , $Z = 5.59$, $P < 0.001$ in a two-tailed test of normal approximation), and there were more cow manure piles ($X^2 = 12.2$, $P \leq 0.001$) and fewer prickly pears ($X^2 = 11.48$, $P \leq 0.001$) at nest sites.

These data further characterize structural subtleties at nest sites selected by Mountain Plovers and support previous observations that some plovers nest near a conspicuous object. Graul (1975) reported 55% of nests

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TABLE 1. Mean percentage grass cover ($\pm$ SD) of 0.5-m² plots, and percentage of plots with dried cow manure and prickly pear.

Plot	Grass	Dried cow manure	Prickly pear
Nest	68 $\pm$ 17	49 ^a	7
Control			
10 m	88 $\pm$ 10	17	28
25 m	85 $\pm$ 11	11	22
50 m	86 $\pm$ 11	11	33
Subtotal	86 $\pm$ 11	13	28

^a Includes count of one large flat rock.

located within 30 cm of a manure pile, and Olson and Edge (1985) reported 27% of nests on prairie dog towns were near a rock 8 cm or more in diameter. We observed 49% of plover nests placed near either a manure pile or a rock.

Relative to physical objects near nests, the only contradiction between our data and observations from earlier studies was the lower prickly-pear densities near nest sites on the grasslands. Olson and Edge (1985) saw no difference in prickly-pear densities at nest sites and random sites on prairie dog colonies, but both nest sites and control sites on those prairie dog towns had lower prickly-pear densities than control sites located outside the area impacted by prairie dogs. Sordahl (1991) noted that Mountain Plover chicks also occur at sites of decreased prickly-pear densities on the Pawnee National Grassland.

Graul (1975) speculated that Mountain Plovers nest near a prominent object to make themselves less conspicuous to predators. This hypothesis has been advanced for many plover species (e.g. Haig 1990), but specific tests for any one species are rare (Grover and Knopf 1982). We wonder, however, why manure piles and rocks would reduce predation on nests when the equally sized, structurally more complex, and physically more ominous prickly pear would not be selected for this purpose. The biological (in addition to statistical) significance of why some birds place nests near objects merits further inquiry.

Olson and Edge (1985) reported 27% bare ground at nest sites in Montana, which is similar to the 32% unvegetated area around nests on the Pawnee National Grassland. Four additional observations suggest that 30% bare ground is likely closer to a minimum habitat requirement than an optimal one in Mountain Plover ecology. First, Mountain Plovers nest in the more xeric landscapes west of the shortgrass prairie province. Second, most nesting attempts by plovers on the Pawnee National Grassland are initiated from late April through May (Graul 1975), a period when the shortgrass species remain dormant. Third, plovers often raise broods in the vicinity of excessive, local disturbance as at cattle watering or loafing areas. Fourth, Mountain Plovers definitely

winter, and occasionally nest and raise chicks, on plowed ground.

Since first collected by J. K. Townsend (1839) near the Sweetwater River (Wyoming), the name of the Mountain Plover has always been considered a misnomer in that the species does not actually occur in montane settings. Rather, most field biologists think of it as either the "you-can-see-the-mountains-from-here" plover or the "prairie" plover. Based on the constancy of bare ground across habitats within the annual cycle of the Mountain Plover, and its former cohabitation with 30 million bison (Roe 1951) and even more prairie dogs (Marsh 1984) on the western Great Plains, we offer that this species is a disturbed-prairie or semidesert species rather than a specific associate of grassland, an interpretation that brings the species more in accord with the bare-ground habitat preferences of other charadriids.

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Mountain Plover Population Trends In Central and Northeastern Montana



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ABSTRACT

Permanent point count transects were established in 1992 in central, northeastern and southwestern Montana to monitor mountain plover (*Charadrius montanus*) population trends in these areas. At the time, these were Montana's 2nd, 3rd and 4th largest mountain plover populations. During the 28-year period from 1992 to 2019, these transects were surveyed during 11 different years with the last counts for the Central and Northeastern Montana Study Areas occurring in 2019, and the last count for the Southwestern Montana Study area occurring in 2004. The count of adult mountain plovers in the Central Study Area declined in a saw-tooth manner from 103 adult birds in 1992 to no birds observed in 2019. In the Northeastern Study Area, mountain plovers counted along the transect started at 17 in 1992, peaked at 36 in 1996, dipped to 12 in 2004, and finished with a count of 13 adult plovers in 2019. Mountain plover numbers in the Southwestern Study Area progressively declined from a high of 33 adult birds in 1992 to no birds found in the Study Area in 2004. Cause of mountain plover decline in the Central Study Area was attributed to conversion of native grasslands to cultivated cropland and introduced grasses, a drastic decline in domestic sheep numbers, and an overall reduction in livestock grazing. In the Southwestern study area, the collapse of the mountain plover population was attributed to a housing development, a log home factory, poisoning of prairie dogs, and the lack of livestock grazing. The Northeastern Study Area was almost entirely public lands, and habitat conditions have been relatively stable over the past 3 decades. Mountain plovers in this study area are associated with bentonitic soils with low plant production and high amounts of bare soil. In the other 2 study areas, mountain plovers were found primarily on private land and were associated with intensively grazed sites and black-tailed prairie dog (*Cynomys ludovicianus*) colonies.

INTRODUCTION

Since the late 1980s, there has been concern about the population status of mountain plovers across their breeding range in the western United States (Leachman and Osmundson 1990). The annual U.S. Fish and Wildlife Service (USFWS) breeding bird surveys from 1963 through 1993 showed a 3.7 percent annual decline in mountain plover numbers, representing a 63 percent overall population decline during that 30 year period (Knopf and Rupert 1999). From 1994 to 2009, the breeding bird surveys suggest a lower rate of decline of 1.1 percent per year (USFWS 2011). From early 1990s up to 2011, the mountain plover was listed as a candidate species for listing under the Endangered Species Act as a threatened species. During this period, the mountain plover was twice reviewed for listing. While the first review determined that listing was warranted it was later rejected because of procedural issues, and the second review determined the mountain plover did not warrant listing under the Endangered Species Act. This history of changing conservation status is quite unique and is not often seen with other rare vertebrate species. Currently the mountain plover has no status under the Endangered Species Act.

In 1999, the U.S. Fish and Wildlife Service (USFWS) proposed listing mountain plovers as "Threatened" based on a declining population trend from Breeding Bird Survey data (about 3.7% per year (USFWS 1999)). This listing effort was undertaken fully by the USFWS as opposed to being petitioned for listing by an outside group. The listing effort was unusual and was based

out of the Lakewood, Colorado USFWS office which apparently did not have full authority to officially list species. As a result, the listing effort was reinstated, but not before an administrative change in Washington D.C. In September of 2003, the USFWS subsequently decided to withdraw the proposed listing of the mountain plover (USFWS 2003). In November 2006, Forest Guardians and the Biological Conservation Alliance sued the USFWS over the withdrawal of the proposal to list the mountain plover as Threatened (*Forest Guardians, et al. v Ken Salazar et al.*, Case No. 3:06-cv-02560-MMA-BLM), and in August 2009, the USFWS agreed to submit a notice in the Federal Register re-opening the proposal to list the mountain plover and provide opportunity for public comment. On 11 May 2011, the USFWS announced the mountain plover did not warrant protection under the ESA citing that about 20,000 plovers remained rather than the previously estimated 11,000-13,000 adult birds (USFWS 2011). In their decision notice, the USFWS noted that the larger population size was not related to increasing numbers of birds, but their belief that there was a better accounting of bird numbers. Since this decision to not list the mountain plover as Threatened in 2011, there has been very little interest by wildlife management agencies in the population status of mountain plovers.

A common criticism of the Breeding Bird Survey data is that it is insensitive to changes in rare species abundance and may substantially over or underestimate overall population change because of sampling bias. For example, so few mountain plovers were detected in Montana on Breeding Bird Survey routes, the USFWS did not project a state-wide trend in their 2011 decision notice to not list the plover (USFWS 2011). Realizing the need for mountain plover focused population data, Knopf (2008) in 1990 decided to establish permanent point count transects for mountain plovers in the Pawnee National Grassland (PNG) in northeastern Colorado which was considered the species' stronghold at the time, and in southern Phillips County, Montana, which also contained a significant population of plovers associated with black-tailed prairie dogs. In 1992, Knopf encouraged us to establish similar permanent point count transects for mountain plovers in 3 other Montana areas where we had documented mountain plover occurrence (FaunaWest 1991), and he provided us details of how to establish permanent point counts similar to his effort.

In 1992, we developed routes along public roads through 3 mountain plover use areas in central, northeastern (Appendices A and B) and southwestern Montana and placed permanent point count stations along these routes. From 1992 to 2004, we surveyed these census routes for mountain plovers a total of 9 times. During this time period we documented the loss of mountain plovers from southwestern Montana, a slow decline of plovers in central Montana, and fluctuating numbers of plovers in northeastern Montana. During the summer of 2014, we were able to resurvey the routes through central and northeastern Montana and documented a continuing decline of mountain plovers in central Montana and a relatively stable population in northeastern Montana. These census routes were surveyed again in 2019, and this report summarizes the results of this survey effort. These data are extremely valuable because they represent identical survey techniques at the same precise census station sites, conducted by the same individuals over an almost 3-decade period.

Study Area

Figure 1 is a list of known mountain plover populations observed in Montana in 1991, their habitat association and population status. Figure 2 shows the general location of those areas. During 2014 and 2019, mountain plover trend counts were only conducted in the Central and Northeastern Montana Study Areas (Areas 2 and 3 in Figure 1 and 2).

Population Area in descending order of size in 1992	Habitat Association	Population Status
1. Phillips, Blaine, N. Fergus & N. Petroleum Counties	Grasslands: Prairie dog colonies & some use of barren areas with glacial till	In 1991, this was the probably the largest mountain plover population. Plovers were found in 18-53% of the prairie dog colonies & in 69% of prairie dog acreage. Mountain plovers remain, but greatly reduced from pre-plague numbers in the 1980s.
2. Wheatland, Golden Valley, & Musselshell Counties (Central Study Area)	Grasslands: Stockwater sites grazed by sheep and cattle. Also in a few prairie dog colonies	118 adults counted in 1992 (includes birds between census stations.) Only 14 adults observed in 2014. No plovers found 2019. Population presumed extirpated .
3. Valley County (Northeastern Study Area)	Dwarf shrub communities associated with silty overflow sites and bentonitic soils	39 adults counted in 1996 in peak year. Plovers remain in this area in low numbers in 2014 and 2019.
4. Jefferson, Madison, & Broadwater Counties (Southwestern Study Area)	Grasslands: Prairie dog colonies, and stockwater sites grazed by cattle	35 adults counted in 1992. Population considered extirpated by 2004.
5. Treasure & Rosebud Counties	Grasslands: Prairie dog colonies, dwarf shrub communities associated with silty overflow sites and bentonitic soils	64 adults counted in 1998. Population status unknown in 2014 and 2019, but plague has decimated prairie dog colonies.
6. Carter County	Dwarf shrub communities associated with silty overflow sites and bentonitic soils	Plovers found here 1994-1997 with 2 adults counted in 1995 the most observed. Population considered extirpated.
7. Carbon County	Dwarf shrub communities and blue grama flats	Plovers recorded here 1996-1998, 2003 -2005 with 3 adults counted in 1997 and 6 adults in 2005. Nests and broods were observed in 1998, 2003 and 2005. No plovers were observed in 2014, but a pair of plovers reported in 2019.
8. Teton County	Grasslands: Ridge grazed by sheep	6 adult birds reported using the area prior to 1996. No birds found in 1996 and 1998 after sheep were removed. Population presumed extirpated.
9. Toole County	Grasslands: Grazed by cattle and Richardson's ground squirrels	2 adults counted in 1996 No birds found in subsequent surveys in 1997 and 1998. Population presumed extirpated.

Figure 1: List of known mountain plover populations found since 1991 in Montana, their habitat association and population status.

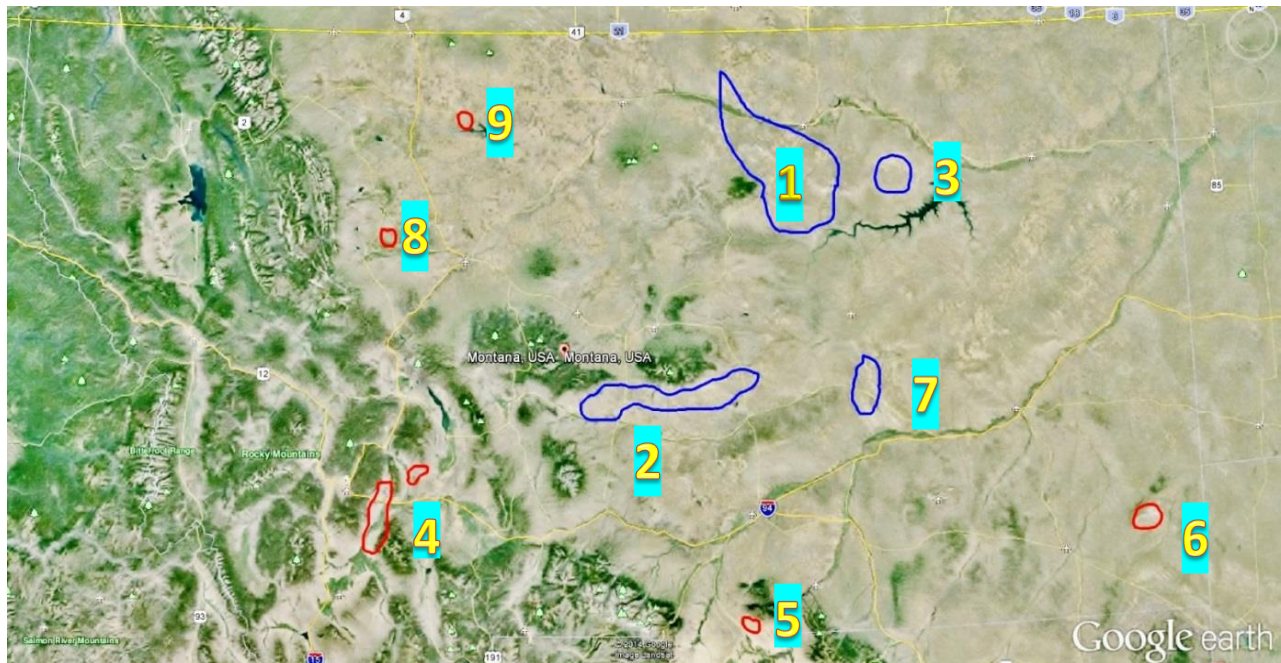


Figure 2: Map of known areas with mountain plover populations in 1991. Map numbers correspond to populations listed in Figure 1.

The Central Study Area

The Central Study Area was located along the southern benches of the Little Belt, Big Snowy and Little Snowy Mountain Ranges (Area 2 in Figure 1 and 2) in central Montana and occupied an area of approximately 2,565 km². Landownership was almost entirely private with a normal complement of State lands (2 sections per township). The only exception was the eastern portion which included some Federal lands managed by the Bureau of Land Management (BLM) and USFWS. These 2 Federal land holdings each contained a black-tailed prairie dog colony used by mountain plovers. The elevation within this study area ranged from 1100 -1700 m.

The major native habitat in this study area was the needle-and-thread grass (*Stipa comata*)/blue grama (*Bouteloua gracilis*) habitat type (STCO/BOGR) (Mueggler and Stewart 1978). Dominant plant species included needle-and-thread grass, blue grama, threadleaf sedge (*Carex filifolia*), June grass (*Koeleria cristata*), fringed sagewort (*Artemisia fridgida*), fleabane (*Erigeron* spp.), and tufted milkvetch (*Astragalus spatulatus*). At higher elevations, scattered bunches of blue bunch wheatgrass (*Agropyron spicatum*) occurred within the STCO/BOGR habitat. Vegetative height at heavily grazed sites in this study area were generally less than 10 cm, while at ungrazed to moderately grazed sites it ranged from 10-20 cm. The western wheatgrass (*Agropyron smithii*)/blue grama habitat type (AGSM/BOGR) occurred in heavily grazed valley bottoms. This habitat type in the Central Study Area contained very little big sagebrush (*Artemisia tridentata*).

Topographically, this study area consisted of broad gravel ridges or benches extending south from the Little Belt and Snowy Mountain Ranges. This topographic condition extended 106 km

from Haymaker Creek on the west to the eastern terminus of the Little Snowy Mountains. In some areas, these ridges were poorly defined and appeared to be more like alluvial fans. Where ridges were well developed, they were separated by broad valleys. Ridges, alluvial fans, and valleys in this area were all inclined 1-2%, sloping southward away from the mountains for 16-24 km. At the southern margins of the ridges in Golden Valley and Musselshell Counties, soils changed from limestone gravels to heavy clays derived from shale, and the topography became more dissected by drainages. Seven black-tailed prairie dog colonies were located along this transition zone. Approximately 9% of the land around census stations had been disturbed by agriculture in 1992 when the trend count transect was established, and by 2014, 27% of the area was disturbed by agriculture. However, since we specifically sited our census stations in areas of native grasslands, the actual amount of land disturbed by agriculture across the entire study area was much greater than this. In 1992, we estimated that 34% of the landscape across the entire study area had been altered by agriculture.

The Northeastern Study Area

The Northeastern Study Area was located 24 km southwest of Glasgow in northeastern Montana and comprised about 648 square km (Area 3 in Figure 1 and 2). Land ownership in this study area was almost entirely Federal and State and included the entire Little Beaver Creek drainage and portions of Miller Coulee and Brazil, Sagehen, and Lone Tree Creeks. This study area had extensive bentonite deposits, some of which were previously mined (a minimum of 10 mined sites). The physiography of the area consisted of broad (> 0.8 km across) low gradient (< 1% slope) valley bottomlands with deeply incised drainages, gently sloping ridge sides with exposed shale and bentonite deposits, and narrow, relatively level ridge tops. Elevation of the study area ranged from 682-804 meters.

The valley bottomlands in the Northeastern Study Area were dominated by silty overflow range sites. These were areas where sheet-flow water occurs during intense rainstorms and deposits fine bentonite alluvium to form barren light-colored hardpan soils. Vegetation on these hard pan soils was sparse and dominated by Nuttall's saltbush (*Atriplex nuttalli*), plains prickly pear cactus (*Opuntia polyacantha*), Nuttall's alkali-grass (*Puccinella nuttalliana*), and blue grama. Big sagebrush and western wheatgrass were also present in these areas. We refer to these silty overflow range sites as the ATNU habitat type. Within these hardpan areas were hummocks of soils dominated by blue grama.

The riparian habitat associated with the incised drainages through these sites were dominated by silver sagebrush (*Artemisia cana*) and western wheatgrass, with virtually no plains cottonwood trees (*Populus deltoides*) or willows (*Sallix* spp.) in these drainages. Generally, there were gentle rises on either side of the valley bottoms dominated by almost pure stands of yellow eriogonum (*Eriogonum flavum*) and Richardson's rubberweed (*Hymenoxys richardsonii*). We referred to these sites as the ERFL habitat. The ATNU and ERFL habitat types had an extremely low vegetative height profile of <10 cm and a high percentage of bare ground (around 90%).

Many of the ridge sides in this study area were dominated by creeping juniper (*Juniperus horizontalis*), elk sedge, (*Carex geyeri*), western wheatgrass and prairie sandgrass (*Calamovilfa longifolia*). We refer to these sites as the JUHO habitat type. The vegetative height profile of the JUHO habitat type was variable, but generally ranged from 10-25 cm. Slopes on these sites were 5-10%.

Other ridge sides in the study area had exposed bentonite deposits. These areas were nearly devoid of vegetation and we referred to them as bentonite barrens. Ridge tops in the Northeastern Study Area were dominated by western wheatgrass, blue grama, and scattered big sagebrush. We refer to these sites as the AGSM/BOGR habitat type. A shallow layer of glacial till covered the ridges, and was characterized by frequent areas of coarse gravel, small cobble and hardpan soils. The glacial till was also found to a lesser extent in the valley bottoms and on the ridge sides. Nuttall's saltbush became locally abundant in some of these hardpan sites. Overall, this study area had extremely depauperate plant communities.

During the 1950s and 1960s, the BLM constructed many trans-valley detention dams and spreader dikes in Little Beaver Creek, Lone Tree Creek and adjacent drainages to reduce the frequency and intensity of flash floods. In addition, many of the bottomland areas dominated by the ATNU and ERFL habitat types were contour furrowed during this period and planted to crested wheat grass (*Agropyron cristatum*). Approximately half of the potential mountain plover habitat in this study area was lost at this time due to these range improvement projects. At present, many of the detention dams have silted in and the dam structures have been breached by flood events. The large mud flats remaining behind the dams are dominated by squirrel-tail grass (*Hordeum jubatum*) and Mexican dock (*Rumex mexicanus*).

METHODS

During 1991, several areas with previous records of mountain plover observations were surveyed for mountain plover occurrence (FaunaWest 1991). Phillips County (Area 1 in Figure 1 and 2) with a known mountain plover population was excluded from this survey at the request of the Bureau of Land Management – which was the primary funding agency of the survey. The Central, Northeastern and Southwestern Montana Study Areas were identified at this time as areas with mountain plover populations that would be suitable for long-term monitoring.

Transect Placement

In 1992, trend count transects were established in each study area. The routes through the study areas and the actual census stations for the trend count transects were determined after carefully surveying each of the study areas for mountain plover occurrence in May and June 1992. The census stations were established at sites where mountain plovers were either observed, or at sites that appeared to contain suitable habitat for mountain plovers even though no mountain plovers were observed at the site. These trend count transects consisted of a series of permanent point count census stations (Appendices A and B).

Initially there were 90 census stations in the Central Study Area and 70 census stations in the Northeastern Study Area, but 2 census stations in the Northeastern Study Area were dropped from the transect due to a washed out road (mountain plovers were never seen at these stations during the years they were surveyed). Mountain plovers were found at only 7 sites in the Southwestern Study Area, so the census in this area was not directly comparable to the other 2 study areas.

All census stations were placed along public roads with legal access. Initially the location of the census stations was based on a legal description with a written description of the location. In the Central Study Area, readily identifiable features along the roads were used to locate the census

stations (e.g. cattle guards, culverts, stock tanks, road signs, road intersections, homesteads, etc.). In the Northeastern Study Area, we used similar descriptions, but the roads were not surfaced with gravel or well maintained, and we placed piles of rock at many of the census stations. Once GPS became available, all the census stations were given a latitude/longitude coordinate. Appendix A lists the latitude and longitude coordinates of each census station.

In 1992, when we set up the permanent census transect across the Central Study Area, we recorded the habitat (i.e. native grass, introduced grass, cultivated wheat) surrounding each of the census stations. In 2014 and 2019, we again recorded the habitat at the census stations. Since most of the stations were located on section lines along roads, it was relatively easy to designate a northeast, southeast, southwest and northwest quarter at each census station, and record the habitat in each quarter quadrant. For the 90 census stations, there were a total of 360 quarter quadrants where we recorded the habitat.

Transect Counts

Mountain plovers were counted at each permanent census station either from, or standing next to, a parked vehicle. A 10-minute scan of the surrounding area was made with binoculars. All mountain plovers observed in the vicinity of the census station were counted and recorded. Due to irregularities in topography and vegetative height, the radius of the survey area at each census station varied considerably between census stations and study areas. In the Central Study Area, changes in land use (e.g. farmed vs. not farmed, grazed vs. not grazed) were common. Similarly, in the Northeastern Study Area, slight undulations in topography frequently resulted in “blind spots” within the area scanned with binoculars. As a result of these issues we did not attempt to extrapolate a mountain plover density estimate for each of the study areas, but rather used the number of mountain plovers counted as an indicator of population trend. Because the census stations were permanent and these issues were relatively consistent among years, the changes in mountain plover numbers were considered reflective of changes in overall numbers of mountain plovers in each study area.

Survey Frequency

The census routes in the Central and Northeastern Study Areas were surveyed in 1992, 1994-2000, 2004, 2014 and 2019 for a total of 11 times in 28 years. The Southwestern Study Area was surveyed 1992-2000 and 2004, but it was not surveyed in 2014 and 2019 because the population appeared to be extirpated in 2004. Generally, we tried to conduct the surveys in late June and early July when most mountain plovers had completed nesting and were accompanied by broods. This time period also preceded the departure of mountain plovers from the study areas for their annual migration.

In this report, the term “population” is used in reference to a local group of breeding mountain plovers within a specified area. It does not imply that the group of birds is genetically distinct, reproductively isolated or otherwise unique. We have no data concerning dispersal and movement between breeding mountain plover populations in Montana, nor how these individual birds might segregate or mix in wintering areas or during migration.

RESULTS

Mountain Plover Census Results for the Central Study Area

The Central Montana Study Area was surveyed for mountain plovers from 9-11 July 2019. The 2019 census count of the Central Montana Study Area resulted in no observations of any mountain plovers at the census stations, and there were also no observations of mountain plovers between census stations. This population is now probably extirpated with little hope of mountain plovers returning. Results for all survey years are shown in figure 3.

Habitat conditions in 2019 were similar to 2014 except the prairie dog colony on BLM land appeared totally abandoned and the USFWS colony on Lake Mason NWR was largely inactive, and 4 old homesteads where mountain plovers could consistently be found had been burned. The 2 prairie dog colonies had a long history of mountain plover use and the loss of prairie dogs in the 2 colonies was probably due to a plague epizootic in 2018. We did not note obvious additional sodbusting of native grasslands from 2014 to 2019.

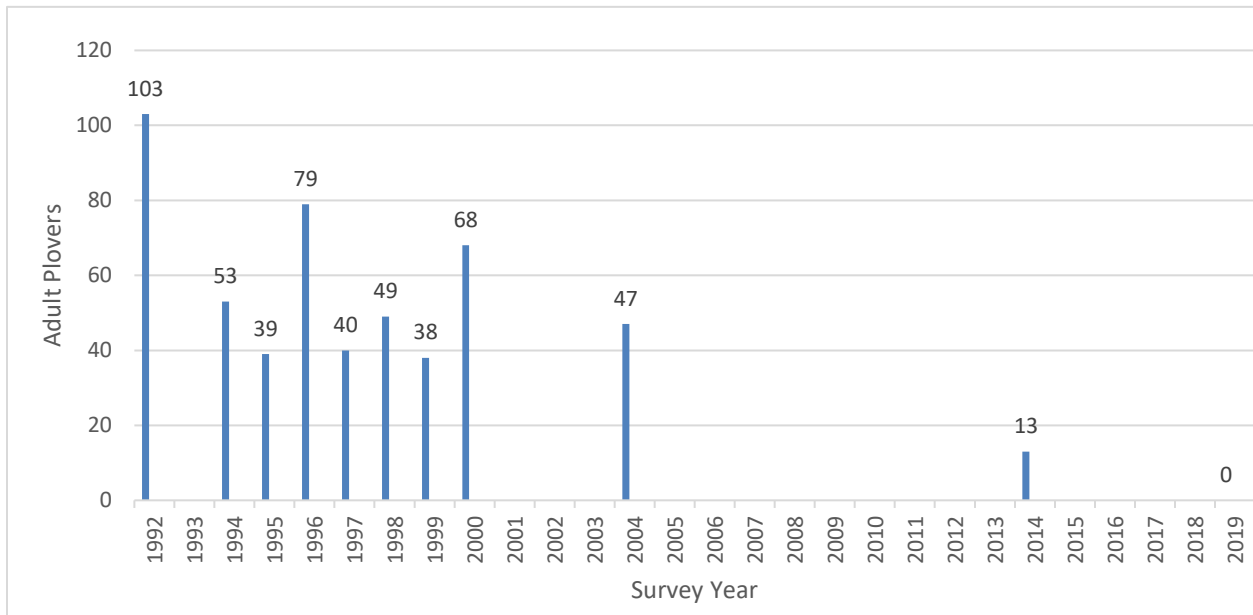
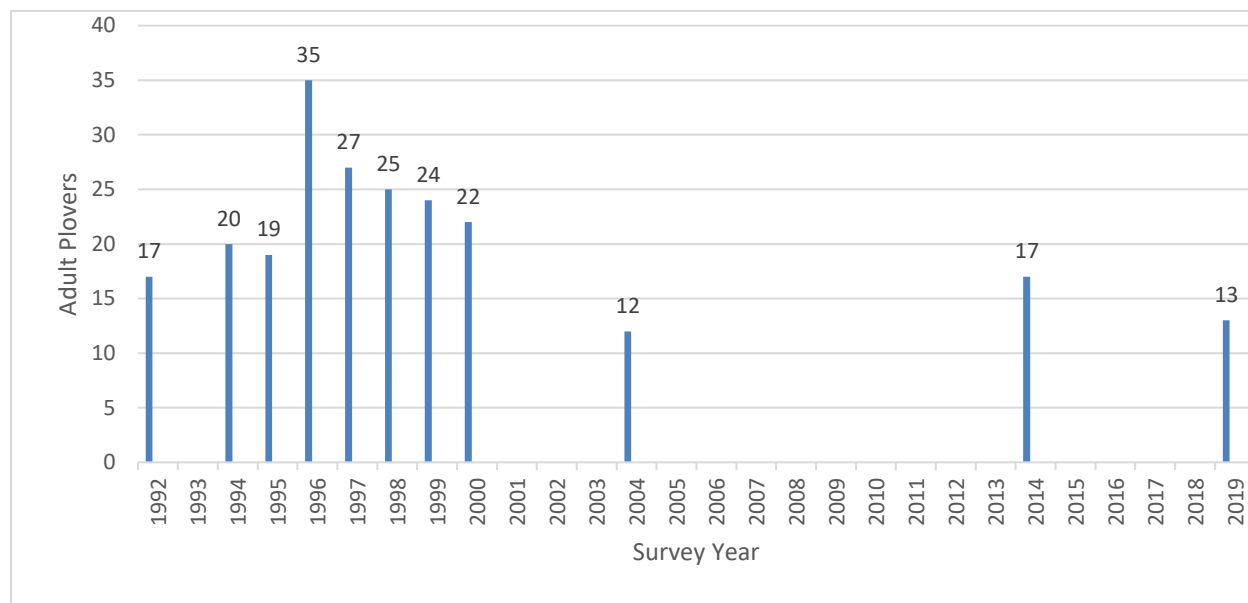


Figure 3: Mountain plover population trend at the Central Montana Study Area from 1992 to 2019

Mountain Plover Census Results for the Northeastern Study Area

The Northeastern Montana Study Area was surveyed for mountain plovers from 4-7 July 2019. Thirteen adult mountain plovers were observed at 10 of the 68 census stations along the survey route. Eight juvenile mountain plovers were also observed with these adults. Another 23 adult and 10 juvenile mountain plovers were observed while traveling between census stations. Overall, in July 2019, we observed 54 mountain plovers representing 27 separate observations with 36 birds classified as adults and 18 classified as juveniles. The 18 juvenile birds represented 11 broods (1.63 chicks per brood). In 2014, we observed 62 mountain plovers representing 36 separate observations while conducting the survey, but we thought that some of these observations could have been the same birds observed on 2 different days. Forty-eight of

Figure 4: Mountain plover population trend on the Northeastern Study Area from 1992 to 2019.



the birds were classified as adults and 14 were chicks representing 9 broods (1.55 chicks per brood). Results for all survey years are shown in figure 4.

DISCUSSION

Central Study Area

Overview

The Central Study Area was previously considered to be Montana’s second largest mountain plover population after the Phillips/Blaine Counties population where mountain plovers are strongly associated with black-tailed prairie dog colonies (Knowles et al. 1982). There are several historical accounts of mountain plovers in what is now our Central Montana Study Area that suggest mountain plovers were once common in this area. Grinnell (1876) reported mountain plovers occurring in the western portion (Haymaker Creek) of our study area in 1876. Silloway (1903) described the mountain plover as being a regular summer resident in Fergus County, Montana from May through September. At this time, Fergus County included all or parts of Judith Basin, Wheatland, Golden Valley, and Musselshell Counties. However, Watts and Eichhorn (1981) noted that 4 bird species associated with short grass prairie in this area (the mountain plover, burrowing owl (*Athene cunicularia*), long-billed curlew (*Numenius americanus*), and grasshopper sparrow (*Ammodramus savannarum*)) were much reduced from Silloway’s description. Pettingill (1981) in 1951 considered the mountain plover as common in the western portion (Haymaker Creek) of our Central Montana Study Area. He stated that plovers could be observed along the road that ran north from Two Dot.

When we began our census of mountain plovers in this area, it is quite likely that mountain plovers were already in decline and that our census effort only captured the tail end of this population collapse. For example, Dr. Robert Eng (pers. comm.) collected a mountain plover on 22 April 1972 about 13 km north of Harlowton, MT (this specimen is in the Montana State

University Vertebrate Museum) within the Central Montana Study Area. He reported the actual collection site to be grasslands at the time, but when we examined the site in the 1990s, it had already been converted to cultivated croplands and no mountain plovers were found. Our highest mountain plover count during the 28-year period of this survey was 103 adult birds at 35 stations in 1992 when we first established the census route. The two lowest counts came in 2014 (13 plovers) and 2019 (0 plovers). The decline of mountain plovers over this time period was initially characterized by fluctuating counts with numbers in peak years being progressively lower (Figure 3). From 2004 to 2014 there was a substantial decline in plover numbers, and we associated this with conversion of native grasslands to croplands, conversion of native grasslands to introduced grasses, a reduction in the number of flocks of sheep, and a general decline in livestock grazing overall. In 2014, we considered this to be a significant decline in mountain plover numbers and we stated that the Central Montana Study Area mountain plover population was on the brink of total collapse. The 2019 survey confirmed this. The decline of mountain plovers in this study area was so drastic and complete there is no need for statistical manipulation of the data to draw a conclusion. The mountain plovers are gone, and it is unlikely they will come back because there are no longer enough suitable sites to maintain a breeding population.

In 1992, while establishing our census route through the Central Study Area, we counted 118 different adult mountain plovers (103 plovers at census stations and 15 in between stations). At that time, it was apparent that there were other areas with mountain plovers that could not be effectively viewed from public roads, and that the actual number of plovers was greater than this minimum count. We estimated that possibly double or triple the number of mountain plovers that we observed could reside in the Central Study Area in 1992 (Knowles and Knowles 1993). However, in 2014 and 2019, we did not see any other areas (e.g. heavily grazed stock water sites) where we thought mountain plovers might be present off of our route suggesting that there was little chance that mountain plovers simply shifted their distribution to areas not along the census route. In fact, during the 2019 survey, while driving across the entire survey area we did not see a single site that appeared to be suitable for mountain plover use. The areas of native grasslands that remained were not grazed sufficiently hard to create the large areas (20 ha or more) of very low growing vegetation that is required by mountain plovers for successful nesting and brood rearing.

The 103 adult mountain plovers observed on our very first census in 1992 was the highest count we obtained during the 28-year period. Subsequent surveys over the next 7 survey years showed a lower but fluctuating population. Due to these annual variations in the census counts during the 1990s, the declining population trend did not become apparent until the 2004 and 2014 census counts when only 47 and 13 adult mountain plovers were observed, respectively. When the 11 census counts are viewed over the 28-year period, it is apparent that the mountain plover population in this area was actually declining throughout the entire period with each peak count slightly lower than the previous peak.

A DETAILED ANALYSIS OF THE POPULATION COLLAPSE

Haymaker Creek in the Central Montana Survey Area

Pettingill (1981 - first edition was published in 1951) stated that the gravel road (now called Haymaker Road) running north from Two Dot, Montana (this road had our census stations 1-10

on the Central Study Area and borders Haymaker Creek) was *the* place in Montana to find mountain plovers. He described mountain plovers to be found on the road and on either side of the road. His descriptions make it sound like mountain plovers were very common in this area in 1951. Haymaker Creek was also the collection site of 4 mountain plovers by Grinnell in 1876 when traveling from Fort Carroll (located on the Missouri River down-stream from the Robinson Bridge) to Yellowstone National Park (Grinnell 1876). Grinnell's collection of mountain plovers near Haymaker Creek clearly shows that mountain plovers were present in the Central Study Area prior to settlement. There is one black-footed ferret record from the Judith Gap area and probably there were black-tailed prairie dogs in this area prior to settlement.

In 1992, we observed 14 mountain plovers at the 10 census stations along Haymaker Road. In subsequent survey years, we were always able to observe mountain plovers along Haymaker Road although the numbers followed the same downward trend observed for the rest of the Central Survey Area. However, in 2014 and 2019, we did not observe a single mountain plover at the 10 census stations on Haymaker Road nor did we see any mountain plovers in between the census stations. These results are highly significant because there have been no obvious habitat changes from 1992 to 2014 at the 10 census stations along Haymaker Road other than absence of grazing. In fact, this area remains dominated by the STCO/BOGR habitat type with virtually no agricultural development. In 2019, the only obvious change we noted was the homestead at station 1 was gone (probably burned) and no cattle and horses were present at this site.

The Haymaker Ranch during the 1990s was managed by an out-of-state owner who traditionally grazed about 2,000 yearling cattle that were brought onto the ranch in the spring and sold in the fall. During our 2004 mountain plover survey, we learned that the ranch had sold. Information posted on the Hall and Hall ranch real-estate website in 2014 states that Haymaker Ranch had been leased the past several years to a local rancher as a cow/calf operation, and that the ranch had just sold again for 8.4 million dollars. The website describes the ranch as being about 30,000 acres of mostly deeded land with only 960 acres cultivated in the Haymaker Creek bottomlands. In 2019, we did not observe any cattle along the census route in this area, but a small flock of sheep was observed about a 1.5 km off the road near station 3.

During the 2014 survey, we did not see any cattle at the census stations 2-9 located on the Haymaker Ranch, but cattle were present at the station 1 located on a ranch immediately north of the Haymaker Ranch. Signage at this ranch showed that the Booth Ranch was being leased by the Miller Brothers. Long-term decline in livestock numbers and grazing practices in the Haymaker Creek area probably have contributed to increased vegetation height and plant density to a level that is not tolerated by mountain plovers. Knopf (2008) considered reduced grazing intensity on the PNG resulted in a gradual increase of vegetation to a level not tolerated by mountain plovers. Augustine and Derner (2012) reported that even intensive spring/summer cattle grazing was not sufficient to return grassland habitat on the PNG to conditions suitable for mountain plover use.

The Lewis Ranch portion of the Central Survey Area

The Lewis Ranch (formerly officially named T-Bench Ranch and now part of the N Bar Ranch) in the Central Study Area is a good example of the importance of intensive livestock grazing to mountain plovers. This ranch was voluntarily entered into the Montana Centennial Register of Natural Areas in the 1980s by the Nature Conservancy because of the abundance of mountain plovers. Part of this ranch classification was a pledge from the Lewis' not to sodbust their ranch.

When we first visited the ranch in May 1985, the area around the ranch headquarters had been intensively grazed during winter and spring and mountain plovers were abundant. Mr. Kenneth Lewis, who managed the ranch, passed away in 1993 and his widow, Janet, did not continue the ranching operation at a similar level. Our surveys documented the decline of mountain plovers following the loss of cattle. In 1992, we counted 18 mountain plovers on the ranch, and by 1997 we were unable to find any mountain plovers. In 2004, we visited with Janet and she commented that plovers were gone from the ranch and that plover numbers in the surrounding area were also way down. During the 2014 survey, we talked to people managing this ranch, and learned that Janet had passed away a few years previous and that the Wilks brothers had recently purchased the ranch when the estate was finally settled. The Lewis Ranch again had cattle on it, but we did not find any mountain plovers at the census stations on the ranch. During the 2019 survey we observed some cattle grazing on the ranch lands, but again no plovers were observed. Vegetation height and density had become too high for mountain plover use under a reduced cattle grazing regime.

Habitat Changes within the Central Survey Area

From 2014 to 2019, the habitat conditions in the Central Survey Area appeared to be very similar with no large areas being sodbusted. One change we noted was that 4 homesteads had been burned. Each of these homesteads had a history of mountain plover observations. These sites were formerly used as loafing areas by cattle and sheep, and with the homesteads gone there was no focal point for livestock to concentrate in the area. Homestead sites from the early 1900s up to the time of abandonment in the 1930s-1950s were probably very intensively grazed by sheep and cattle. During the homesteading period, much of this study area had 4 homesteads on each square mile of land. During peak sheep numbers in the 1930s and 1940s, there must have been many sites suitable for mountain plover use.

Another change was noted at the prairie dog colonies located on BLM and USFWS land (Stations 85 and 86). A suspected plague epizootic occurred throughout central and north-central Montana in 2018 (Randy Matchett, pers. comm.), and these 2 colonies with previously documented mountain plover use were both severely impacted. When we examined the BLM colony in 2019, we did not observe any prairie dogs, nor did we see any sign of prairie dog activity. At the USFWS prairie dog colony only a few prairie dogs remained in 2 small areas on Federal land, and in 1 area of adjacent private land several acres of active colony remained. At both of these colonies we normally observed mountain plovers and burrowing owls, but in 2019 we did not observe either species.

Although there were no obvious habitat changes (although there was a change in land use) on the Haymaker Creek portion of the Central Study Area, there were considerable habitat changes elsewhere in the study area. During the 28-year period, there was a significant decrease in native grass habitat and a corresponding increase in introduced grasses, alfalfa, and cultivated wheat at the census stations. Surprisingly, many of the wheat fields documented in 1992 had subsequently been planted to introduced grasses, and much of the gain in wheat came from sodbusting of native grassland. Figures 5 and 6 show this decline of native grasslands from 91% of the quarter quadrants at census stations in 1992 to 73% of the quarter quadrants in 2014. An assessment of habitat at the census stations in 2019 did not show additional sodbusting since 2014. At the same time, wheat increased from 4% to 14% and introduced grass increased from

Figure 5: Percentage of 360 quarter quadrants at 90 permanent census stations in the Central Montana Study Area in July 1992.

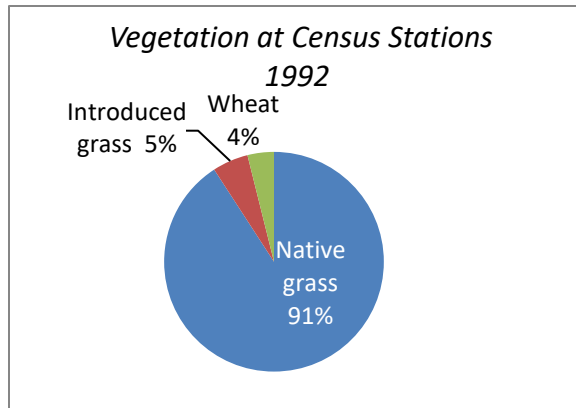
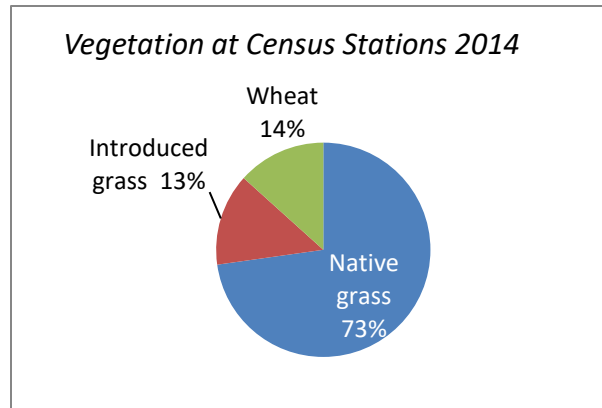


Figure 6: Percentage of 360 quarter quadrants at 90 permanent census stations in the Central Montana Study Area in July 2014.



5% to 13%. Thus, wheat and introduced grasses increased from 9% to 27% of the quarter quadrants from 1992 to 2014. It is important to note that these figures do not accurately represent the amount of wheat and introduced grass across the entire study area as a whole, since the census stations were initially placed in areas with native grasslands where mountain plovers were found or were likely to be found. The actual percentage of cultivated wheat and introduced grass pasturelands across the study area was much greater than this. In 1992, we estimated that only 66% of the Golden Valley and Wheatland Counties portion of the Central Study Area remained in native grassland.

The conversion of native grasslands to wheat and introduced grass during this 28-year period has been an ongoing process that we noted early in the survey period. In the early years of this survey we were suspicious that the Conservation Reserve Program (CRP) had encouraged sodbusting. Our suspicions were based on windmills and stock tanks located in wheat fields with piles of fence posts and rolls of old barb wire along the field edges, and immediately adjacent to these wheat fields were fields of crested wheatgrass. This suggested that the crested wheatgrass fields were formerly wheat fields that had been placed into the CRP, and that pastureland (as indicated by water developments) had been sodbusted. When we questioned the District Conservationist at the Natural Resource Conservation Service office for Musselshell County about this, he acknowledged that this was a problem, but refused to let us examine their farm files to document the extent of sodbusting.

Twenty-eight years later we now have a measure of sodbusting for 90 specific points, and it was significant. Sodusting in the 1980s was probably even more significant following the start of the CRP program in 1983 when there were absolutely no provisions to discourage sodbusting. In 1992, we were told by ranch-hands that were rebuilding fences drifted over with dirt from wheat fields, that the area in western Musselshell County had a 2-township area (72 square miles) sodbusted during the 1980s. During the 1990s, farmers were required to file a farm conservation plan prior to sodbusting (only necessary if they wanted to remain in government farm programs) which may have curtailed some sodbusting but certainly did not prevent sodbusting during the period we conducted mountain plover surveys.

Mountain Plover Response to Conversion of Native Grasses to Introduced Grasses

At the census stations that had been converted to wheat or introduced grasses, we continued to monitor the stations for mountain plovers, and during all 11 surveys we had only a single observation of a mountain plover using a census station converted to wheat. In this case, it was using a chemically fallow field in an area where wheat stubble had been flattened by equipment. During the 2014 and 2019 surveys, none of the census stations with wheat or introduced grasses had mountain plovers. Two native grassland census stations (22 and 65) used by mountain plovers early in the survey were converted to crested wheatgrass, and mountain plovers were never seen at these sites after the conversion. Crested wheatgrass has a vegetative height profile too tall for mountain plovers.

Much of the privately-owned native rangelands in eastern Montana has incrementally been converted to crested wheatgrass and other non-native grasses over the past century. All of the Bankhead Jones Act lands reclaimed by the Federal government and now managed by the BLM were also planted to crested wheatgrass in the 1930s. This massive and widespread conversion of native prairie to introduced grasses across eastern Montana permanently excluded mountain plovers from broad areas. When the USFWS (2011) stated that 31 million acres of eastern Montana were grasslands and that sodbusting was not an important issue, they failed to note that the vast majority of these grasslands were not suitable for mountain plover use. Mountain plovers require broad areas of relatively level land, with short growing vegetation and lots of bare ground. Montana's mixed grass prairies are not suitable for mountain plover use without intense mammal herbivory (i.e. black-tailed prairie dogs, historical bison numbers, and probably large flocks of domestic sheep). For the most part, it is very difficult to create suitable mountain plover habitat by grazing cattle.

In Nebraska, Oklahoma, and eastern Colorado there are reports of mountain plovers using fallow fields of cultivated wheat, millet and corn, but there is also a high level of nest destruction in these fields (Shackleford 1997, Knopf and Rupert 1999, Bly et al. 2008). Shackleford (1997), after documenting mountain plover use in fallow cultivated fields in Oklahoma, conducted a mountain plover survey across the distributional range of mountain plovers from Oklahoma to Montana looking specifically at cultivated fields. He found very little use of cultivated fields from Wyoming northward.

Association of Mountain Plovers with Sheep

Early in our survey efforts of the Central Study Area, we observed the association of mountain plovers with sheep. We frequently saw mountain plovers associated with flocks of sheep and feeding on insects flushed by the grazing sheep. Sheep graze grasses closer to the ground than cattle and appear to more evenly graze a pasture creating the appearance of a well-groomed lawn. When we first noted this association of mountain plovers with sheep, we suggested that the USDA develop an incentive program for sheep producers in the Central Montana Study Area to continue raising sheep in areas with mountain plovers. We were concerned that most sheep ranchers appeared to be nearing retirement age and we thought that the new ranch managers would switch from sheep to cattle. Even in the 1990s it was apparent that there was a long-term decline in sheep numbers in Montana (Figure 7). The loss of sheep in Montana has been a long-term trend starting in the 1940s. Peak sheep numbers in Montana were recorded in the 1930s, and this probably explains why mountain plovers persisted during this period despite the massive prairie dog poisoning campaigns of the 1920s and 1930s.

During the 2014 survey, we observed only 1 small flock of sheep in Haymaker Creek bottomlands immediately north of Two Dot (this area was not officially part of the census route), and a larger flock of sheep in a crested wheatgrass field in the Hopley Creek area (station no. 22) that had been sodbusted. In 2019, we observed a flock of sheep further north on Haymaker

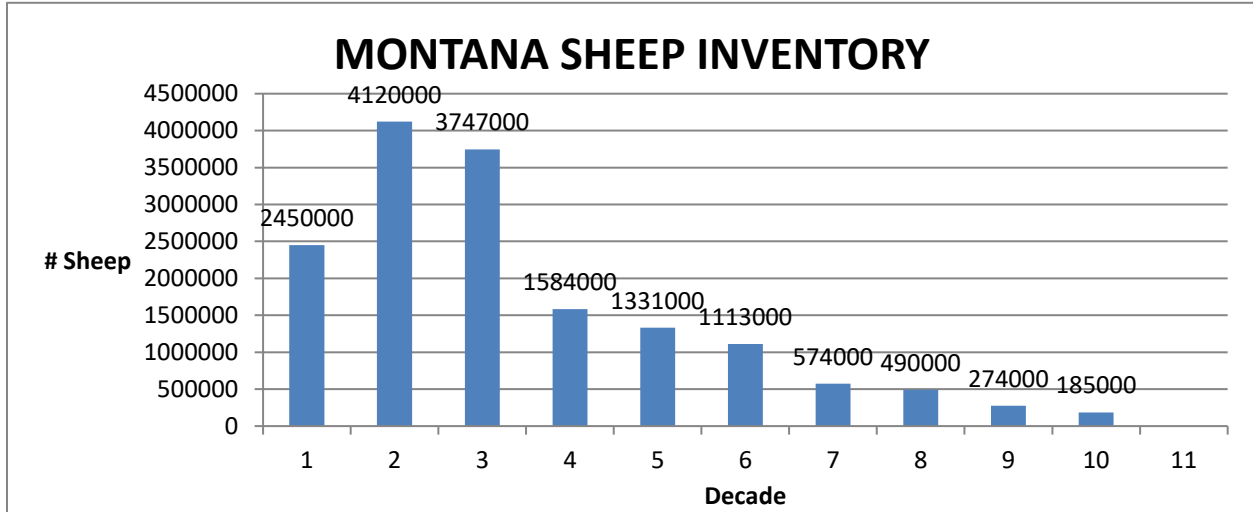


Figure 7: Montana sheep inventory from 1920 to 2010 showing the rise and fall of sheep numbers in Montana.

Creek and the same large flock of sheep on Hopley Creek at station no. 22. During the 2014 survey we talked to a fuel truck driver delivering diesel fuel to ranches in the area, and the driver confirmed our observations that most large flocks of sheep were gone. The truck driver also mentioned that livestock numbers overall were down across the area. In 2019, we talked to an elderly individual east of Judith Gap and when we mention the scarcity of sheep, he stated that all the sheep east of Highway 191 were gone (“There are no sheep left in this country”). The absence of cattle that we observed along Haymaker Creek in 2014 and 2019 was also apparent in other areas of the Central Study Area.

Another aspect associated with sheep dominated ranges was intensive predator control which might also have benefited mountain plovers through increased reproductive success. Knopf (2008) commented that predator control prior to the 1972 ban of compound 1080 was beneficial to mountain plovers, and that without predator control on the PNG the swift fox (*Vulpes velox*) became the dominant predator of mountain plover nests and chicks. During the 1990s, when sheep were more abundant on the Central Montana Study Area, we frequently saw coyote carcasses draped across the top strand of barb-wire fences which was an indication that predators were actively being controlled at that time.

The association of mountain plovers with sheep has only been briefly mentioned by 2 other authors. Plumb (2004) working in Wyoming noted that grazing by cattle and sheep was pervasive in areas that he found mountain plovers. McGaugh (1998) noted that wintering mountain plovers in the Antelope Valley and near Harper Dry Lake in California were using irrigated alfalfa fields that were grazed by wintering flocks of sheep. (Note: We have conducted desert tortoise surveys in the Harper Dry Lake alfalfa fields - the wintering flocks of sheep are gone, and all of the irrigated fields have now been converted to solar energy plants. These fields were specifically chosen for solar development because the desert had already been disturbed by

agriculture. The 2011 USFWS (2011) finding of not warranted for mountain plover listing did not even mention this loss of a known wintering area.)

Other Habitat Changes including windfarms

There have been other changes to the Central Study Area besides conversion of native grassland to wheat and introduced grasses, and the loss of sheep and cattle. A large wind farm is now present south of Judith Gap in an area which had recorded mountain plover use (Flath 2003 and TRC 2008). Although the wind farm was not placed directly on any of our census stations, wind turbines were in the relative vicinity of two census stations (31 and 32). These two stations are located next to Highway 191, and both previously had consistent mountain plover use during previous surveys. In addition to the windfarm, in 2014 at these same 2 census stations, we observed that Montana Dept. of Transportation had built large wooden snow fences along this entire stretch (1.6 km) of the highway. No mountain plovers were found in this area in 2014 and 2019.

At these 2 stations there was also a change in livestock grazing that may have contributed to the abandonment of these sites by mountain plovers. One site was formerly grazed summer-long by both cattle and sheep while the other site was grazed by sheep. In 2014, both sites were only grazed by cattle, and in 2019 neither sites were not grazed. Augustine and Derner (2012) noted that even with double the recommended grazing rates by cattle during spring and summer, it was not sufficient to provide suitable habitat for mountain plovers on the PNG in northeastern Colorado. They also reported that mountain plovers remaining on the PNG were associated with black-tailed prairie dog colonies and burned areas.

Change in Mountain Plover distribution

The distribution of mountain plovers in the Central Study Area has changed over the years. In 1992, mountain plovers were distributed along the entire length of the 90 census stations all the way from Haymaker Creek on the west to the Lake Mason National Wildlife Refuge prairie dog colony on Willow Creek on the east (about 106 km). Some areas such as Haymaker Road, Highway 191 census stations, the Lewis Ranch, and the homestead cluster were initially mountain plover hot spots. As mountain plover numbers began to decline at these and other sites due to changing habitat conditions, a higher percentage of mountain plovers were found at the 2 prairie dog colonies (1 on BLM, 1 on USFWS) located at the east end of the census route.

In 2004, 32 of the 47 (68%) adult birds counted at the census stations were observed in the prairie dog colonies. In 2014, 46% (6 birds) of the adult plovers were found on these colonies. However, the observed decline from 32 birds on the colonies in 2004 to 6 birds in 2014 was of concern because both colonies had high levels of prairie dog activity. We did visit these 2 prairie dog colonies in early July 2005 and found 21 mountain plovers at that time (Knowles and Knowles 2006). These prairie dog colonies were severely impacted by an apparent sylvatic plague epizootic in 2018 and no mountain plovers were found on the colonies in 2019. This 2018 plague epizootic was widespread through central and northcentral Montana and had a significant impact on prairie dog populations throughout the area (pers. comm. Randy Matchett).

Also in July 2005 we visited known mountain plover “hot spots” along the census route and observed 3 adults and 5 young on gravel roads west of Highway 191 and 5 adults and 1 young on gravel roads east of Highway 191. We attribute these distributional shifts to an overall decline of

mountain plovers in the Central Montana Study Area. This decline also represents a decline in the mountain plover range distribution due to changing habitat conditions.

Comparison of the Declines of the Central Montana and Pawnee National Grasslands Mountain Plover Populations

We have included a graph of the mountain plover population trend for the Pawnee National Grasslands (PNG) (Knopf 2008) (Figure 8) because the PNG decline appears very similar to the Central Montana Study Area decline (i.e. fluctuating numbers and each peak count lower than the previous peak). The main difference is that the collapse of the mountain plover population at the PNG occurred over a much shorter period than what we observed for the Central Montana Study Area, but the end results appear similar. Based on Knopf's (2008) documentation of the mountain plover population collapse within the PNG in the mid-1990s, there is little chance of mountain plover populations recovering following a dramatic decline such as this.

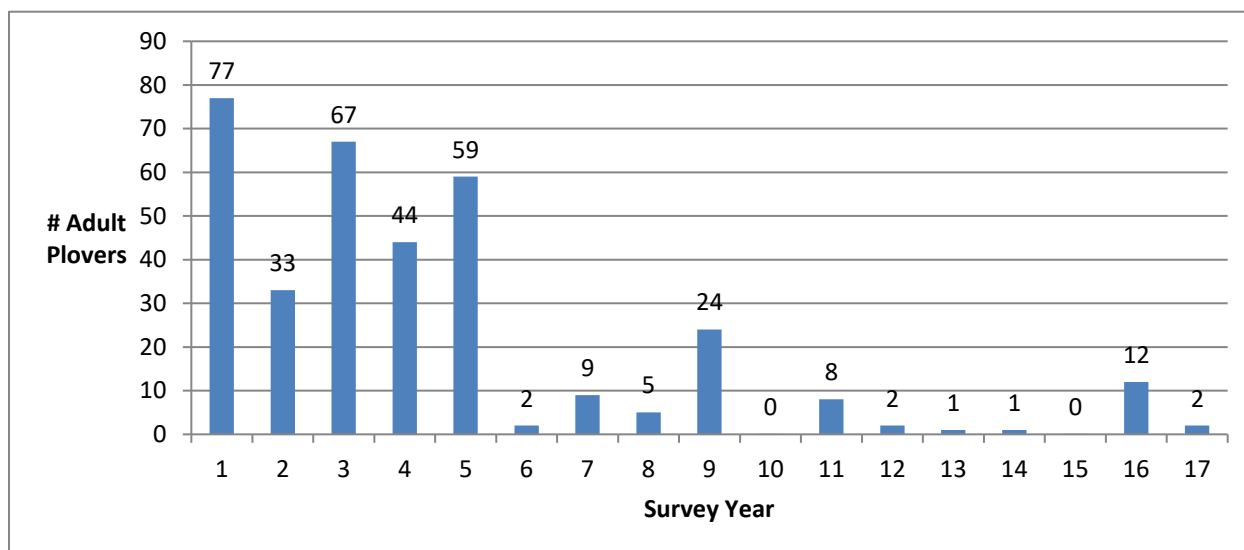


Figure 8: Mountain plover population trend at 112 census stations on the Pawnee National Grassland from 1990 to 2006. Data from Knopf 2008. Survey years 10 and 15 represent zero birds observed.

Knopf (2008) established his permanent trend count transect on the PNG in 1990. Knopf's (2008) trend count transect on the PNG had 112 census stations with 17 years (1990-2006) of survey data. His highest count occurred in 1990, his first survey year, with 77 adult birds observed. This can be compared to our highest count in the Central Study Area of 103 birds in 1992 at 90 census stations.

The decline of mountain plovers on the PNG followed a similar trend as seen on the Central Montana Study Area i.e. fluctuating numbers with population peaks showing a steady decline. On the PNG, a dramatic decline in mountain plover numbers was noted following a year of

above average precipitation. Knopf (2008) believes that mountain plovers will not return to the PNG in similar numbers because traditional use of this area has been lost, and because of long-term habitat changes due to only moderate grazing intensity by cattle. Graul and Webster (1976) considered the PNG to be the "stronghold" for mountain plovers during the 1970s and had estimated over 20,000 mountain plovers in this area in 1970. Today, the mountain plover is

considered a rare bird on the PNG (Augustine and Derner 2012). Knopf (2008) thought that mountain plover numbers on the PNG were actually at their peak in historic times during the 1930s, that they had been in a long-term decline ever since then, and that the population collapse that he documented was actually just a quick end to this long-term decline.

Mountain plovers on the Central Montana Study Area probably had been in decline for many years before we started our census effort similar to that described by Knopf (2008) for the PNG. At some low number, the mountain plover population becomes dysfunctional which is expressed as a population collapse like that documented in 2019. In 2014, we speculated that the few mountain plovers remaining at prime habitat sites (homestead cluster, prairie dog colonies), were too few to effectively recover the population. The Southwestern Study Area (Jefferson/Broadwater/Madison Counties), Toole, Teton, and Carter Counties mountain plover populations are other examples where remnant populations have gone extinct. The Central Montana Study Area mountain plover population has now joined the list of these other Montana populations that have disappeared.

Northeastern Study Area Discussion

Overview

The Northeastern Study Area census route has been surveyed 11 times since 1992, and the number of adult mountain plovers observed at census stations along the route has ranged from a low of 12 plovers at 9 stations in 2004 to a high of 35 plovers at 21 stations in 1996 (Figure 4). We attribute the high number of mountain plovers observed in 1996 to the loss of prairie dog habitat in Phillips County as a result of a sylvatic plague epizootic among black-tailed prairie dogs in the early to mid-1990s. With the reduction in suitable prairie dog habitat mountain plovers may have searched surrounding areas for suitable nesting habitat. However, we did not see a similar increase in mountain plovers in 2019 following the 2018 plague epizootic in Phillips County.

At one time, prairie dog colonies in adjacent Phillips County provided habitat for Montana's largest mountain plover population (Knowles et al 1982, Knowles and Knowles 1984). Childers and Dinsmore (2008) estimated the number of plovers in this area at 758, but this estimate was after the initial plague epizootic in the 1990s. A decline of mountain plovers in Phillips County has been associated with the decline of prairie dog acreage (Knowles 1999, Dinsmore et al. 2005). With this decline of prairie dog acreage in Phillips County, some mountain plovers may have looked elsewhere for suitable habitat and moved into the bentonite areas of Little Beaver Creek and adjacent drainages during the mid-1990s (survey year 5). However, the sylvatic plague epizootic in southern Phillips County in 2018 did not result in increased plover numbers in the Northeastern Study Area in 2019. It is possible the mountain plover numbers in Phillips/Blain Counties never recovered to their pre-plague numbers. In addition, there could be many more factors influencing the Northeastern Study Area mountain plover numbers than just sylvatic plague in Phillips County.

The 13 adult mountain plovers observed at 10 census stations in 2019 was the second lowest count of the 11 survey years but was comparable to the 2014 count when we observed 17 mountain plovers at 11 census stations. Both counts, although they were at the lower end of the previous survey results, were within the range of the number of mountain plovers observed during the previous survey efforts. Overall there appears to be no discernable upward or

downward trend of mountain plovers in this area from 1992 to 2019. The result of our census effort shows that mountain plovers remain in southern Valley County in low numbers.

Green (1982, 1983) and Green and Engle (1984) conducted mountain plover surveys in what is now our Northeastern Study Area in relation to bentonite mining. During his surveys of this area in the early 1980s, Green estimated mountain plover densities to range from 6.3-1.7 plovers per square kilometer during the 3 years (1982 – 1984) that he studied mountain plovers in the Northeastern Study Area. In 1992 (Knowles and Knowles 1993), we resurveyed Green’s survey areas and estimated 1.9 birds per square kilometer. Childers and Dinsmore (2008) estimated a mountain plover density in this area of 1.6 birds per square kilometer, but their survey area may not have exactly duplicated Green’s survey areas. However, these data provide a density estimate of mountain plovers in the same general area over a 22-year period (1982-2004) that shows some consistency in density from at least 1982.

Based on our density estimate of 1.9 birds per square kilometer in 1992 (Knowles and Knowles 1993) and using the cumulative area that mountain plovers were observed during Green’s surveys and our surveys, we estimated about 100 adult mountain plovers in this area in 1992. While we have no actual quantitative data on the total number of mountain plovers occurring in this area in 2019, we have walked through most of the suitable mountain plover habitat in Little Beaver Creek and adjacent drainages and have a feel for how many mountain plovers might be in the Northeastern Study Area. In our opinion, this area currently supports less than 100 adult mountain plovers.

Childers and Dinsmore (2008) estimated the total number of mountain plovers in this area of Valley County to be about 160 adult birds. This estimate was based on 110 randomly selected point counts within the ACEC area of Little Beaver Creek using a technique based on studies by Wunder (2003) in South Park Colorado, and Plumb (2004), Plumb et al. (2005) in Wyoming. This population estimation technique involves randomly placed point counts yielding a density estimate which is then expanded across a survey area to estimate the entire population.

While point counts can accurately estimate mountain plover numbers around a point, meaningfully applying this density over a broad area is a different story. Unlike many species, mountain plovers are extremely site specific and not randomly distributed across the landscape. Thus, errors in density are amplified by projecting point count data to broad areas.

Both latter studies (Wunder, 2003, Plumb, 2004 & Plumb et al., 2005) provided population estimates that were about double of the previous estimates for their respective survey areas (USFWS 2011). We believe that the estimate of 160 adult birds by Childers and Dinsmore (2008) is also too high an estimate for the Northeastern Study Area. Since mountain plovers are so site specific in this area, a better total count for a population estimate would be to systematically walk through the known sites used by plovers in late June/early July and count the number of adult mountain plovers flushed or otherwise encountered.

Habitat Changes

There appeared to be shifts in mountain plover distribution in the Northeastern Montana Study Area from 1992 to 2019. In 2014 and 2019, we did not observe mountain plovers at stations near the abandoned bentonite plant and in the adjacent Brazil Creek. Early in our survey efforts these

were good places to find mountain plovers, and Green (1982, 1983) and Green and Engle (1984) recorded many mountain plover observations in this area. In 2014 and 2019, the vegetation in this area appeared too tall for mountain plover use.

Changes in cattle grazing may also have been a factor with changing mountain plover distribution. In 2004, no mountain plovers were found in Lone Tree Creek and the area appeared ungrazed that year. In 2014, a large number of cattle were present in Lone Tree Creek and we made 3 observations of mountain plovers in this area. However, in 2019 cattle were not present in that portion of Lone Tree Creek within the survey route, but we did observe 2 adult mountain plovers. In 2014, we did not observe any mountain plovers around Big Rock Reservoir, Grub Reservoir, and Sage Hen Creek where we normally find mountain plovers. Cattle were not present at Big Rock Reservoir or Sage Hen Creek and only a few cattle were present at Grub Reservoir in 2014. In 2019, Grub Reservoir and Sage Hen Creek had been grazed and we did find mountain plovers in this area. Intensive cattle grazing is probably very important for mountain plovers even in this area of depauperate plant communities.

In 2004, we noted that the BLM had recently dug pit reservoirs at 2 census stations (16 and 26) that normally received mountain plover use. In 2014, mountain plovers were observed at both census stations close to the reservoirs, and at station 26 we observed a mountain plover standing on the spoils mound adjacent to the reservoir and a second mountain plover was in the area. Knopf (per. comm.) stated that, on the PNG, if water had leaked on the ground at stock tanks, killdeer (*Charadrius vociferus*) would be present and displace mountain plovers, but this did not seem to be an issue in the Northeastern Study Area. We did not find mountain plovers at these sites in 2019.

The Northeastern Montana Study Area had previously been mined for bentonite at 10 sites. Six of the sites were old unreclaimed mine pits and 4 were newer (1980s) mine sites that were reclaimed at the start of our surveys. The reclaimed sites were initially planted with a seed mix of native grasses and sagebrush. Although there was good initial germination and growth, none of these plant species persisted at the reclaimed sites. Instead, a small native forb, rillscale (*Atriplex diocuis*), invaded these sites and dominated the vegetation (Knowles and Knowles 2014). While conducting a vegetation analysis of these reclaimed sites in August 2013, we did observe mountain plovers to use this rillscale-habitat at 1 reclamation site, and in 2019 we observed a mountain plover at another rillscale dominated reclaimed site. We did not observe mountain plovers in 2013 and 2014 to use the unreclaimed sites, but they were found immediately adjacent to 3 of the unreclaimed sites (Knowles and Knowles 2014).

CONSERVATION CONSIDERATIONS

The formula for population extinction is to fragment the habitat and isolate populations, and then impose a catastrophic event on the remaining population. Since settlement of Montana, mountain plover populations have been fragmented and isolated due to prairie dog control and sylvatic plague epizootics, conversion of native grasslands to cultivated cropland and introduced grasses, and changing grazing intensity and patterns by large herbivores.

We have gathered sufficient data to demonstrate that mountain plover populations are now extinct at 2 of our 3 long-term study areas (Southwestern and Central), and at 3 other small

isolated sites. It is apparent that the mountain plover population remaining in the Northeastern Study Areas is small, isolated, and vulnerable to extinction. The habitat conditions in each of the study areas have certainly been degraded from presettlement conditions. Prairie dog colonies are reduced, fire has been virtually eliminated, intensive grazing by migratory bison herds is absent, and much native grassland has been converted to cultivated cropland or introduced grasses. Specific to the Northeastern Study Area are large trans-valley dams, spreader dikes, and contour furrowing.

Of the 9 recently identified mountain plover populations in Montana, extinction appears to have already occurred in 5 of these. These extirpated populations are the Central Study Area (Golden Valley, Wheatland and Musselshell Counties), the Southwestern Study Area (Jefferson, Broadwater and Madison Counties), and the Teton, Toole and Carter Counties populations. An occasional mountain plover is still observed along Gyp Spring Road in Carbon County (Mike Lesnik pers. comm.), but this population is so small it is hard to understand how it survives. The Phillips/Blaine and Treasure/Rosebud County populations are probably greatly reduced due to reoccurring plague epizootics in prairie dogs (Knowles 1999, Dinsmore et al. 2005), but there is no recent population data on these 2 populations following the most recent plague epizootic. Mountain plovers in the Northeastern Study Area (Valley County population) have fluctuated over the past 3 decades but remain in low numbers and are certainly vulnerable to catastrophic events. It would not take much to push one or more of the remaining mountain plover populations towards extinction. An above average precipitation year occurring during a widespread sylvatic plague epizootic could be devastating for mountain plovers.

In the Northeastern Study Area, the BLM implemented a large-scale range improvement program that destroyed at least half of the suitable mountain plover habitat in the 1950s and 1960s. There has also been past bentonite mining in the core area used by mountain plovers. Since all bentonite deposits in this area had been claimed prior to the ACEC designation, the designation does not restrict future bentonite mining at the claim sites, and indeed there was some mining (1 new pit) that occurred between 2014 and 2019. Other catastrophic events which could cause local extinction would include unusual weather events (hailstorms, spring blizzards, flash flooding etc.), sylvatic plague in prairie dogs, the elimination of sheep grazing, and government policies which favor sodbusting. As metapopulations become fragmented and isolated, the probability of local populations recovering following catastrophic events decreases and the probability of losing the entire metapopulation increases proportionately with the loss of its member populations.

In our opinion, the small and isolated mountain plover populations that we have studied in Montana are repeated throughout their breeding range on the Great Plains. The largest population of 2000-3000 plovers in South Park, Colorado is, in reality, a small isolated population (see discussion below). The same can be said for the Phillips/Blaine Counties population in Montana. What we have witnessed with the loss and decline of small and isolated mountain plover populations in Montana is likely being repeated elsewhere. The PNG is certainly an example of how vulnerable these small populations are to habitat change and catastrophic events. The PNG population was believed to contain 20,000 plovers in 1970 but had totally collapsed 3 decades later.

USFWS 2011 Ruling

The USFWS (2011), in their decision to not list the mountain plover as threatened, made many outrageous statements, some of which applied to Montana directly. They attributed 18.5 million acres of suitable mountain plover habitat in Montana and later stated there was 31 million acres of grassland habitat available for mountain plovers. They totally ignored the fact that the mountain plover is a very site-specific bird and if exact habitat characteristics are not met, they are not capable of successfully nesting and rearing young. (Briefly stated, these habitat requirements are broad level areas >20ha, intensively grazed or otherwise very short vegetation, a high percentage of bare ground, and such sites need to be well distributed over a large area to support a functional population.) Without any doubt, only a fraction of one percent of Montana's grassland habitat is suitable for mountain plover nesting and brood rearing. Where mountain plover habitat is lost, birds do not simply move over to a new location since it is unlikely that additional suitable habitat is available. While there may be plenty of potential mountain plover habitat in Montana, very little of it is suitable for mountain plover use. Mountain plovers require large level upland areas (>20 ha) of very short vegetation (< 8 cm tall), and lots of bare ground (>30%) for successful nesting. Additionally, these areas need to be sufficiently abundant and closely spaced to support a viable population.

USFWS (2011) claimed that the black-tailed prairie dog is a resilient species not likely to decline and that rangeland conversion to agriculture remains insignificant. For Montana, they specifically stated that the threat of future destruction of both prairie dog and mountain plover habitat through agricultural conversion was minimal. These statements are in direct conflict with what is actually happening with plague epizootics in Montana's major prairie dog colony complexes, rozoil poisoning of prairie dogs on private lands, and sodbusting in Montana. The document also treated all prairie dog acres in Montana as being mountain plover habitat, when in fact most of Montana's prairie dog acreage is not suitable for mountain plovers because of the topographic setting or size and distribution of the colonies. For example, mountain plovers require at least 20 ha of upland prairie dog habitat in broad level prairie to be suitable for nesting, but the majority of prairie dog colonies in Montana are less than 20 ha and most of the prairie dog colonies in southeastern Montana are located in drainages.

The 2011 USFWS mountain plover assessment stated that part of the reason for not listing mountain plovers was the discovery of a high-density mountain plover population in South Park Colorado. In 2001, the density estimates for this area that was used in the USFWS assessment was 12.8 plovers per square kilometer. However, a 2016 density estimate for South Park placed the density less than a quarter of that (2.8 per square kilometer) (Pierce 2017). The USFWS stated that even though long term trend data showed mountain plovers declining, a better accounting of mountain plover numbers showed that there were almost twice as many mountain plovers (15,000 to 20,000) as compared to their earlier estimate of 11,000 to 13,000 birds.

MANAGEMENT SUGGESTIONS

Although the remaining mountain plover populations may exhibit resilience on a short-term basis, there is no guarantee that these populations will persist in the long-term under present habitat conditions. These Montana mountain plover populations will be vulnerable to extinctions due to catastrophic events on the breeding grounds, wintering areas, and along migratory routes. Further declines in habitat suitability can also be expected. A conservation strategy should be

developed and implemented immediately for each area of Montana where mountain plovers still persist in Montana. Of the 4 areas where mountain plovers are known to remain (Northeastern Study Area, Phillips/Blaine Counties, Rosebud/Treasure Counties, Carbon County) there is significant Federal landownership, and there are opportunities to preserve and enhance mountain plover habitat. Unfortunately, mountain plovers that were associated with private lands in Montana are pretty much gone. Mountain plover conservation efforts on the PNG following the collapse of that mountain plover population have demonstrated that it is extremely unlikely that the population can be recovered once it is lost. Conservation efforts in Montana should be focused on areas with public lands and in areas that still contain viable mountain plover numbers.

Examples of management actions that might benefit mountain plovers would be:

- 1) Increased cattle grazing in areas with mountain plovers both in numbers and length of grazing season - there should be no rested pastures,
- 2) Prairie dogs should be encouraged on public lands such as in Phillips/Blaine and Rosebud/Treasure Counties – this could include increased livestock grazing and restriction of prairie dog shooting.
- 3) Burning small patches of level upland prairie during fall or early spring may be helpful at providing suitable sites for mountain plover nesting. Mountain plovers are attracted to burned areas.

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APPENDIX A

LIST OF PERMANENT CENSUS STATIONS

Table A1. List of census stations for the Central Montana Study Area showing the latitude/longitude coordinates. Latitude/longitude coordinates are in decimal degrees North and West respectively.

Station Number	Latitude	Longitude
1	46.60596	-110.09472
2	46.60608	-110.08334
3	46.59613	-110.08315
4	46.55727	-110.08284
5	46.53366	-110.08288
6	46.51907	-110.08292
7	46.51188	-110.08295
8	46.49002	-110.08300
9	46.47514	-110.07729
10	46.46618	-110.07201
11	46.51888	-109.89285
12	46.52661	-109.89333
13	46.52818	-109.91395
14	46.53316	-109.92274
15	46.53334	-109.89279
16	46.55288	-109.89285
17	46.56258	-109.89306
18	46.56279	-109.95605
19	46.59184	-109.95655
20	46.61501	-109.97758
21	46.63176	-109.97757
22	46.64759	-109.97766
23	46.66096	-109.97754
24	46.67890	-109.97737
25	46.67910	-109.91117
26	46.67885	-109.89067
27	46.67133	-109.87207
28	46.66442	-109.86518
29	46.62099	-109.83911
30	46.62097	-109.77496
31	46.61966	-109.76950
32	46.62809	-109.76614
33	46.65017	-109.51240
34	46.65016	-109.49814
35	46.65015	-109.49142
36	46.61286	-109.45195
37	46.60671	-109.45203
38	46.61347	-109.53565
39	46.64763	-109.52934

40	46.60658	-109.61997	
41	46.60662	-109.60806	
42	46.60658	-109.44386	
43	46.60654	-109.43655	
44	46.60654	-109.43082	
45	46.60660	-109.41395	
46	46.60660	-109.40586	
47	46.60669	-109.36837	
48	46.60664	-109.32040	
49	46.60680	-109.30458	
50	46.61783	-109.31550	
51	46.63231	-109.32567	
52	46.63588	-109.31505	fence across road
53	46.64294	-109.32587	
54	46.64998	-109.32602	
55	46.60644	-109.26247	
56	46.56431	-109.26241	
57	46.55555	-109.26235	
58	46.54858	-109.26791	
59	46.54918	-109.28334	
60	46.55755	-109.28333	
61	46.57518	-109.28342	
62	46.60641	-109.28363	
63	46.60664	-109.24155	
64	46.60660	-109.22053	
65	46.60659	-109.21114	
66	46.62338	-109.17834	
67	46.62561	-109.17580	
68	46.63139	-109.16905	
69	46.63550	-109.15769	
70	46.64280	-109.15739	
71	46.63561	-109.14703	
72	46.63562	-109.13628	
73	46.63517	-109.12624	
74	46.63471	-109.11590	
75	46.63486	-109.10516	
76	46.63500	-109.09187	
77	46.62880	-109.11581	
78	46.62022	-109.10533	
79	46.61196	-109.09927	
80	46.60567	-109.09454	
81	46.60559	-109.08385	
82	46.60511	-109.07491	
83	46.59466	-109.07377	
84	46.58724	-109.07378	
85	46.56785	-108.82985	

86	46.69587	-108.87565
87	46.60540	-109.10485
88	46.60510	-109.11410
89	46.60655	-109.16782
90	46.60657	-109.17841

Table A2. List of census stations for the Northeastern Montana Study Area showing the latitude/longitude coordinates and number of mountain plovers observed at each station in 2014.

Latitude/longitude coordinates are in decimal degrees North and West respectively.

1	48.15575	-107.02760
2	48.15440	-107.02740
3	48.13466	-107.02284
4	48.13266	-107.02419
5	48.13889	-107.02692
6	48.12982	-107.02615
7	48.12601	-107.02884
8	48.11735	-107.03214
9	48.11483	-107.03256
10	48.11535	-107.03613
11	48.10678	-107.03414
12	48.10302	-107.03478
13	48.10043	-107.03376
14	48.10013	-107.02390
15	48.11532	-107.03661
16	48.10579	-107.04050
17	48.10529	-107.04828
18	48.10112	-107.04193
19	48.09737	-107.04634
20	48.09306	-107.04366
21	48.08993	-107.04343
22	48.08805	-107.04140
23	48.08783	-107.03280
24	48.08779	-107.02836
25	48.08863	-107.02379
26	48.06009	-107.01414
27	48.05466	-107.01249
28	48.05399	-107.00594
29	48.07309	-107.11197
30	48.07385	-107.11865
31	48.07511	-107.12421
32	48.07529	-107.13184
33	48.07777	-107.14201

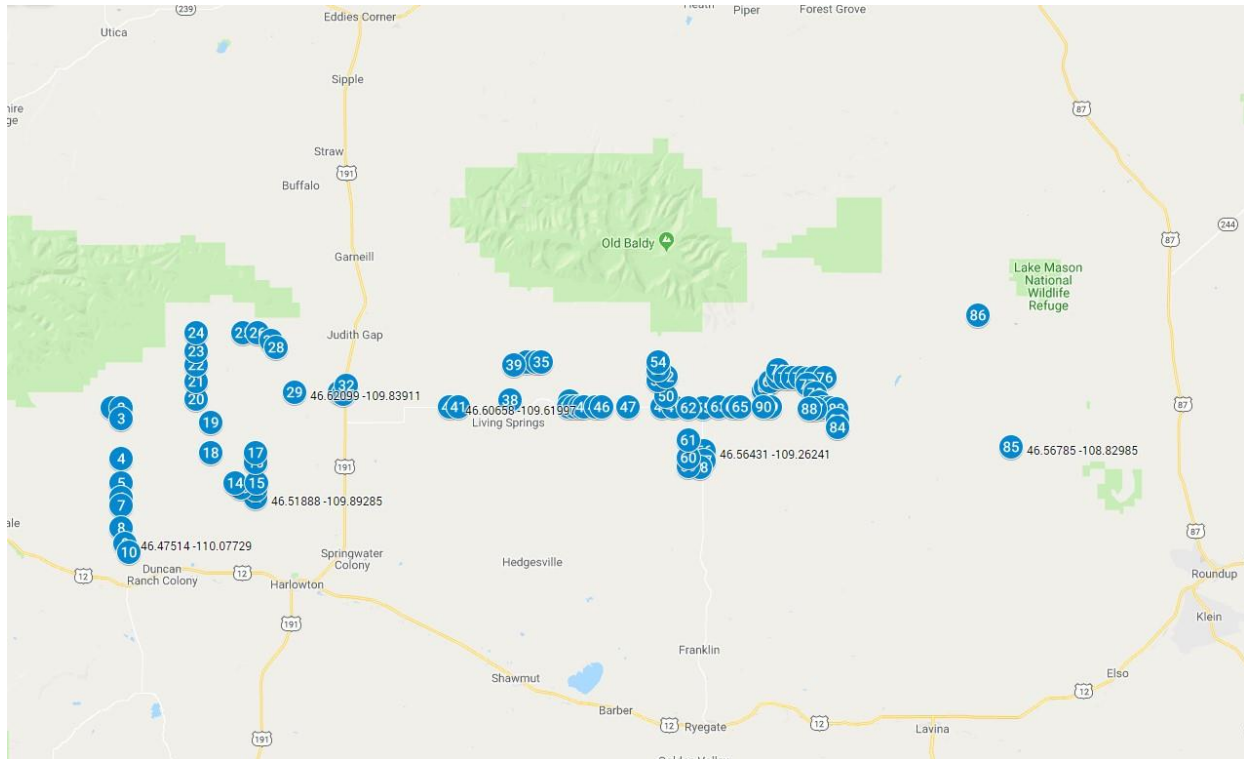
34	48.07799	-107.14642
35	48.08155	-107.15601
36	road washed out	
37	road washed out	
38	48.08615	-107.16241
39	48.09138	-107.17580
40	48.09561	-107.18223
41	48.10162	-107.18877
42	48.10085	-107.19588
43	48.09694	-107.19980
44	48.10851	-107.15733
45	48.11052	-107.14880
46	48.11267	-107.13735
47	48.10622	-107.11801
48	48.10314	-107.08270
49	48.10348	-107.07739
50	48.10389	-107.07132
51	48.10468	-107.05924
52	48.14025	-107.01911
53	48.14863	-107.01536
54	48.15352	-107.00993
55	48.12182	-107.00578
56	48.11659	-107.00550
57	48.11319	-107.00552
58	48.10936	-107.00404
59	48.10670	-107.00240
60	48.09931	-106.99402
61	48.08543	-106.96106
62	48.07757	-106.87993
63	48.05785	-106.90051
64	48.05422	-106.90260
65	48.05147	-106.90413
66	48.02833	-106.87733
67	48.03789	-106.91533
68	48.03460	-106.92613
69	48.02771	-106.93740
70	48.04697	-106.89822

Appendix B

Maps of Permanent Census Stations

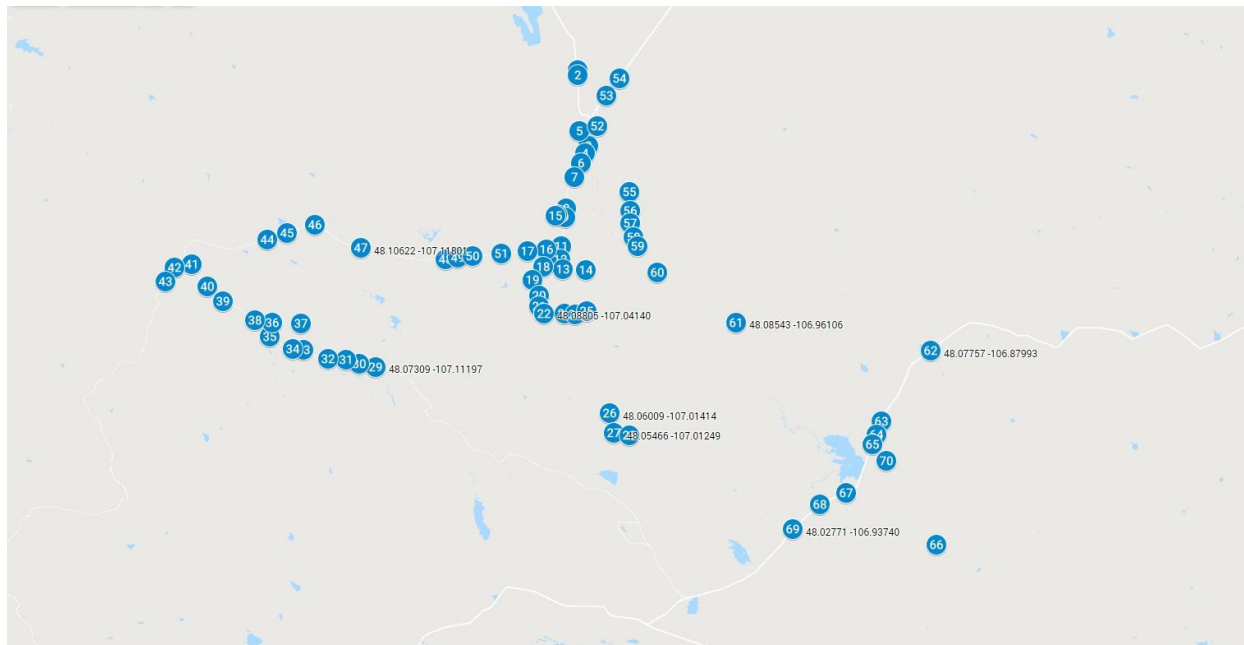
Map of Central Census Stations (with link):

<https://drive.google.com/open?id=1uULmBg919DtRnAZoMErbtsv5-m5BjeCw&usp=sharing>



Map of Northeastern Census Stations (with link):

https://drive.google.com/open?id=1zWq4Y4N_RJNNk5GM87oF05b04XIncYIV&usp=sharing



DRAFT

**AN EVALUATION OF THE IMPACTS OF RECREATIONAL SHOOTING
ON BLACK-TAILED PRAIRIE DOGS**

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Montana Department Fish, Wildlife and Parks
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Abstract: The black tailed prairie dog is a native Montana wildlife species. In Montana, prairie dogs breed in March and April and pups are born in April and early May. Pups emerge from natal burrows from mid-May through early June. Average above ground litter size over a 3 year period in 2 un-shot north-central Montana prairie dog colonies was 3.4 and 1.6 pups. Approximately 40% of the females in north-central Montana bred. Normal summer and yearly prairie dog mortality in colonies protected from shooting was 17-23% and 39-53%, respectively. The mean generation time for prairie dogs protected from shooting in north-central Montana was approximately 2.7 years. In 1 colony, the average female replaced herself with 1.2 female offspring during her lifetime and in another colony the average female produced only 0.3 female offspring in her lifetime. During the late 1980s and 1990s sylvatic plague impacted several major Montana prairie dog colony complexes. During this same period, recreational shooting of prairie dogs increased in popularity. Two published Montana studies have investigated the impacts of shooting on prairie dogs. One study, conducted on the Charles M. Russell National Wildlife Refuge (CMR) from 1978 to 1980, evaluated the use of shooting as a prairie dog control technique, and concluded that it was effective at reducing prairie dogs and preventing the growth of small colonies. The other study evaluated the impacts of recreational shooting on prairie dogs in southern Phillips County. This study documented a 15% average summer mortality rate on un-shot colonies and a 35% average summer mortality rate on shot colonies. Data collected by the conservation agencies in this area found that the average prairie dog shooter spends about 3 days shooting prairie dogs, fires about 150 to 160 rounds of ammunition per day and hits 40 to 60 prairie dogs per day. Using simple calculations based on the number of licensed prairie dog shooters and acres of prairie dogs on the Fort Belknap Reservation, up to 45% of the prairie dog population may be removed by shooting in some years. Neither Montana shooting study determined if shooting mortality is compensatory to natural mortality, and neither study determined if there is an annual surplus of prairie dogs. Colony size growth rates for frequently mapped prairie dog complexes indicate that the concept of sustained annual yield cannot be directly applied to prairie dogs since negative average growth rates were noted in 51 (36%) of 140 years monitored. Recreational shooting has the potential to impact prairie dog associated species both directly (mortality) and indirectly (disturbance and reduced prairie dog density). It is recommended that management objectives for prairie dog complexes be established and then develop management strategies that will achieve those objectives. Depending on the objective, shooting may or may not be an appropriate activity. Montana's prairie dog conservation plan goal is to conserve prairie dogs and associated species.

INTRODUCTION

The black tailed prairie dog is a native Montana wildlife species.

It was originally found in most grassland and shrub/grassland habitats east of the Continental Divide. During the late 1980s and 1990s prairie dog populations in some areas of Montana showed substantial declines. Sylvatic plague was active during this time period and probably was responsible for much of this decline. During this same time period, recreational shooting of prairie dogs increased in popularity as sporting arms technology increased the range and accuracy of small caliber rifles. Although, the impact of recreational shooting on prairie dogs over a broad region has not been investigated, there have been 4 studies (3 in Montana and 1 in North Dakota) that have evaluated specific aspects of shooting on a limited number of prairie dog colonies. In addition, there is prairie dog management data from Fort Belknap Indian Reservation that has tracked prairie dog acreage and numbers of recreational shooters over an extended period, and there is also information from Fort Belknap and Phillips County on the number of shots typically fired by recreational shooters and the number of prairie dogs hit.

A REVIEW OF PRAIRIE DOG POPULATION ECOLOGY

Knowles (1987) reported on prairie dog reproductive ecology in southern Phillips County, Montana. He found that prairie dog breeding occurs during a 4 week interval from early-March to early April, but late winter and early spring weather can influence mean conception dates considerably. Prairie dogs have approximately a 30 day gestation period, and young were born from early April through early May. Pups were observed to emerge from their natal burrow from mid-May to early June when approximately 44 days old. Prairie dogs breed only once per year. The average *in-utero* litter size was 4.4, but ranged from 3.8 to 5.0. Reproduction in yearling females was highly variable with an average of only 43% breeding. About 90% of females older than 1 year bred. Approximately 25-44% of the *in-utero* reproduction failed to survive to emergence of pups above ground (6 weeks of age). Consequently the above ground litter size is considerably less than the *in-utero* litter size, and over a 3 year period in 2 un-shot north-central Montana prairie dog colonies it averaged 3.4 and 1.6 pups per litter. Mean generation time for prairie dogs in these 2 colonies was 2.6-2.8 years. In 1 of these 2 colonies the average female replaced herself with 1.2 female offspring during her lifetime and in the other colony the average female produced only 0.3 female offspring in her lifetime.

A REVIEW OF MONTANA SHOOTING STUDIES

Knowles (1988) conducted a controlled shooting experiment at 2 small prairie dog colonies (2.1 and 14.6 ac) on the Charles M. Russell National Wildlife Refuge well before (1978-1980) plague was documented in this area (1992). The purpose of the experiment was to evaluate the effectiveness shooting as a control technique. The shooting was conducted primarily in spring and early summer using 0.22 caliber rim-fire rifles. The time spent shooting, number of shots fired, and prairie dogs hit were recorded (Table 1). Effects of shooting were documented by measuring prairie dog activity levels (maximum counts) on the 2 shot colonies and 1 colony that was not subjected to shooting. The results clearly demonstrated that shooting reduced prairie dog activity levels when compared to the un-shot colony (Figure 1). By the second year of shooting, nearly all prairie dogs were eliminated in the smallest colony (1 prairie dog remained). Moreover, it was apparent that neither colony could sustain the level of harvest resulting from as little as 1.6 hours of shooting effort per acre of prairie dog colony. An estimated 5.1 to 7.0 prairie dogs per acre were removed from the colonies with 1.6 to 8.3 hours of shooting effort per acre of colony. The peak early summer prairie dog density estimates based on mark-recapture estimates for 3 undisturbed colonies in this same area during the same time period ranged from 5.0 to 10.1 prairie dogs per acre. The removal of 5 to 7 prairie dogs per acre is considered significant. These 2 colonies were located close to a 320-acre colony and immigration of prairie dogs into the smaller colonies from the larger colony was known to influence prairie dog numbers the year after terminating shooting.

Vosburgh and Irby (1998) studied the effects of recreational shooting at 10 prairie dog colonies in southern Phillips County in 1994 and 9 colonies in 1995 and compared the results to 8 colonies protected from shooting on the Charles M. Russell National Wildlife Refuge. Apparently only data from 1995 were suitable for determining changes in prairie dog density from June through August. In 1995, prairie dog population size declined an average of 35% in the 9 shot colonies while density declined an average of 15% in un-shot colonies during the same time period. These differences were considered significant. Shooting appeared to more than doubled the summer mortality as compared to the un-shot colonies. Shooter registration at the study colonies showed that recreational shooting began in May and extended through September suggesting that the actual changes in density due to shooting would be greater than 35% since the prairie dogs in the study colonies were counted in June and August. The peak number of shooters registering at the study colonies during both years of the study occurred during June, but in 1995 a considerable number of shooters registered in July and August as well. Two

colonies received a disproportionate amount of shooting (57% of the registered shooters). The shooting effort expended at the 9 study colonies is presented as an average in Table 1 and would be a minimum estimate since not all shooters registered. Currently this study is the best and only effort to document population changes due recreational shooting. The 35% decline in summer prairie dog density in the shot colonies is considerably higher than the early summer to early fall mortality (17-23%) reported by Knowles (1982) for 2 prairie dog colonies on the CMR protected from shooting (Table 2). The 15% decline in prairie dog density for un-shot colonies on the CMR studied by Vosburgh and Irby (1998) was comparable to the early summer to early fall mortality reported by Knowles (1988) for protected colonies on the CMR 15 years earlier. Year-long prairie dog mortality reported by Knowles (1982) for 2 un-shot colonies over a 2-year period averaged 39% for 1 colony and 53% for another colony (Table 2).

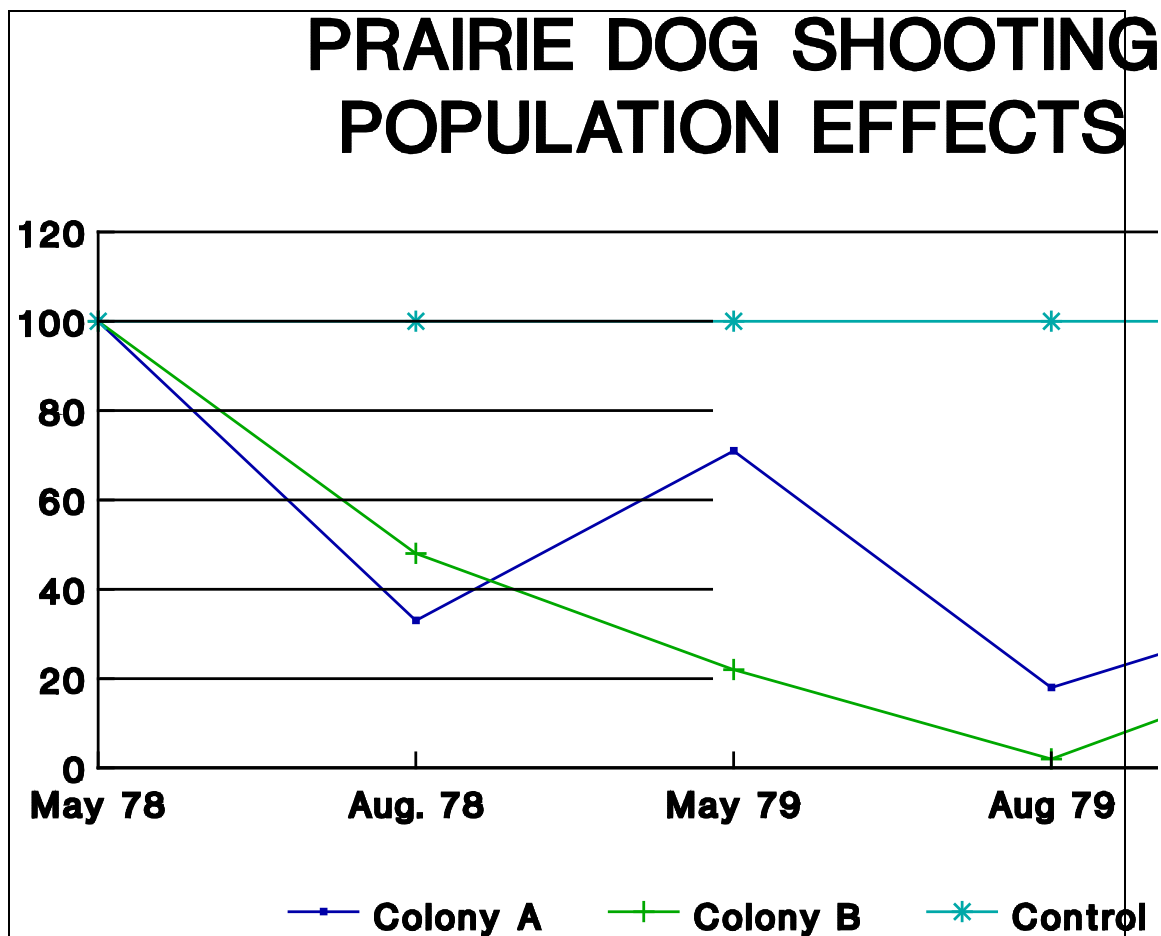


Figure 2. Population impacts of experimental shooting at two Charles M. Russell National Wildlife Refuge prairie dog colonies in 1978 and 1979 relative to an un-shot colony. Colonies were not shot during 1980.

Table 1. Summary of shooting at a 14.6-acre (Colony A) and a 2.1-acre (Colony B) colonies on the Charles M. Russell National Wildlife Refuge during 1978 and 1979. The shooting was conducted with a 0.22 caliber rifle in 1978 and a 0.22 caliber magnum rifle in 1979. Also presented is information from Vosburgh and Irby (1998) and Vosburgh (1999) for comparison purposes.

Colony	Hours	Dogs	Shots/	Dogs/	Shots/	Dogs
Year	shooting	hit	hour	hour	dog	
removed/ac	Shots					
Colony A						

1978	22.8	503	99	22.1	4.3	5.1	6.8
1979	36.4	239	102	6.6	2.8	2.3	7.0
Colony B							
1978	17.5	217	23	12.4	1.3	9.4	6.9
1979	6.1	30	16	4.9	2.6	1.9	5.1
Vosburgh ¹	2.6	70	23	26.9	8.8	3.0	--
	8.5	166	58	19.5	6.8	2.9	1.3
Ft. Belk. ² day ³		150	45	21.4	6.4	3.3	--
Phillips ²	7	160	60	22.3	8.6	2.6	--

1 Data represent averages from Vosburgh and Irby (1998). These are

minimum estimates since not all shooters registered.

2 Data for Fort Belknap and Phillips County are from Vosburgh (1999).

3 A day of shooting is assumed to be 7 hours.

Vosburgh (1999) also compared counts of prairie dogs on 4 shot and 3 un-shot colonies on Fort Belknap Reservation during 1999. The number of prairie dogs counted declined 20% on shot colonies and 10% on un-shot colonies (Vosburgh 1999). In 1999, 250 shooters were licensed at Fort Belknap and 14,230 acres of prairie dog were mapped (estimated 0.37 hours of shooting per acre). In 2000, the number of licensed shooters declined to approximately 100 probably due to a plague outbreak that was detected in 1999, and to a 3 day shooting limit on licensed shooters. This study also showed that guided shooters with the hi-tech guns and ammo who spend all day in the field, shot about 150 rounds per day and hit 40-50 prairie dogs. A similar study conducted by Bureau of Land Management (BLM) and MT Dept. Fish Wildlife and Parks (FWP) indicated that the average shooter hits about 60 prairie dogs per day during 7 hours of shooting. Vosburgh and Irby (1998) reported most shooters spend 2-3 days shooting prairie dogs and kill about 200 prairie dogs during their visit.

Table 2. Estimates of peak prairie dog density (prairie dogs per acre) during summer and percent mortality in 3 un-shot prairie dog colonies on the CMR from 1978 through 1980. Data is from Knowles (1982).

	Density	Yearlong Mortality	Summer Mortality
Large stable colony	10.1	39%	17%
Colony maintained	5.4	53%	23%

through immigration

Small expanding colony	5.0	--	--
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These 2 studies (Vosburgh and Irby 1998 and Vosburgh 1999) indicate that summer population declines are greater on shot colonies than on un-shot colonies with a minimum of 0.2 to 0.4 hours of shooting effort per acre of prairie dog colony. Prairie dog density estimates in these 2 studies were made after prairie dog pups emerged from natal burrows in late May and early June, and did not consider the impact of shooting in spring (March through May) when pregnant females or females with very young pups are particularly vulnerable. Although June through August are the primary months for shooters (Vosburgh and Irby 1998), some recreational shooting does take place during May and September (Vosburgh and Irby 1998).

The data from Vosburgh and Irby (1998) and Vosburgh (1999) shown in Table 1 reflect information gathered from recreational shooters using small caliber high velocity center-fire rifles. The number of shots taken per hour and prairie dogs hit per hour were generally more than what was recorded by Knowles (1988) under controlled conditions. This could be due to the longer effective range of high velocity center-fire cartridges providing an opportunity to shoot at a greater number of prairie dogs with a relatively high probability of hitting a prairie dog versus rim-fire cartridges with a limited effective range.

In the study conducted by Knowles (1988), approximately 1.6 and 2.4 hours of shooting were expended on each acre of the larger prairie dog colony for each year, and 8.3 and 2.9 hours of shooting were expended on each acre of the smaller prairie dog colony for each year. Vosburgh and Irby (1998) recorded 0.2 hours of shooting effort per acre in 1995 based on shooter registration forms left at the 9 survey colonies (this is a minimum estimate). Shooting effort based on hours spent shooting per acre by Knowles was 6 to 41.5 times greater than reported in the Vosburgh and Irby (1998) study. However, the actual removal of prairie dogs on a per acre basis was only 3.9 to 5.4 times greater in the study conducted by Knowles (1988). This difference is probably due to the differences between rim-fire and center-fire rifles described above. The comparison of these studies (Knowles 1988, Vosburgh and Irby 1998, and Vosburgh 1999) illustrates that shooting can impact prairie dog populations and that it is just a matter of the number of hours of shooting effort expended on a colony in relation to the size of the colony that determines the level of the impact.

Knowles (1988) noted that shooting prairie dogs during the spring

(April and May) when females were pregnant or lactating may have a substantially greater population impact than shooting prairie dogs during summer. There is no question that shooting females with dependent young in the burrow results in the starvation death of the pups as well. During the controlled shooting conducted by Knowles (1988), it was apparent that young prairie dogs pups emerged prematurely from their natal burrows following the death of their mother. Prairie dog pups are extremely altricial; they are naked the first week after birth, and their eyes do not open until 40 to 45 days of age. It is only after their eyes open that they emerge from the burrow. During the first week or 2 above ground prairie dog pups are extremely naive and are slow to respond to alarm barks of adults. Prairie dogs breed only once a year (March and April) and it is likely that shooting mortality during spring is additive to natural mortality that occurs from summer through winter. Spring is when prairie dog densities within a colony are at a low point.

The study by Knowles (1988) did not address what the population consequences might be on prairie dog colonies that were shot at by recreational shooters. Unknown factors at this time were the number of shooters, the amount of time spent shooting, the distribution of the shooting effort across the landscape and the persistence of prairie dog shooters at a colony. In such a context, shooters have free movement among colonies and may distribute their shooting effort to colonies that are perceived to provide the most recreation. Vosburgh and Irby (1998) found that 2 colonies accounted for 57% of the total recorded shooting effort during their study. It is not known if shooters will move on to other colonies when a critical threshold population level is reached.

It is believed that in some years there is an annual surplus of prairie dogs that could be removed without negatively impacting an established prairie dog population, but this assumption has not been validated with empirical data. Prairie dog colony expansion (Table 3) and prairie dog dispersal (see Knowles 1985) are both evidence that there is a surplus of prairie dogs in some years. If prairie dog acreages are reflective of a prairie dog population, it is apparent that following termination of poisoning prairie dog populations can expand at 50% or more per year for several years when the initial colony size is very small and there are old burrows available for colonization. However, such colony growth rates are rarely maintained over an extended period (Table 3). Moreover, Table 3 shows that prairie dog colony growth rates are highly variable and that negative growth rates are common. Growth rates for the frequently mapped prairie dog complexes in Table 3 indicate that the concept of sustained annual yield cannot be directly applied to prairie dogs since negative average growth rates were noted in 51 (36%) of 140 years monitored. Knowles (1985) also noted that prairie dog dispersal

was not consistent between years. As a minimum, it can be concluded that a surplus of prairie dogs is not necessarily available every year and that when there is a surplus it is not consistently the same.

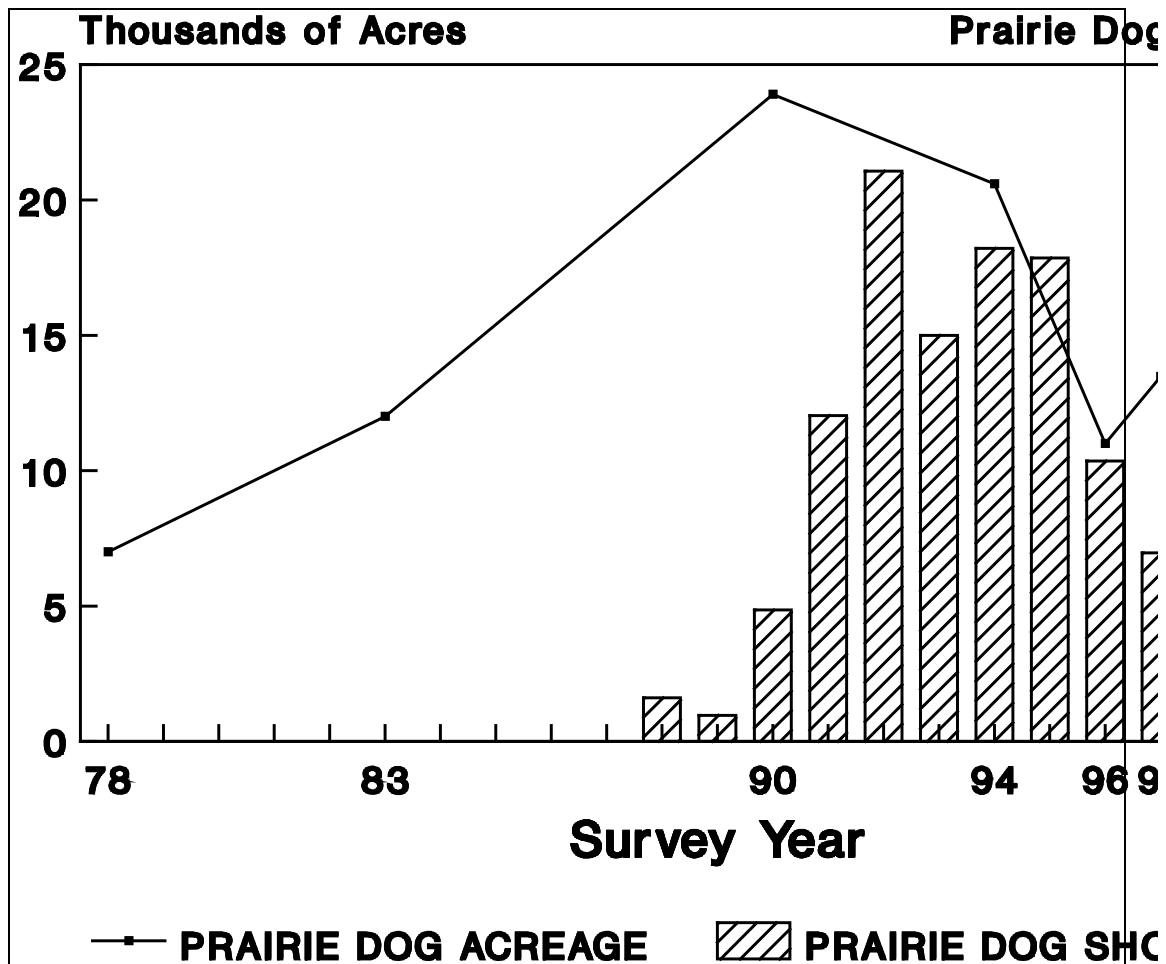


Figure 3. Summary of prairie dog acreage and number of licensed prairie dog shooter on the Fort Belknap Indian Reservation from 1978 to 2000.

Table 3. Annual prairie dog colony growth rates for Theodore Roosevelt National Park in western North Dakota and for 4 areas of Montana.

Area	Annual Rate of Change	Source
Roosevelt NP western ND	1947-53 51% 1953-56 -21% 1956-57 -26% 1957-63 29% 1963-65 1% 1965-73 -7% 1973-77 -1% 1977-82 2% 1982-85 12% 1985-88 -5% 1988-91 20% 1991-92 9% 1992-95 -3% 1995-97 3%	TRNP files
C.M. Russell NWR north-central MT	1964-70 71% 1970-74 15% 1974-79 2% 1979-84 7% 1984-88 5% 1988-94 -5% 1994-95 -20% 1995-97 0%	Knowles 1982 & CMR files
Phillips County north-central MT	1981-84 15% 1984-88 3% 1988-92 -10% 1992-93 -3% 1993-98 1%	Reading et al. 1989 and Stoneberg 1993 John Grensten (pers. comm.)
Northern Cheyenne Reservation, south-central MT	1984-90 12% 1990-94 -23% 1994-95 -36% 1995-97 25% 1997-98 39% 1998-99 63% 1999-00 37%	FaunaWest 1994 Steve Fourstar (pers. comm.)
Fort Belknap Reservation, north-central MT	1978-90 12% 1990-94 -4% 1994-96 -23% 1996-97 22% 1997-98 11% 1998-99 -5% 1999-00 -9%	FaunaWest 1991 BIA Files Tim Vosburgh (pers. comm.)

Fort Belknap has collected information on numbers of licensed prairie dog shooters and prairie dog acreage since 1978. This information is displayed in Figure 2. In 1994, prairie dog acreage was mapped at 20,600 acres and there were 510 licensed shooters. Using simple calculations and assuming 10 prairie dogs per acre (see Table 2), Fort Belknap had a prairie dog population of approximately 206,000 individuals. Using information from Vosburgh and Irby (1998) of the average shooter firing 160 rounds per day and hitting 60 prairie dogs and the average shooter spending 3 days shooting (Vosburgh 1999); then the average shooter would kill 180 prairie dogs. This would equal about 91,800 prairie dogs being shot on the Fort Belknap Reservation or about 45% of the estimated prairie dog population in that year. Although these may be gross estimates of shooter effort and the total prairie dog population on Fort Belknap, these figures illustrate that cumulatively across a broad area recreational shooting does have the potential to influence prairie dog populations. The decline in prairie dog acreage from 1990 to 1996 on the Fort Belknap Reservation (Figure 2) could have been due to shooting (Figure 3). Fleas were collected from several prairie dog colonies across the Reservation in 1996 and none of the fleas tested positive for plague (Knowles 1996). Significant positive plague titers in coyotes collected for plague monitoring purposes on the Reservation were not detected until 1996. Declines in prairie dog acreage on Fort Belknap from 1996 to 1998 and from 1999 to 2000 were likely due in part to a plague epizootic. The reduction of prairie dog shooters shown in Figure 2 was in response to increases in license fees, a 3 day shooting limit imposed in 2000, and a declining prairie dog population. However, prairie dog acreage did increase following a 67% reduction in licensed prairie dog shooters.

Recreational shooting may have other impacts on prairie dogs beside increased mortality rates. Shooting may disrupt prairie dog social behavior, and is certainly selective against prairie dogs that sit on mounds and issue alarm barks. Under natural conditions, alarm barks decrease the risk of predation within a prairie dog colony and it is assumed that barking prairie dogs are more likely to pass on their genes. Stockrahm and Seabloom (1988), working in western North Dakota, studied prairie dog reproductive rates on 2 colonies that received intensive recreational shooting and 2 colonies that did not receive recreational shooting. They found fewer males, smaller litter sizes and very few females breeding as yearlings in the 2 shot colonies when compared to 2 colonies where shooting was not a factor. These authors suggested that shooting disrupted the prairie dog social system. This study did not demonstrate an inverse relationship between prairie dog density and natality

(principle of inversivity). Vosburgh and Irby (1998) reported a higher juvenile to adult female ratio on their shot colonies, but stated they were unable to demonstrate an unambiguous relationship to compensatory reproduction. Vosburgh and Irby (1998) found no significant differences in sex ratio at shot and un-shot colonies during 3 of the 4 sampling periods. However, their last sampling period resulted in a higher male to female ratio on shot colonies as compared to un-shot colonies.

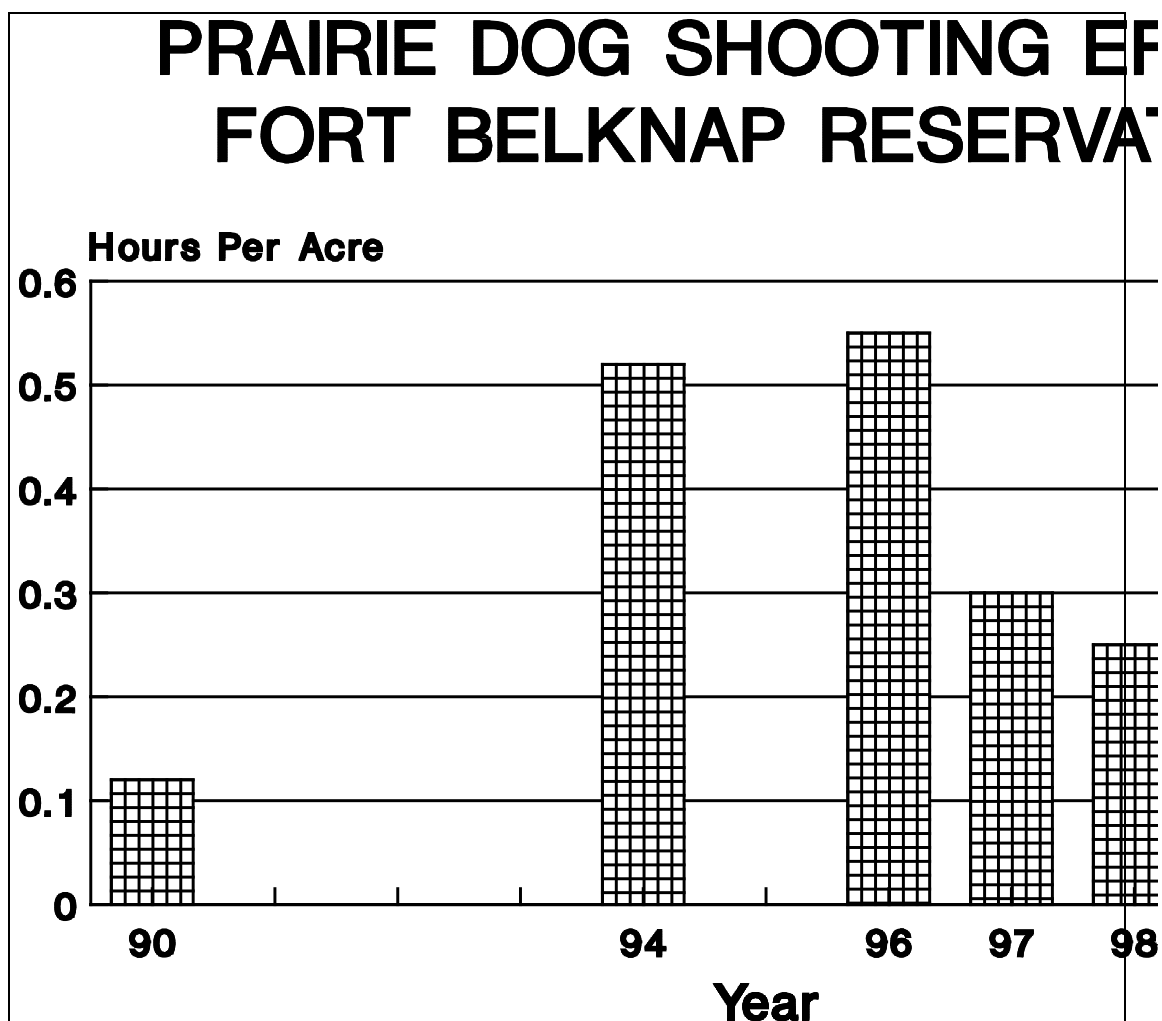


Figure 4. Prairie dog shooting effort (hours/acre) at the Fort Belknap Reservation from 1990 to 2000.

Figures 4 and 5 are presented to compare and contrast prairie dog colony acreage trends for 2 segments of the same prairie dog complex. The BLM portion of the prairie dog complex was subjected to recreational shooting and plague starting in 1992. The CMR

portion of the complex was protected from recreational shooting but was also impacted by plague.

IMPACTS OF RECREATIONAL SHOOTING ON ASSOCIATED SPECIES

Recreational shooting can impact prairie dog associated species through direct mortality and indirectly through disturbance and reduced habitat quality resulting from lower prairie dog density in shot colonies. The incidental take by recreational shooting of protected bird species associated with prairie dogs has been reported. This includes burrowing owls (FaunaWest 1998, John Grensten pers. commun.), mountain plovers (John Grensten pers. commun.), and ferruginous hawks (FaunaWest 1998, John Grensten pers. commun.) being found dead on prairie dog colonies. Other birds observed dead on prairie dog colonies include black-billed magpies and California gulls. Dead badgers have also been observed on prairie dog colonies (FaunaWest 1998). There is also opportunity for ground nesting birds to have nests and un-fledged chicks crushed by off-road vehicle use. The number of nests crushed is directly related to the amount of off-road vehicle use during the nesting period. Mountain plovers would be particularly vulnerable to this activity since their nesting is concentrated on prairie dog colonies. Mountain plover numbers are sufficiently low that any man-caused mortality should be considered significant. The population significance of direct mortality of associated species resulting from recreational prairie dog shooting has not been studied. However, on the Pawnee National Grassland incidental take due to recreational shooting is believed to be a significant local loss of burrowing owls (letter from Jason Woodard to John Sidle, March 2001).

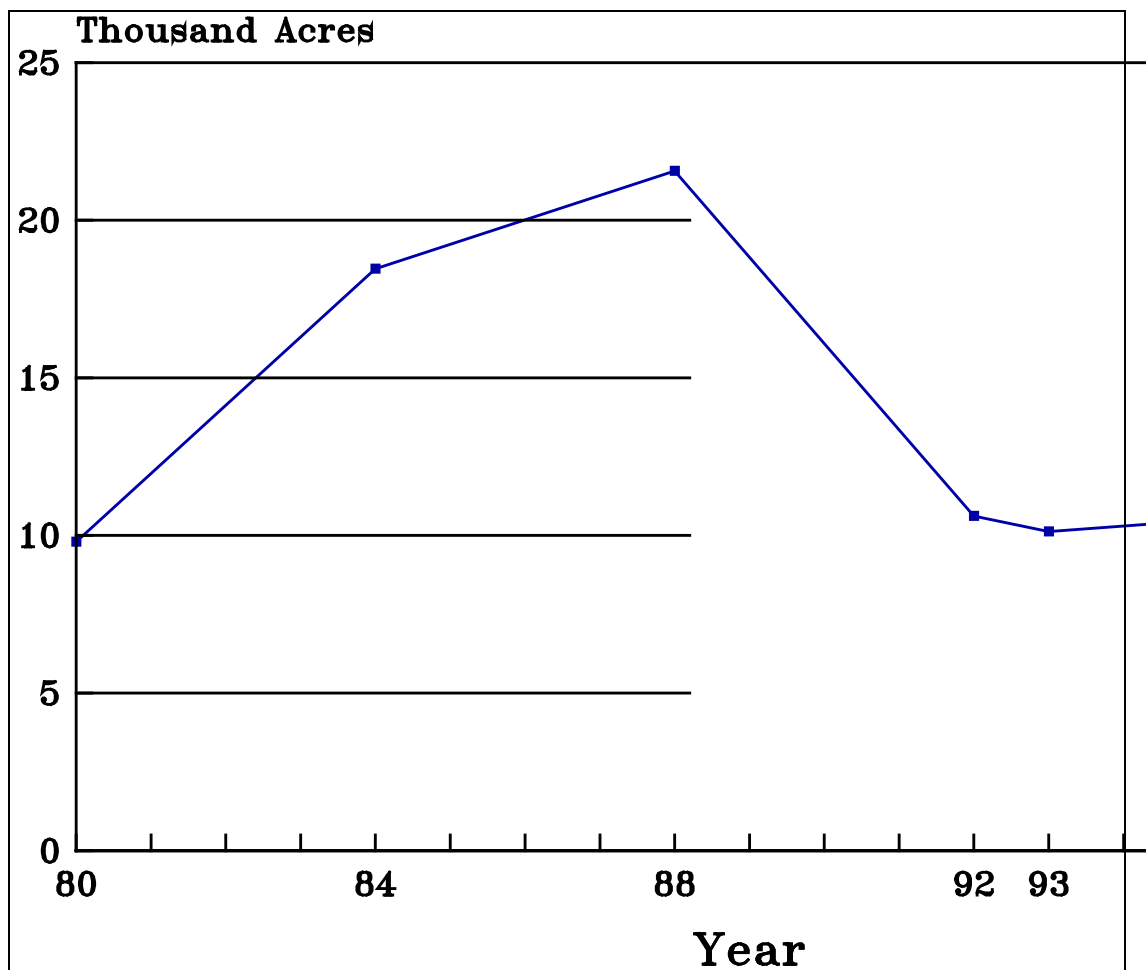


Figure 4. Prairie dog acreage trend in Phillips County, Montana on BLM, state and private lands from 1980 to 1998. Plague was noted in 1992.

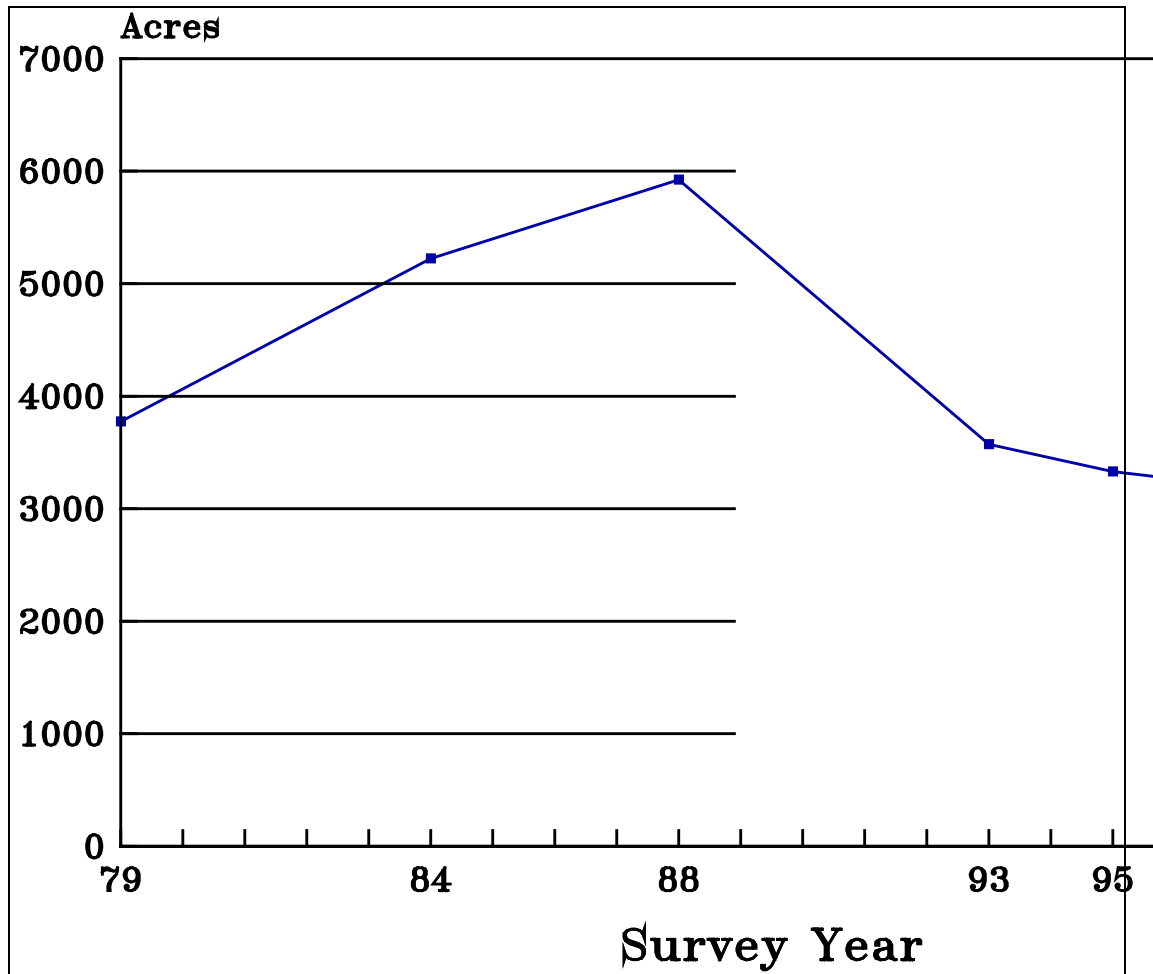


Figure 5. Prairie dog acreage trend for the UL Bend and western portion of the Charles M. Russell National Wildlife Refuge, Montana. Plague was noted in the area in 1992.

Lead poisoning may be another source of mortality for prairie dog associated bird species. Fragments of lead ingested by raptors when scavenging shot prairie dog carcasses have the potential to kill or severely disable raptors. Burrowing owls are reported to scavenge poisoned prairie dogs (Butts 1973) and would also be expected to feed on prairie dogs killed by recreational shooting. Ferruginous hawks and golden eagles are 2 other raptors known to scavenge on dead prairie dogs. Shooting in some areas has been sufficiently intense during the past decade to literally put millions of pieces of lead on the ground. It is unknown if passerine birds are picking up pieces of this toxic heavy metal. Mortalities in morning doves have been noted with ingestion of only 2 lead pellets. Ingestion of lead is a known significant

problem for birds (Lewis and Ledger 1968 and Wiemyer et al. 1988).

The disturbance associated with recreational shooting is also an unknown factor and potentially could cause ground nesting birds to temporarily vacate a nest or abandoned it entirely. Burrowing owl density and nesting success on prairie dog colonies is thought to be directly related to prairie dog density (Desmond and Savidge 1998). Recreational shooting reduces prairie dog density and this may change the qualitative value of prairie dog habitat to associated species.

Mapping of prairie dog colonies throughout Montana from 1996 through 1998, indicated that recreational shooting was widespread (FaunaWest 1998). Vehicle tracks through prairie dog colonies were common, and it was not unusual to encounter shooters in the field. The study by Vosburgh and Irby (1998) demonstrated that June is the month receiving the most shooting activity. June is also the month with the greatest average precipitation in Montana east of the Continental Divide, and off-road vehicle use by prairie dog shooters results in deep ruts when the soil is soft.

REASONS FOR SEASONAL RESTRICTIONS ON THE TAKE OF PRAIRIE DOGS

1) The shooting of lactating female prairie dogs in April through early June results in the starvation death of dependent young. Based on a study by Vosburgh and Irby (1998) 15% of the recreational shooting from May through August occurs in May. Another 39% occurs in June when prairie dog pups are not well acclimated to above ground activity. Shooting mortality during April and May would have high probability of being additive to natural mortality.

2) Shooting efforts with as little as 1.6 hours of shooting per acre of prairie dog colony with rim-fire rifles can negatively impact prairie dog populations, and shooting efforts of 0.2 hours of shooting per acre of prairie dog colony with center-fire rifles can double the normal summer (June through August) mortality.

4) The available information on prairie dog populations suggests that we have a poor understanding of what might be an annual surplus of prairie dogs and that there is not a consistent surplus between years.

5) On a state-wide basis, the amount of recreational shooting is largely unknown. On a regional basis, only Fort Belknap Indian Reservation has tracked the number of shooters through license sales. Based on anecdotal information, recreational shooting is widespread and occurs at significant levels.

6) Frequently mapped prairie dog complexes have not increased under a regime of unrestricted shooting and sylvatic plague (see Figures 2 and 4).

7) A spring through early summer closure of prairie dog shooting on Federal lands would:

- a) defer shooting to a period when prairie dog pups are weaned and have been acclimated to above ground activity.
- b) defer shooting to a period when prairie dog associated bird species have completed most of their nesting activity
- c) defer shooting activity during spring and early summer to private, state, and tribal lands. Only 29% of the Montana prairie dog population is known to occur on Federal lands, and about 20% of the Federal prairie dog acreage is protected on the CMR. Some shooters may pursue their activities in states lacking seasonal restrictions on the take of prairie dogs, and some may choose to not shoot prairie dogs because they are unable to adjust to a seasonal closure.

8) The Fish and Wildlife Service has determined that the black-tailed prairie dog is threatened with extinction, and its listing as a threatened species has been precluded by species with higher listing priorities.

9) Recreational shooting does result in some incidental take of prairie dog associated species. For the mountain plover, burrowing owl, and ferruginous hawk, much of this mortality occurs during the nesting season and may be additive to natural mortality. The ingestion of lead fragments by raptors scavenging prairie dog carcasses is a concern, as well as the long-term accumulation of lead fragments on or near the surface of prairie dog colonies.

10) The main purpose of prairie dogs on Federal lands should be to provide suitable habitat for prairie dog associated species, and not to provide recreation to prairie dog shooters. Montana's 4 main associated species (black-footed ferret, mountain plover, burrowing owl, and ferruginous hawk) are currently near or below long-term viable population levels.

REASONS FOR NO SEASONAL RESTRICTIONS ON THE TAKE OF PRAIRIE DOGS

1) The annual number of prairie dog shooters would likely decline with a seasonal shooting closures. Most prairie dog shooting occurs during the month of June when the weather is cooler, the grass is greener and there are no mosquitoes. Vosburgh and Irby (1998) found that the number of shooters who registered on individual colonies in 1994 and 1995 increased from 10 shooters

in May to 26 shooters in June and then dropped to 16 in July and 14 in August.

2) The Fish and Wildlife Service has determined that shooting is not responsible for significant range-wide declines in prairie dog populations. Their decision was based on comments from experts. Landowners also have noted that shooting is not a major factor that impacts prairie dog populations.

3) Prairie dog populations (acreage) in north central Montana have expanded under unrestricted shooting regimes. Since 1996, BLM colonies in Phillips County that are open to shooting appear to be increasing faster than colonies on the CMR that are closed to shooting.

4) Additional research is needed to determine the seasonal impact of shooting on prairie dog populations. The amount and timing of shooting pressure varies from year to year but studies to date have been short-term (less than 1 year). There is insufficient evidence justifying seasonal closures.

5) Research from South Phillips County during the 1995 shooting season indicated a 20 percent shooting mortality. A similar study on Fort Belknap during summer 1999 and found a 10 percent higher decline of prairie dogs on shot towns compared to un-shot towns. Both studies were conducted during years of relatively high shooting pressure.

6) There have seen no evidence that indicates shooting has negative population impacts on species associated with prairie dogs. Marco Restani radio-marked 30 burrowing owls on Fort Belknap Reservation during 2000 to address the question of shooting mortality. However, technical difficulties interfered with this study. Accidental or intentional shooting of burrowing owls has not been noted at Fort Belknap. A long-term mountain plover study by Steve Dinsmore has not found proof that shooting disrupts mountain plover nesting activity or brood survival.

7) Most pups are weaned before the bulk of shooting takes place. Local businesses rely on June shooting activity as does the Tribal prairie dog shooting program. Heavy shooting pressure in May could have significant impacts on prairie dog populations but it does appear that recreational shooters prefer to wait until the pups have emerged from natal burrows before they take to the field. Studies indicate that very little shooting occurs in May.

8) Landowner support is critical in the development of a state conservation plan for prairie dogs. A large proportion of prairie dogs occur on private land. Landowners support recreational shooting of prairie dogs and are opposed to seasonal restrictions. Any unnecessary restrictions might erode landowner

support in the development of a conservation plan, and in tolerance of prairie dogs on private land.

9) Restricting recreational shooting of prairie dogs during early summer may reduce the wariness that prairie dogs have toward humans. Studies have shown that prairie dogs are more wary of vehicles and humans on foot in shot colonies than in un-shot colonies. Prairie dogs may lose some of this fear during periods of restricted shooting making them more vulnerable to being shot later in the season.

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SELECTIVE USE OF BLACK-TAILED PRAIRIE DOG TOWNS BY MOUNTAIN PLOVERS

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ABSTRACT.—Habitat use by Mountain Plovers (*Charadrius montanus*) was studied in north-central Montana during 1978 and 1979. Mountain Plovers were found to selectively inhabit black-tailed prairie dog (*Cynomys ludovicianus*) towns. Horizontal visibility and bare ground were significantly greater inside prairie dog towns used by plovers than adjacent areas. Total plant cover and grass cover were significantly lower inside prairie dog towns than on adjacent areas. Most towns on the study area were associated with an area that was intensively grazed by cattle. Plovers used only the active towns larger than 3 ha located on level upland sites (n = 16 out of 35).

The ecology and behavior of the Mountain Plover (*Charadrius montanus*) have been studied in southeastern Wyoming and north-eastern Colorado (Laun 1957; Baldwin 1971; Graul 1973a, b, 1974, 1975; Graul and Webster 1976). None of these reports mention Mountain Plovers using prairie dog towns. Cameron (1907) found these plovers to be associated with prairie dog towns in southeastern Montana. Black-tailed prairie dog (*Cynomys ludovicianus*) towns occupy level sites, are intensively grazed by cattle, and have short vegetation. Prairie dog towns represent a distinctive habitat in this region and also are used by Horned Larks (*Eremophila alpestris*), Killdeer (*Charadrius vociferus*), and Burrowing Owls (*Athene cunicularia*). The purpose of our study was to investigate the association of Mountain Plovers with prairie dog towns, and to describe related habitat characteristics.

STUDY AREA AND METHODS

Our study area, comprising 560 sq km on the north side of the Missouri River, was 100 km southwest of Malta in Phillips County, Montana on the Charles M. Russell National Wildlife Refuge (CMR; Fig. 1). It is within the timbered breaks of the river and is characterized by alternating deep-cut coulees and steep-sided ridges. Major ridgetops are broad and flat, becoming progressively wider with increasing distance from the river. Ponderosa pine (*Pinus ponderosa*) and Rocky Mountain juniper (*Juniperus scopulorum*) dominate slopes with northerly exposures. The dominant plant species on the level ridgetops are western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloua gracillis*), prickly pear (*Opuntia polyacantha*), fringed sagewort (*Arte-*

misia frigida), and big sagebrush *A. tridentata*). Knowles (1975) described fully the vegetation of this area. The mean annual precipitation and temperature are 35 cm and 6.6°C.

To obtain distributional data on Mountain Plovers, we established a system of 18 vehicular transects throughout the study area (Fig. 1). Nine of the transects, totalling 19.2 km, were in prairie dog towns, and nine others, totalling 18.5 km, were outside of towns. The route was run 10 times, generally in the morning, at approximately one-week intervals from 1 June to 8 August 1979 using a three-wheeled "all-terrain" motorcycle. Cruising speed along the transects was 15 km/h; we stopped only to record observations of Mountain Plovers visible from the vehicle. A chi-square test of homogeneity was used to test the hypothesis that numbers of plovers within and outside of towns were homogeneous.

Horizontal visibility within and adjacent to six prairie dog towns used by Mountain Plovers was measured with a coverboard 2 m high, 1 dm wide and divided in 1 dm intervals. One transect was placed inside and one adjacent to each of the six towns. Each visibility transect consisted of two parallel, 150-m lines spaced 60 m apart. Six stakes were placed along each line at 30-m intervals. Coverboard sightings were taken from each stake along one line perpendicular to the corresponding stake on the opposite line, and diagonally to the closest stake left and/or right of the corresponding stake (stake 1, line A to stake 2, line B, etc). This scheme allowed 16 measurements per transect. Eye level for the sightings was at 1 m and visibility was estimated to the nearest 5%. A Mann-Whitney U-test was used to test

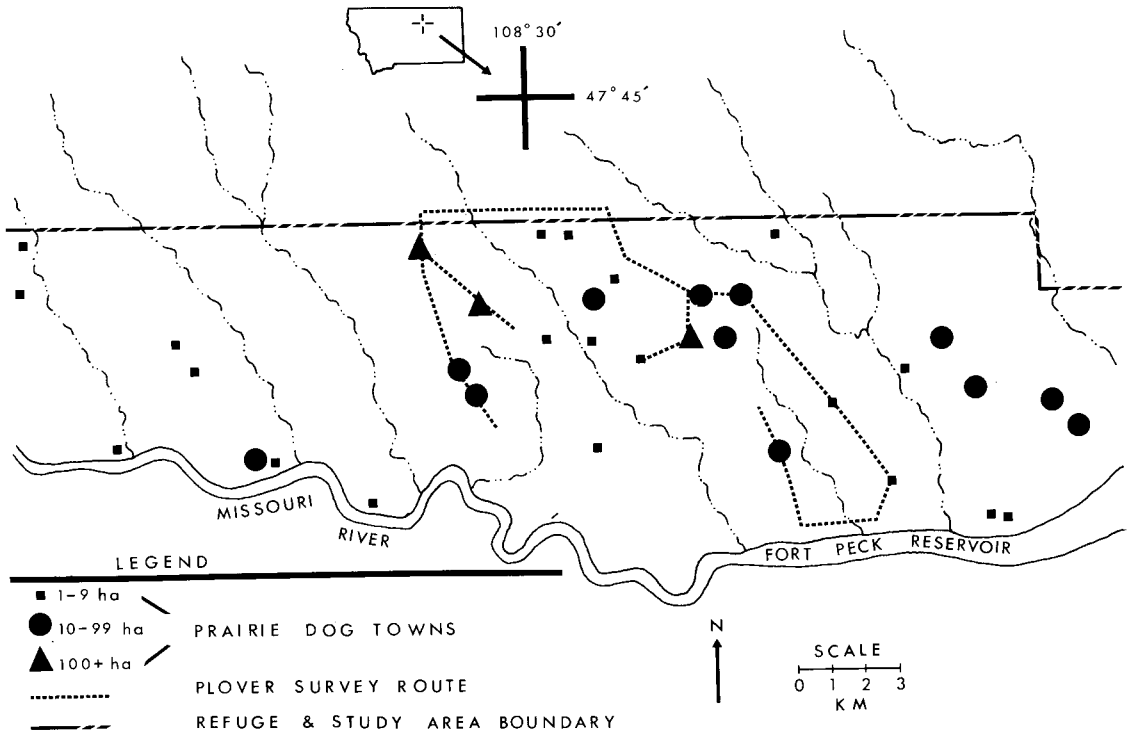


FIGURE 1. Map of study area showing Mountain Plover census route and prairie dog towns.

the hypothesis that the median visibility value within prairie dog towns was equal to that outside of prairie dog towns. Similar visibility transects were also established at four towns in bottomland sites not used by plovers. At each stake along all of these visibility transects, slope was measured with a slope meter similar to that described by Koepl (1979).

Amount of bare ground and canopy coverage (Daubenmire 1959) of litter, total plant cover, grasses, forbs, and shrubs were determined inside and adjacent to five prairie dog towns used by Mountain Plovers. One transect was placed inside and one adjacent to each of the towns. Each transect consisted of five parallel 30-m lines spaced 15 m apart. Ten 2×5 dm plots were sampled at 3-m intervals along each line. A Mann-Whitney *U*-test was used to test the hypothesis that median cover values inside prairie dog towns were equal to median cover values in adjacent areas.

RESULTS

We recorded 91 Mountain Plovers during the 10 survey runs; 90 of these were in prairie dog towns. Association with prairie dog towns was highly significant ($P < 0.005$). The plover seen outside of a town during the surveys, plus two seen outside of towns during May, were single birds within 0.5 km of a town on level, sparsely

vegetated sites with considerable amounts of bare ground. During July and August 1979, we recorded sightings of plovers in conjunction with other work in the study area, and all 71 birds seen were in prairie dog towns. We found three nests of plovers in towns during May; broods were frequently observed in towns during June and July. We also found that plovers could not be readily chased out of towns. When pursued on foot they would run in front of us up to the boundary of the town and then fly a circuitous route back into the town. Plovers also roosted in towns at night. In 1979, Mountain Plovers were in prairie dog towns from 3 April to 21 August.

Horizontal visibility within prairie dog towns used by Mountain Plovers was significantly ($P < 0.001$) greater than visibility adjacent to these towns (Fig. 2). The amount of bare ground and coverage of forbs was greater in towns than adjacent areas but the difference was significant ($P < 0.05$) only for bare ground. Coverage of litter, total plant cover, and grass were less in towns as compared to adjacent areas; only the latter two were significant ($P < 0.05$ and $P < 0.025$, respectively). Shrubs accounted for less than 1% coverage at all sites except one, where big sagebrush covered 28% of the ground adjacent to a town. All slopes recorded along the visibility transects inside

of towns were less than 12%. In general, prairie dog towns and the surrounding areas were very level; this was especially true of towns located on upland sites. In several of the towns used by plovers, small areas had slopes of 12%–25%; occasionally plovers were seen on these slopes.

Thirty of the 35 prairie dog town sites that occurred on the study area were active in 1979. Plovers were seen at 16 of the active towns and at none of the inactive towns. Half of the active towns were larger than 10 ha, while 81% of the towns used by plovers were larger than 10 ha ($\chi^2 = 6.25$, $P < 0.025$). The smallest town in which a plover was found was 3 ha. We did not find Mountain Plovers in any of the six town sites that were located on the bottomlands of the Missouri River and its tributary coulees. Towns in the bottomland sites were smaller ($\bar{x}$, 4.8 vs. 29.3 ha) and had lower visibility values ($\bar{x}$, 78 vs. 96%) than those on upland sites. Most (83%) of the towns on this study area were associated with intensive grazing by cattle or with some other physical disturbance. Fourteen of the 16 prairie dog towns used by plovers were located next to stock ponds. The other two towns were more than 1 km from a stock pond, but cattle were frequently seen loafing and feeding in one of the towns. All towns used by plovers were grazed by cattle, while stock pond sites without prairie dogs were not used by plovers. Many of the towns were closely associated with one or more other towns, and during late August 1978 two small flocks of plovers were seen flying between closely associated towns. Also, during August 1979, plovers used a town that they had not used earlier in the year. Thus, at least during August, there was some interchange of plovers between towns.

Larger prairie dog towns usually contained more than one pair of plovers. An intensive search in May 1979 of a 100-ha town revealed at least 13 adult plovers. We considered the density of Mountain Plovers in this prairie dog town to be representative of that which we encountered in other large towns.

DISCUSSION

The data from the census routes and our general observations both show that Mountain Plovers selectively inhabit prairie dog towns on the CMR. These towns furnished the necessary habitat for plovers from their arrival in April until their departure in August; breeding, rearing of young, feeding, and roosting all appear to take place in prairie dog towns. Plovers may be responding to differences in vegetative cover, plant species composition, topography, and/or food availability in selection of towns over areas not occupied by prairie dogs.

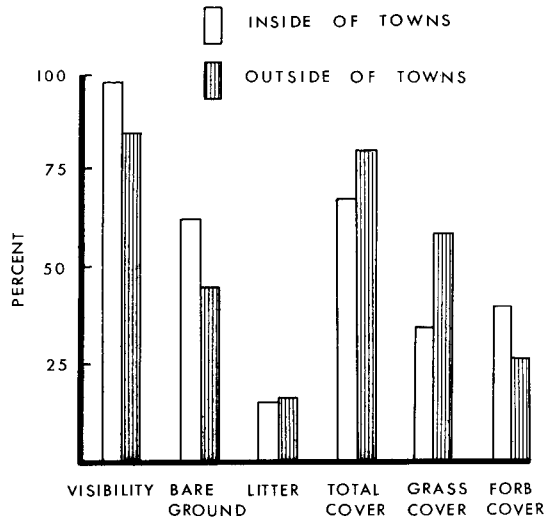


FIGURE 2. Horizontal visibility, bare ground, and canopy coverage of litter, total plant cover, grass cover and forb cover inside of and adjacent to prairie dog towns used by Mountain Plovers.

Mountain Plovers were associated with the larger prairie dog towns in upland areas. Towns less than 10 ha were marginal sites for plovers to raise young successfully as no young were sighted in the three towns used in this category. Although most towns used by plovers were next to stock ponds, the presence of plovers at two towns without water suggests that they can survive without a source of free water. Others (Bradbury 1918, Laun 1957) have reported that Mountain Plovers nest in areas remote from free water.

Towns used by plovers were very level with slopes rarely exceeding 12% (see also Gaul 1975). Mountain Plovers in Colorado occur with greatest densities in areas with short grass, level topography, and intensive livestock grazing (Graul and Webster 1976). The towns on our study area offered an excellent combination of these three factors.

Our study provides evidence that Mountain Plovers live commensally with herbivorous mammals. Plovers were always found in intensively grazed areas. Here, near the northern limits of the present range of Mountain Plovers (Graul and Webster 1976), the combined effects of prairie dogs and cattle on the vegetation are apparently needed to provide suitable nesting conditions for the birds. Plovers were not found in areas of intensive grazing without prairie dogs, and prairie dogs were dependent on cattle for conditions to successfully establish a town. The plovers cope with approaching grazing ungulates by flying at their faces in order to divert them from nesting areas (Walker 1955, Gaul 1975).

Graul and Webster (1976) found the density of nesting Mountain Plovers in Colorado to range from 4 to 32 birds per sq km with about 20 birds per sq km being most representative. The density (13 plovers per sq km) that we found in one of the larger towns on the study area is lower than what Graul and Webster (1976) considered average for northeastern Colorado. Prairie dog towns occupied only 1.6% of our study area, and overall densities probably did not exceed 0.2 birds per sq km.

Skaar (1980) listed Mountain Plovers as breeding in five areas in Montana, and he listed another eight areas as showing "circumstantial evidence for breeding." However, a recent state-wide survey of non-game mammals and birds found plovers breeding only in Phillips County (Flath, pers. comm.), which includes two of the breeding areas listed by Skaar (1980). Bureau of Land Management records show that plovers are found in prairie dog towns throughout the south half of Phillips County (Shryer, pers. comm.). These records also include a sighting of two plovers in a town immediately south of our study area. Dood (1980) noted a plover in a prairie dog town in Custer County, Montana in August 1979 but considered it to be a migrant. In Montana, breeding populations of Mountain Plovers now appear to be confined to prairie dog towns in the north-central part of the state. The decline of Mountain Plovers in Montana may be related to the near-extermination of prairie dogs earlier in the century (Koford 1958).

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BLACK-TAILED PRAIRIE DOG ABUNDANCE AND DISTRIBUTION IN THE GREAT PLAINS BASED ON HISTORIC AND CONTEMPORARY INFORMATION

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ABSTRACT Recorded presettlement observations of black-tailed prairie dogs (*Cynomys ludovicianus*) are not adequate to fully determine their abundance and distribution. Early naturalists and explorers only made casual reports of prairie dogs on an opportunistic basis; their written records do not represent systematic surveys. Cumulative accounts of prairie dog control efforts, together with the known current prairie dog distribution in North Dakota and Montana, clearly show that most journalists failed to record prairie dog colonies, and that they restricted their travels to a few common routes resulting in only a very small and select portion of the landscape being surveyed. The hypothesis that prairie dogs dramatically increased in abundance following settlement is highly speculative. It ignores the fact that the Great Plains were once populated by large numbers of native ungulates, and that prairie dog control efforts began as early as the 1880s. Many lines of evidence suggest that the black-tailed prairie dog was common prior to European-American settlement, and occupied 2-15% of large landscapes (400,000 ha or more). This evidence includes systematic accounts of prairie dogs at the time of settlement, government records concerning poisoning efforts, physical evidence of abandoned historic colonies, and contemporary information on prairie dog ecology, dispersal, distribution and abundance as well as presettlement accounts of large colonies measured in miles. The association of the black-footed ferret (*Mustela nigripes*), an obligate predator, and a commensal bird species (e.g. mountain plover (*Charadrius montanus*) and burrowing owl (*Athene cunicularia*) with prairie dogs (*Cynomys* spp.) is considered additional evidence that prairie dogs were abundant and widespread for an extended period. The presence of black-tailed prairie dogs throughout the short- and mixed-grass regions of the Great Plains from southern Canada to northern Mexico provided an import and unique habitat to a variety of wildlife species.

INTRODUCTION

The ecological importance of the black-tailed prairie dog (*Cynomys ludovicianus*) was

not fully appreciated until the latter half of the 20th century well after implementation of massive government eradication efforts. Early pleas to conserve small areas of prairie dogs for black-footed ferrets were largely ignored (Murie 1937) and reveals that even professional wildlife biologists did not understand the importance of expansive, closely spaced prairie dog colonies to assure viable populations of associated species. In contrast to the need of large closely spaced colonies for associated species viability, prairie dogs were and still are commonly viewed by farmers and ranchers as destroyers of the range and competitors of domestic livestock for limited forage resources, and as such should be eradicated or severely controlled. This negative view of prairie dogs by the private landowners resulted in a pattern on the landscape of small widely spaced colonies interspersed by areas of local extirpation. This pattern developed in the early 1900s under government sponsored poisoning campaigns and has been maintained by periodic bouts of poisoning. The intense dislike of prairie dogs by private landowners is mirrored in state laws designating prairie dogs as a pest species, and has fostered a situation where state and Federal conservation agencies aided and abetted prairie dog control. State wildlife management agencies, for the most part, abdicated any management authority of prairie dogs to the behest of private landowners.

Due to continuing population declines resulting from sylvatic plague, poisoning, habitat loss and shooting, the black-tailed prairie dog was petitioned for listing as a threatened species under the Endangered Species Act in July 1998. In February 2000, the U.S. Fish and Wildlife Service ruled that the prairie dog warranted listing, but that listing was precluded by a backlog of other species with higher listing priorities. The Fish and Wildlife Service evaluated the petition based on the five listing criteria as required by law. These were: 1) present or threatened destruction, modification, or curtailment of habitat, 2) over-utilization for commercial, recreational, scientific or educational purposes, 3) disease or predation, 4) the inadequacy of existing regulatory mechanisms, and 5) other natural or man-made factors affecting its continued existence (Federal Register 1980). Presettlement abundance and distribution of prairie dogs was not a factor in the listing process. The Fish and Wildlife Service determined that 1) a significant portion of prairie dog habitat had been permanently lost to agricultural conversion of grasslands, 2) recreational shooting of prairie dogs is an unregulated and a common practice, 3) sylvatic plague has impacted prairie dog numbers over a significant portion of its range, 4) state laws classify prairie dogs as a pest species and promote prairie dog control, and 5) prairie dog poisoning remains a common management practice. The Fish and Wildlife Service noted that the black-tailed prairie dog is a colonial species, and that many remaining colonies through out much of the range are small and isolated. Consequently, eradication of colonies through control efforts, plague, habitat loss and other impacts may over time sequentially lead to local

extirpations and range contractions. Since prairie dogs are a highly colonial species, the reduction in size and number of colonies represents a reduction in distribution even though geographic range distribution has not decreased proportionately to the reduction in numbers. Although the black-tailed prairie dog still occurs over a vast region and numbers in the millions, its colonial characteristics make it vulnerable to impacts identified in the five listing criteria.

Virchow and Hyngstrom (2002) challenged the Fish and Wildlife Service decision that the black-tailed prairie dog warrants listing, and suggested that presettlement distribution and abundance of the black-tailed prairie dog was not carefully considered. In their analysis, they contend that little evidence exists to suggest black-tailed prairie dogs were historically "superabundant" in the Great Plains. Although presettlement abundance and distribution is not part of the listing criteria, past and present prairie dog distribution and abundance is an important issue that needs to be addressed. Evidence suggests that the black-tailed prairie dog was once significantly more common in the Great Plains than they are today. We define common as occupying 2-15% or more of large landscapes (400,000 ha). This would represent local populations of 200,000 to 1,000,000+ individual prairie dogs. In this paper, we examine historical and biological literature regarding prairie dog distribution and abundance. In particular, we focus on evidence from the northern Great Plains, where domestic livestock were not introduced until the late 19th century and initiation of widespread homesteading did not occur until the early 20th century (Howard 1959). We conclude that black-tailed prairie dogs were very common and widespread in this area and that within this region prairie dogs have been greatly reduced from their original abundance as evidenced by: 1) habitats prairie dogs currently occupy and the availability of these habitats; 2) the number, distribution and size of extant prairie dog colonies; 3) the ability of prairie dog colonies to expand into suitable habitats; 4) the dispersal abilities of prairie dogs; 5) visible remains of old abandoned prairie dog colonies; 6) historic accounts of prairie dogs at the time of settlement; and 7) records of early government efforts to eradicate prairie dogs.

METHODS

We reviewed many of the 19th century natural history notes for Montana and the western Dakotas (Knowles and Knowles 1993). This review consisted of determining the routes taken by early explorers and naturalists, and determining the quantity and quality of natural history notes recorded. Whenever possible, copies of the original journals were obtained through inter-library loan, and the journals were read.

We have recently mapped prairie dog colonies in Montana (Fauna West 1998), and North Dakota (Knowles 2002). These mapping efforts included a systematic ground survey in Montana, and aerial and ground surveys in North Dakota. In Montana, a 1:150,000 scale map of prairie dog colony locations developed by Campbell (1989) was used as the basis for the mapping effort. However, if Federal land management agencies had current mapping information available, these data were used where ever available. For the North Dakota mapping effort, we assimilated all agency records of prairie dog colonies since 1980 and flew to each of the sites. Active colonies were then mapped during ground surveys. Standing Rock and Fort Berthold Reservations were not included in the ground surveys. Theodore Roosevelt National Park had current prairie dog mapping data and was not included in the survey. During the ground survey, presence of abandoned prairie dog colonies were plotted as points on 1:200,000 scale maps.

For the Fort Belknap Indian Reservation in north-central Montana, a copy of a map compiled in 1921 depicting areas where black-tailed prairie dogs and Richardson's ground squirrels (*Spermophilus richardsoni*) were poisoned on the Reservation was obtained from the National Archives in Washington, D.C. We digitized this map and then compared it to a 1999 map of prairie dog colony size and location on the Reservation. There was no information on the map to indicate if all colonies on the Reservation were poisoned, but we believe that the 1921 map accurately portrays those areas that were poisoned. It is possible that other colonies (especially smaller colonies) existed on the Reservation that were not poisoned.

Also for eastern Montana, we created a model to predict suitable black-tailed prairie dog habitat within this area (Proctor 1998). By combining existing vegetation, slope, and soil data with a Geographic Information System, we created maps outlining varying degrees of prairie dog habitat suitability for large areas. Initially, the model was developed for Phillips and Blaine Counties in north-central Montana and later expanded to the entire Montana prairie dog range distribution in eastern Montana. Prairie dog presence was found to correlate well with vegetation and slope. Soil texture correlated only minimally, and soil depth did not appear to be a significant factor. When the model was extrapolated to a much larger area of Montana, 94.5 percent of prairie dog colony locations fell within the higher potential habitat categories (Proctor 1998, maps on file with Montana Fish Wildlife and Parks, Helena).

RESULTS

PRESETTLEMENT ACCOUNTS

An uncritical analysis of the historical record can lead to inaccurate estimates and conclusions that prairie dogs did not become prevalent until the early 20th century because they were not repeatedly mentioned by early naturalists. For example, Koford (1958) claimed that prairie dogs had increased in abundance following settlement of the Great Plains because the journals of Lewis and Clark and others who crossed the region make few references to prairie dogs where they were considered abundant early in the 20th century. It is clear, however, that Lewis and Clark, and other early explorers did not include every possible encounter with prairie dogs in their journals. Their failure to mention prairie dogs does not mean that prairie dogs were not present. The majority of early explorers and naturalists had little interest in prairie dogs and generally filled their journal pages with accounts of hardships of travel through wilderness areas, encounters with Indians, forage conditions for horses, observations of bison (*Bison bison*) and other large mammals, and the number of animals shot.

A careful review of the Lewis and Clark expedition (Burroughs 1961), which recorded some of the best information on prairie dogs during the 19th century, shows how much went unreported concerning prairie dogs. For example, Lewis and Clark made journal entries on 7, 11, 16, and 17 September 1804 when they first encountered prairie dogs in southeastern South Dakota. They reported that there were prairie dog colonies along the White River and the Missouri River. Their next prairie dog journal entry came on 23 May 1805 near the Mussellshell River in Montana where Lewis noted a large colony along the river and noted that prairie dog colonies were located on south and southeast exposures, implying that other colonies were seen in similar circumstances. Lewis also noted that they had found colonies 8 to 9.6 km from water, implying again that there were observations of unreported colonies since all journal records were of colonies next to rivers. Two weeks later on 5 June Lewis reported passing for 11-km along the skirts of a large prairie dog colony near the Marias River and stated that it was the largest yet seen. The next journal entry is on 2 August near Whitehall, Montana when Clark reported passing prairie dog colonies. Lewis provided a general description of prairie dogs on their return trip on 1 July 1806 while in the mountains of western Montana outside of the range distribution of prairie dogs. He stated that colonies were several hundred acres in size, but gave no indication of the frequency that colonies were encountered. Also, this statement ignored large colonies reported on 17 September 1804 and 5 June 1805 that were clearly larger than several hundred acres. The next reference to prairie dogs came on 30 and 31 August when near the Niobrara River. From these accounts, it is clear that Lewis and Clark made only intermittent notations of prairie dog occurrence.

Based on observations of several other early naturalists as well as contemporary information, we know that many of the terraces of the Missouri River from the Niobrara River in Nebraska to Holter Dam in western Montana were suitable prairie dog habitat and likely occupied at the time that Lewis and Clark traversed the area. For example, Maximilian reported on a prairie dog colony on an island in the Missouri River in South Dakota, and when in North Dakota he stated that in this neighborhood are many villages of the prairie dog (Twaites 1966). He also reported prairie dog colonies at Beauchamp Creek (same general area of the 23 May 1805 note by Lewis) and Cow Creek in Montana. Cooper (1868 and 1869) reported seeing prairie dog colonies along the Missouri River from Fort Benton to the Dearborn River in Montana. Bailey (1926) reported on a series of prairie dog colonies along the Missouri River in North Dakota from Fort Yates to the Yellowstone River.

Also, our recent mapping of prairie dog colonies in Montana (FaunaWest 1998) recorded a series of 18 prairie dog colonies on terraces of the Missouri River along the Wild and Scenic River portion which is still relatively pristine, and seven active and inactive colonies on the Charles M. Russell National Wildlife Refuge located along the River above Fort Peck Reservoir. These observations document the habitat availability to prairie dogs along a river segment where early explorers recorded only one prairie dog colony. During Clark's descent of the Yellowstone River he failed to even mention prairie dogs when in fact terraces of this River were latter described by Stuart (1902) in 1863 as having many prairie dog colonies. Five prairie dog colonies still remain along the River segment (Shields River to the Bighorn River) that Stuart covered (FaunaWest 1998). Given this information, it is apparent that the Lewis and Clark did not comprehensively report all prairie dog colonies along the Missouri and Yellowstone Rivers.

Also, early explorers and naturalists had limited transportation options and so frequently restricted their travels to the same well established trails usually along rivers. These transportation corridors were selected for the ease of travel, and safety. Expeditions following the Missouri River through North Dakota and Montana (e.g. Lewis and Clark, Maximilian) never had the opportunity to observe optimal prairie dog habitat in the upland prairie because they traveled close to the river. Therefore, their descriptions cannot be used to extrapolate to upland areas in Montana and North Dakota where the topography has permitted the development of large complexes of prairie dog colonies. Some observers who did traverse the upland prairie found prairie dogs to be "quite abundant on the plains" (Grinnell 1876), and described them as the characteristic mammal of the prairies (Coues 1878) or stated that they were innumerable (Mead 1899).

INFLUENCE OF EARLY SETTLEMENT

Determination of the date at which major influences by settlers occurred is important. Virchow and Hyngstrom (2002) use 1860 as the start of the settlement period and so assumed that any report of prairie dogs after this period has been influenced by settlement. Although they noted that settlement across the Great Plains was not uniform, they failed to take this into consideration. For example, although Spanish occupation of the southwest and introduction of their domestic livestock that could have led to overgrazing likely dates back to the 1700s (Oakes 2000), cattle did not come to central Montana until 1880 (Howard 1959). Virchow and Hyngstrom (2002) two early accounts of prairie dogs in Montana and South Dakota (1871 (Messiter 1890) and 1859, Hayden (1863) respectively) into the postsettlement period, yet in fact settlement of these areas had not yet occurred. Interestingly, both Messiter and Hayden reported large prairie dog colonies in these areas. Coues (1878) observations of prairie dogs north of the Milk River in Montana in 1874 also preceded settlement there. In addition, Messiter returned to central Montana in 1882 and reported that cattle and cowboys made a poor substitute for bison and Indians indicating that during his first trip to Montana (1871-1872) settlement was not significant. Also, in western South Dakota, the Sioux tribes successfully stalled European settlement until the Custer expedition of 1874 into the Black Hills.

Nor did the introduction of cattle on the prairies in eastern Montana and western North Dakota bring about an immediate change in the intensity of land use. Early settlement in central and eastern Montana were large ranching efforts (Howard 1957), which often followed immediately on the heels of bison extermination, and in this case cattle were substituted for bison (Messiter 1890). It is difficult to develop a case for increased levels of grazing during the early settlement period when there were many accounts of large bison herds, and situations where bison had so severely grazed the landscape that horses were in poor condition due to lack of feed (Hazlitt 1934, Burroughs 1961, Reynolds 1868, Audubon 1897, Hafen and Hafen 1961). In Montana, large-scale homesteading did not begin until 1909 (Howard 1959), and stock water did not become widely available in the upland prairies until the 1930s. Thus, in the northern Great Plains it is unlikely that the transition to cattle provided an environmental release for prairie dogs.

Virchow and Hyngstrom (2002) also suggested that estimates of abundant prairie dog populations resulted from increased geographic range distribution and numbers following settlement of the Great Plains, and from a few grossly exaggerated reports of prairie dog abundance made to justify rodent control efforts. Prairie dogs associate with intensively grazed

areas (Koford 1958, Knowles 1986, Licht and Sanchez 1993) and, frequently, prairie dog colonies in Montana and North Dakota are found surrounding old homestead sites and stock water developments (Knowles 1986, Licht and Sanchez 1993). Thus it is not surprising that when Merriam (1902) interviewed farmers in east-central South Dakota that he received reports of prairie dogs showing up at homesteads. Merriam (1902) also gives similar reports from Kansas and Arizona where prairie dogs increased when the land was settled. However, Mead (1899) stated that in Kansas prairie dog numbers declined following extirpation of bison, but recovered as domestic livestock were brought into the area. It is possible that Merriam only documented prairie dogs re-occupying former range.. However, none of these reports represent a systematic assessment of regional prairie dog populations and trends. All that can be concluded from these anecdotal reports is that there were already prairie dogs in these areas at the time of settlement.

In addition, claims have been made (Virchow and Hyngstrom 2002) that early range-wide estimates of prairie dog abundance were greatly exaggerated. Yet, although Nelson's (1919) estimate of 40,469,500 ha of prairie dog (*Cynomys* spp.) across vast areas of the Great Plains and intermountain west was compiled from estimates provided by field agents of the Bureau of Biological Survey and not through systematic surveys, it is corroborated by a series of independent estimates. For example, for New Mexico in 1921, Oakes (2000) found Bureau of Biological Survey estimates of prairie dog abundance of approximately 6 million ha to be fairly consistent with estimates of the areal extent of prairie dogs estimated in 1971 minus the area poisoned over the period 1921-1971. In addition, Burnett (1919) in eastern Colorado estimated that 2.8 million ha of black-tailed prairie dogs, with a total of 5.8 million ha for all three prairie dog species in the state (Burnett 1918). Furthermore, in Texas Bailey (1905) estimated there were 23 million ha of prairie dogs. Lantz (1903) estimated there were 0.8 million ha of black-tailed prairie dogs in Kansas. In addition, in South Dakota Rose (1973) reported an early estimate (1923) for black-tailed prairie dogs at 0.7 million ha, and in Montana Flath and Clark (1986) estimated early black-tailed prairie dog abundance at 0.6 million ha. The total for these six states alone is 37 million ha given these various independent estimates. Including the area in the other six states with prairie dogs (*Cynomys* spp.), one would have to conclude that the Bureau of Biological Survey estimates were well founded.

Moreover, the 1919 estimates did not account for 10 to 20 years of agricultural cropland conversions and the 30 plus years of control work that preceded organized Federal poisoning programs against prairie dogs. Habitat conversion was extensive. Choate et al. (1982) estimated that two-thirds of the area within the geographic distribution of the prairie dog in Kansas was

converted to cropland after settlement. Merriam's (1902) report clearly shows that formulation of cheap, effective prairie dog poisons were already available by 1902. Strychnine could be purchased in most agricultural communities, and poisoning of prairie dogs by private ranches was already underway. Merriam (1902) lists several other control methods that were in use and effective on a limited scale. Clark (1989) found that eradication of prairie dogs began about 1880 with an organized control program in northwestern Wyoming reported as started in the 1880s (Clark et al. 1986). In Kansas, the statutory requirement to control prairie dogs began in 1903 (Lantz 1903). Carbon bisulphide, a toxic fumigant used was "popular" in prairie dog control by 1888 (Hubbard and Schmidt 1984). "Lees Peerless Gopher Killer" was a patented rodenticide in wide use at the turn of the century (Lantz 1903). In New Mexico, farmers were drowning and plowing prairie dogs in the mid 1880s (Oakes 2000). Indeed, by the time the Bureau of Biological Survey became involved with prairie dog control programs in 1915, prairie dog poisoning by private ranches had been an ongoing process for at least two decades. As one commentator noted, "...the ranch men had been poisoning prairie dogs for years and had... completely cleared the country of the pest" (Oakes 2000).

Under government organization and sponsorship, prairie dog poisoning became a systematic attempt at total eradication. Merriam (1902) realized that the extreme colonial nature of black-tailed prairie dogs made them highly vulnerable to such an organized extermination program. He identified cheap effective poisons available at that time, addressed the need to develop coordinated prairie dog control programs to effect large scale extermination, and conceptually outlined how such a program could be implemented. Bailey (1926) provided records of colonies destroyed in North Dakota by 1913 and noted that the Bureau of Biological Survey and the North Dakota Department of Agriculture were investigating the prairie dog situation in North Dakota in 1915. Grondahl (1973) reported that prairie dogs had been subjected to various degrees of control for 100 years in North Dakota. Although grazed rangelands around homesteads may have increased habitat suitability for prairie dogs, this factor was countered by habitat conversion to croplands and early prairie dog control efforts. Consequently, it is not possible to make generalizations about prairie dog population trends early in the settlement process.

RECORDS OF PRAIRIE DOG CONTROL EFFORTS

Government reports of hectares treated with poisons and quantities of poisoned grain bait applied were an honest attempt to quantify rodent control efforts, and are valuable documentation of prairie dog abundance at the time of settlement. Clark (1989) reviewed information compiled by Burnett in a series of reports on annual prairie dog and ground squirrel (*Spermophilus* spp.) poisoning in Colorado from 1912 to 1923. Using the graph in Clark (1989)

we estimated 17,750,000 ha of land were treated with poisoned grain bait during this period, and the records showed that 595,926 litters of treated grain bait were applied. In eastern Colorado, Clark (1989) quotes Payne (in Johnson 1912) that low and high estimates of black-tailed prairie dog abundance in 1903 was between 2 and 10% of the landscape occupied by their colonies.

Furthermore, Anderson et al. (1986) cited a report by Bell (1921) that documented poisoning of 2,832,860 ha in Montana and 2,428,166 ha in North Dakota of prairie dogs and ground squirrels during 1920. By comparison, in Montana, mapped prairie dog colonies totaled about 27,000 ha in 1998 (FaunaWest 1998), and in North Dakota mapped prairie dog colonies totaled about 8,000 ha in 2002 (Knowles 2002). Also, in Phillips County, Montana during a 3-year period (1931-1933) 69,000 ha of prairie dogs were poisoned with 33,000 kg of poison grain bait as well as 170,000 ha of ground squirrels treated with 19,100 kg of poisoned grain bait. In South Dakota, several reports exist of prairie dog poisoning activity for from different areas and time periods in the early 1900s (Table 1). These records are specific for black-tailed prairie dogs, and they indicate that over 400,000 ha were poisoned during the 1920s and 1930s. In Wyoming, Anderson et al. (1986) cited Martley (1954) that 1,120,290 ha of prairie dogs (black-tailed and white-tailed prairie dogs (*Cynomys leucurus*) were poisoned between 1915 and 1923. In northeastern Wyoming (Campbell, Niobrara, and Weston Counties) an additional 445,080 ha of black-tailed prairie dogs were poisoned from 1923 to 1928 (Day and Nelson 1929 cited in Anderson et al. 1986). One colony in this area was reported to be 160 km long.

In New Mexico, during the period of 1917-1932, a large poisoning campaign was conducted against prairie dogs (black-tailed and Gunnison's (*Cynomys gunnisoni*) with approximately 4.5 million ha treated with poison grain bait (Hubbard and Schmitt 1984); no information exist on how many hectares of each species were poisoned. Shriver (1965) estimated prairie dog (both species) abundance in New Mexico in 1919 at 4.8 million ha or about 15.3% of the total landscape (Hubbard and Schmitt 1984). Several records from the early 1900s suggest that the black-tailed prairie dog in New Mexico was very abundant (Hubbard and Schmitt 1984). Collectively, early reports and these documents of prairie dog poisoning efforts clearly show that prairie dog poisoning occurred on a local level began as early as the 1880s and that it was conducted on a broad scale across the geographic range of the black-tailed prairie dog starting in 1915 and continuing into the 1930s.

EARLY SETTLEMENT PERIOD RECORDS OF PRAIRIE DOGS

During the early settlement period, there was opportunity to record prairie dog distribution and abundance as the land was surveyed. In at least one case, prairie dogs were

noted as the land was surveyed from 1908-1914 prior to homesteading. Flath and Clark (1986) were able to review land use classification maps for about 25% of southeastern Montana where prairie dog colonies were noted on maps by the surveyors from 1908 to 1914. They looked at each 16-ha parcel, and if a surveyor noted prairie dogs in the parcel, Flath and Clark (1986) counted the parcel as containing 8 ha of prairie dogs. They assumed that all prairie dog colonies were recorded. The results of this study estimated that prairie dogs occupied 2.8% of the surveyed sections (1 square mile), and the percentage of surveyed sections with prairie dog colonies averaged 25%. However, for counties with more than 100 surveyed sections, the occurrence of prairie dogs ranged from 1% to 48% indicating considerable regional variation in prairie dog abundance. Flath and Clark (1986) stated that homesteading in the survey area primarily occurred later, from 1915-1917 after the land survey. The survey excluded the Crow and Northern Cheyenne Reservations, and both Reservations contain characteristic prairie dog habitat. Flath and Clark (1986) also prepared detailed maps of prairie dog distribution in the Tongue River and the Powder River areas. These maps show that prairie dogs were distributed primarily along the major drainages with some colonies exceeding 16 km. They also noted that General George A Custer reported several extensive prairie dog colonies along Rosebud Creek in 1876 (Fulton 1982 cited in Flath and Clark 1986). Physical evidence of abandoned historic colonies in these drainages is still visible (personal observation).

Similar maps may exist for other areas of Montana, but no systematic effort has been made to investigate this possibility. We examined land use classification maps for Jefferson County, in southwestern Montana and found one of two known historic prairie dog colonies noted on the maps. In this case, the mappers indicated the colony as "dog town" written in small letters indicating a colony of 2-4 ha in size. This mapping technique is consistent with Flath and Clark's (1986) observations. Both the historical colonies in Jefferson County were large (> 300 ha), and it is likely that the colonies had already been poisoned when the maps were drawn in the early 1900s (exact dates unknown). The discovery of gold in this area in the 1860s led to settlement of southwestern Montana ahead of the eastern plains (Howard 1959). The available early settlement records also support a relatively high occurrence of the black-tailed prairie dog.

RECORDS OF LARGE COLONIES

There are many reports of large prairie dog colonies, measured by miles, written prior to or at the time of settlement. Some of these are listed in Virchow and Hyngstrom(2002: Table 3). In Texas, one colony was estimated to be 400 km long by 160-240 km wide (estimated at 64,753 square km) and was mentioned by both Merriam (1902) and Bailey (1905). This colony no longer exists (Kevin Mote, Texas Game Fish and Parks, pers. commun.). Another large colony

was reported between the North and South Wichita Rivers in what is now King and Knox Counties, Texas (Halloran 1972). Also, in southeastern Arizona, Mearns reported in 1907 (cited in Hoffmeister 1986) that burrows of prairie dogs were scattered for miles over the plains south of the Pinaleno range or Sierra Bonito. The black-tailed prairie dog is now considered extirpated from Arizona. In Kansas, one colony was described as 96 km long (Baker 1889). In north-central Kansas, Mead (1899) noted that in 1859 a prairie dog colony on the divide between the Saline and Solomon Rivers from Ellsworth County and west was continuous for miles. He described the prairie dogs as being "innumerable". In southern Logan County Kansas, Merriam (1902) reported that about 777 square km constituted one continuous colony. In north-central Montana between the Missouri and Milk Rivers, Messiter (1890) described prairie dog colonies to be 48-64 km long. These colonies were noted by early settlers in this area (see below), even though they were not noted by the Lewis and Clark (Burroughs 1961) and Maximilian Expeditions (Twaites 1966, Thomas and Ronnefeldt 1982) that passed just south of these colonies. (Under good conditions prairie dog colonies can be observed at 1-2 km distance with binoculars.) Physical evidence of these colonies can still be found (see below). In this area there are currently approximately 12,000 ha of prairie dog colonies. Finally, in southeastern Montana, Flath and Clark (1986) reported many complexes along drainages extending more than 16 km, and some complexes covered more than 9,216 ha at the time of settlement.

In South Dakota, Hayden (1863) estimated the largest colony he observed was 130 square km. Rose (1973) reported that many old timers in South Dakota spoke of prairie dog colonies occurring for distances of 24-32 km along major drainages. He also noted that prairie dogs occurred in great abundance between Rapid City and Faith, South Dakota a distance of 240 km. On the Grand River National Grassland in northwestern South Dakota, an elderly rancher (L. Lyon, pers. commun.) reported to us in May 2002 that his grandfather talked about a prairie dog colony between Faith and Newell that required three days to cross on horseback in one direction and two days to cross on horseback in the other direction. He specifically stated that "this was before there were towns and stuff like that". Merriam (1902) said that prairie dog colonies 32-48 km long were not rare. In Oklahoma, a virtually continuous prairie dog colony in tall grass prairie stretched from Kingfisher Creek to Fort Reno, Oklahoma, a distance of 35 km according to Lewis and Hassien (1973) who cited Strong (1960). In northeastern Wyoming, Anderson et al. (1986) cited Day and Nelson (1929) for a prairie dog colony that was 160 km long. In New Mexico, Auto of Xavier, in 1680 referred to the northern end of the Jornada del Muerta plainas Paraje de las Tusas (Place of the Prairie Dogs), implying a large prairie dog colony existed in the broad valley (Oakes 2000). These were all significant prairie dog colonies for which there is no comparison with present prairie dog colonies in the United States.

There is credible evidence that large colonies existed on short grass and mixed grass prairies. The question is how many large prairie dog colonies existed on the prairies, and what percent of the landscape was occupied by prairie dogs. Baker (1899), Mead (1899), Hayden (1863), Messiter (1890), Merriam (1902), and Rose (1973) imply that there were more than one large colony. However, Messiter (1890) noted that the large colonies in north-central Montana were larger than others that he had seen elsewhere. In Montana, Allen (1874) traveled the divides between the Yellowstone and Missouri Rivers and the Yellowstone and Mussellshell Rivers during 1873, and described prairie dogs as generally distributed throughout the region traversed, but nowhere very numerous. This suggests that he did not encounter extraordinarily large colonies. However, even with 2-10% of the landscape occupied by prairie dogs, 90-98 km of each 100 km of the region transected would be outside of prairie dog colonies. Based on these records it is apparent that the black-tailed prairie dog was widely distributed across the Great Plains and that in many areas it occurred in extensive colonies.

PHILLIPS AND BLAINE COUNTIES, MONTANA

Some of the best documentation of prairie dog abundance during the early 1900s exists for the area occupied by Phillips and Blaine Counties in north-central Montana which included part of the area that Messiter (1890) traveled through in 1871. In October 1974, we talked to two elderly men who had worked on Civilian Conservation Corp crews during the early 1930s poisoning prairie dogs in Phillips County, Montana. They reported that there was a colony that stretched from the base of the Little Rocky Mountains to the UL Bend on the Missouri River; it was called 40-mile town. They described this colony as a series of large colonies 65 km long as opposed to a single continuous colony, and that the goal of the poisoning effort here was total extermination (interview notes October 1974). The thorough nature of this effort was confirmed by Murie (1937) when he conducted a faunal survey of the area that became the Charles M. Russell National Wildlife Refuge. There is also physical evidence of a large colony that extended from the eastern portion of the Fort Belknap Indian Reservation into central Phillips County, a distance of about 48 km (Figure 1). This information is consistent with Messiter's (1890) observations of prairie dogs colonies 48-64 km long in north-central Montana.

Prairie dog colonies on the Fort Belknap Indian Reservation (north-central Montana) were also mapped in 1921 (Figure 2). The Reservation includes some of the area crossed by Messiter in 1871. These maps recently were located in the National Archives in Washington D.C., and we have digitized and consolidated these maps. Based on this information, there were approximately 16,336 ha of prairie dog colonies on the Reservation in 1921 which represented

about 8% of the Fort Belknap Reservation rangelands. The Fort Belknap Reservation was established in 1888 and settlement there occurred at 3 locations: Fort Belknap Agency, Hayes, and Lodge Pole. The latter two sites were in the Little Rocky Mountains, and the former site was on Milk River bottomlands. The Reservation was never opened to homesteading, but grazing by non-member cattle and horses was permitted in the early years (Howard 1957). Significant conversion of grasslands to croplands did not occur until the 1970s, and development of homes outside of established communities did not take place until the 1980s (personal observation). In 1999, there were approximately 6,000 ha of prairie dog colonies on the Reservation (Tim Vosburgh, Fort Belknap Fish and Game biologist, pers. commun.), or about 38% of the mapped acreage in 1921.

Rodent control records for Phillips County, Montana show that 72,480 ha of prairie dog colonies were poisoned from 1924 through 1939, with 68,825 ha of this total being treated from 1931-1933 (BLM 1982). There were also 1.5 million ha of Richardson's ground squirrels poisoned from 1918-1939 which could have included some prairie dog colonies. The 68,825 ha of poisoned prairie dog colonies represents about 6% of the County including the Little Rocky Mountains and the Missouri River Breaks areas of the County which contain non-suitable habitat for prairie dogs. In 1998, only 5,700 ha of prairie dog colonies remained in Phillips County, or about 8% of the acres poisoned in the early 1900s. Yet, Phillips and Blaine Counties contain Montana's largest and most extensive prairie dog colony complexes.

PHYSICAL EVIDENCE OF LARGE PRAIRIE DOG COMPLEXES

Occupation of sites by prairie dogs for extended periods (perhaps centuries) can alter the appearance of the soil surface. In some cases, actual prairie dog mounds remain visible long after the prairie dogs are gone. This evidence can be used to corroborate estimates of numbers. Bailey (1926) stated that the old burrows and mounds remain for many years and that the sites of ancient prairie dog towns are marked by little swells of grassy turf scattered over the prairie. In northwestern Wyoming, Clark et al. (1986) reported that prairie dog mounds in abandoned white-tailed prairie dog colonies remained visible for 60+ years after the colonies were poisoned. In Montana, we have observed similar situations especially in mountain valleys and benches in the western portion of the black-tailed prairie dog range. In native prairie sites in eastern Montana, southwestern North Dakota and northwestern South Dakota, we frequently encounter a pattern on the soil surface of alternating raised areas that are well vegetated, and depressed areas that are less vegetated, often with pan spots. Our interpretation of these patterns is that these sites were historic prairie dog colonies, and the soil surface is a result of centuries of prairie dog activity interacting with erosional forces (wind and water). In South Dakota, Rose (1973)

reported that remnants of old colonies are still evident along the Bad River between Philip and Fort Pierre. Physical evidence of abandoned prairie dog colonies is still evident near Faith and St. Onge, South Dakota and along the Belle Fourche River, near Colony, Wyoming (personal observations). Cheyenne, Wyoming was built on the site of a large prairie dog colony (Day and Nelson 1929). Hayden (1872) mentions walking out of Cheyenne and seeing prairie dogs. Mounds of this colony are still visible some 8 km east of Cheyenne off Interstate 80, and north of Cheyenne. When mapping prairie dog colonies, it is not unusual to find a series of small colonies remaining in these areas that were once large prairie dog colonies (Knowles 2002). Cultivation of rangeland sites destroys this physical evidence of past occupation by prairie dogs, but even in areas with limited cultivation it is possible to plot the general distribution of former prairie dog colonies (Knowles 2002).

In north-central Montana, physical evidence of the large former prairie dog colonies is still very evident in Phillips and Blaine Counties. This is consistent with Messiter's (1890) observations, with early maps of the Fort Belknap Reservation, accounts of early residents of this area, and reports of prairie dog control efforts for this area (see above). It is possible to use a map of existing prairie dog colonies in this area to estimate the general outline of the large colonies that apparently once occurred in this area. Although we have observed evidence of large former prairie dog colonies in other locations in Montana, most of those areas are too fragmented by croplands to determine the full extent of the colonies even though a few scatter prairie dog colonies remain.

In western North Dakota, while mapping prairie dog colonies along the Little Missouri River corridor, and the upper portions of the Knife, Heart, Cannonball, and North Grand Rivers, we found physical evidence at 153 sites of former prairie dog colonies. This was not a comprehensive survey of old colonies and there was no attempt to determine the aerial extent of these colonies. However, it was apparent that this area at one time contained significant prairie dog colonies. The upper drainage basins from 10 km north of Belfield and Fryburg south to Amidon, a distance of approximately 53 km appeared to have contained extensive prairie dog colonies. Some of this area is upland prairie within the Little Missouri National Grassland and has never been cultivated, but cultivation of many of the sections in this area makes it difficult to precisely trace this colony complex. Bailey (1926) stated that upland prairie was the primary habitat of prairie dogs in North Dakota. Within this area, we located 47 sites that appeared to be former prairie dog colonies. However, a 1939-1942 map of prairie dog colonies within the Medora Ranger District shows only three small colonies in this area (Bishop and Culbertson 1976), while our 2002 mapping effort located 31 small to moderate-size colonies. It is apparent

that prairie dogs were greatly reduced in this area by 1939-1942, but have recovered somewhat in recent years.

PRAIRIE DOG ECOLOGY

Our knowledge of prairie dog ecology suggests that once a colony is established that it is capable of expanding into areas with slopes up to 12% and into areas with herbaceous vegetation up to 20-30 cm (personal observation). Although shrubs like big and silver sagebrush (*Artemisia tridentata*, *A. cana*) can restrict prairie dog colony expansion, over a number of years these shrubs will be eliminated or modified to permit occupation of a site by prairie dogs. Prairie dogs are capable of constructing burrows in a variety of clay and clay/loam soil that are common in the Great Plains (Koford 1958). Much of the short-grass and mixed-grass prairie is suitable habitat for prairie dog colonization based on soils, vegetation and slope.] *

We have developed a map of potential prairie dog habitat within their range distribution in Montana, based slope, soils, and vegetation data found at existing prairie dog colonies. This mapping effort identified 1.1 million ha of preferred habitat, and an addition 11.3 million ha of potential habitat. This analysis excluded approximately 4.5 million ha of cultivated croplands even though cropland sites frequently are suitable prairie dog habitat based on slope and soils (Bailey 1926). In Montana, it is apparent that the 27,000 ha of documented prairie dog colonies are not limited by habitat features, and that prior to massive poisoning campaigns, cultivation of upland prairie and the introduction of sylvatic plague, the available habitat would have supported a substantially greater prairie dog population. This verified by historic accounts (Messiter 1890), early land surveys (Flath and Clark 1986), and records of early poisoning efforts (BLM 1982, Anderson et al. 1986).

Despite anecdotal accounts of seemingly high prairie dog colony growth rates, recorded long-term growth rates over broad areas on the northern Great Plains are generally not supportive of these accounts (Table 2). Annual growth rates at these frequently mapped prairie dog complexes exceeded 50% only where prairie dogs were recovering from poisoning programs (Theodore Roosevelt National Park 1947-1953, Charles M. Russell National Wildlife Refuge 1964-1970) and plague (Northern Cheyenne Reservation 1998-1999). While mapping prairie dogs in North Dakota we encountered one 23.5-ha colony next to a ranch headquarters that the landowner reported to have started in the early 1960s and had never been poisoned. To attain large areas occupied by prairie dogs such as 48-64 km long prairie dog colonies is a long-term process. It is doubtful that, the large prairie dog colonies reported at the time of settlement

could have developed in the few years from the start of homesteading to initiation of prairie dog control programs.

Prior to settlement of the Great Plains, black-tailed prairie dogs had thousands of years to invade and colonize suitable habitats. Dispersal distances of prairie dogs are normally under 10 km (Knowles 1985, Garret and Franklin 1988). Maps of prairie dog colony distribution at the time of settlement (Flath and Clark 1986), and during the latter portion of the 20th century shows that colonies are typically relatively close to each other which reflects prairie dog dispersal ability and availability of suitable habitat (see Figure 1). For example, Flath and Clark (1986) reported mean inter-colony distances for two areas surveyed from 1909-1914 in southeastern Montana were 3.4 and 2.9 kms. On the Charles M. Russell National Wildlife Refuge following 15 years without any prairie dog control, Knowles (1982) recorded a mean inter-colony distance of 2.5 km. Based on maps supplied by Reid (1954), Coppock (1981), Scheelhaase (1973), and Hillman (1978), Knowles (1982) calculated mean inter-colony distances of 1.2 km for Theodore Roosevelt National Park, 2.4 km for Wind Cave National Park, 3.8 km for southern Saskatchewan, and 2.4 km for southwestern South Dakota, respectively. Based on our knowledge of prairie dog colony distribution today, it is unlikely that presettlement of prairie dog distribution was characterized by small isolated, but instead colonies would be within a normal dispersal range of each other.

The short dispersal distances of black-tailed prairie dog, combined with their extreme coloniality, means that establishment of a geographic range distribution throughout the Great Plains, extending from southern Canada to northern Mexico and from the Rocky Mountains to the 98th meridian, would have required the development of a large metapopulation in which colonies were relatively closely spaced within the normal dispersal range of prairie dogs. Nothing in modern prairie dog mapping data suggests that isolated small colonies are a normal pattern in prairie dog colony distributions. If accurate, Bailey's (1905) observation of colonies in Texas being separated by 16 to 32 km is a clear indication that prairie dogs had already been controlled severely in that area. In Montana and North Dakota our observation is that prairie dog colonies are rarely found separated from other colonies by such distances.

Mapping of prairie dog colony complexes typically reveals a characteristic pattern of colony size class distribution. A significant portion of prairie dog colony acreage is usually contained in a few large colonies, but smaller colonies are numerically more common. (FaunaWest 1998). We assume that prairie dog colony size class distribution prior to settlement would have been similar; however, many of the smaller colonies present today are actually just

remnants of colonies that were once much larger prior to control efforts. In northern Mexico, Ceballos et al. (1993) and List et al. (1997) provided information on a large prairie dog colony complex prior to prairie dog control and agricultural land conversion. In 1986, the main colony was 34,000 ha while the entire complex contained 55,000 ha of prairie dog colonies. During the past decade, cattle ranching and conversion of grasslands to irrigated agricultural croplands has resulted in the fragmentation of this complex. The main 34,000-ha colony has been broken into smaller colonies, and many of the smaller satellite colonies have been exterminated. This process of fragmenting large colonies into smaller colonies, and then working to exterminate the smaller colonies, was probably used in the past to break up large prairie dog complexes in the United States. This complex in northern Mexico was probably the best contemporary example of how prairie dog colony complex might have looked prior to settlement of the Great Plains.

In the absence of poisoning and plague, it has been repeatedly demonstrated in the past 50 years that prairie dogs have the capacity to re-colonize and re-occupy previously occupied habitat (Table 2). Given the centuries that this species had to colonize the Great Plains and its extensive range distribution, the black-tailed prairie dog likely expanded into most of the available suitable habitat and obtained some level of equilibrium with its environment. For example, the glaciated plains of north-central Montana (includes Phillips and Blaine Counties) were heavily impacted by continental glaciation, but since the end of the Pleistocene prairie dogs appeared to be able to establish colonies in much of this area and occupy 6-8% of the landscape.

No one has articulated what factors likely limited prairie dog populations prior to settlement. We do not know if it was availability of suitable habitat, soils, disease, drought, severe winters, flooding, predation, interaction with large ungulates, or a combination of these factors. In much of the short-grass and mixed-grass prairie, little in the prairie environment seems to represent a barrier to prairie dog colony growth; since the topography and vegetation are generally well within the range of habitat that prairie dogs can colonize. Thus, we hypothesize that at the time of settlement of the Great Plains, black-tailed prairie dogs were up against the habitat limitations of their environment, and that active colony sizes fluctuated in relation to environmental perturbations. The most important of these would have been extended long-term drought, periods of excessive precipitation, fire, and bison grazing patterns. The response of prairie dog populations to these perturbations may have varied across their range. For example, drought on the eastern tall grass portion of their range would have allowed opportunities for expansion, but drought on the western semi-arid portion of the prairie dog range would be met with reduced productivity (Knowles 1987). Such environmental perturbations likely influenced prairie dog numbers more than any settlement activities,

exclusive of poisoning.

DOCUMENTED PRAIRIE DOG DECLINES

In western North Dakota Bishop and Culbertson (1976) provided an account of prairie dog decline within the Medora Ranger District. Bailey (1926) stated that prairie dog colonies within the area subsequently studied by Bishop and Culbertson (1976) were already being poisoned by 1913 and that the U.S. Biological Survey and North Dakota Department of Agriculture assessed the prairie dog situation in this area in 1915. By the time of the 1939-42 accounting of prairie dogs, government-organized poisoning had going on for at least 24 years; thus presettlement prairie dog acreage in this area would have been considerably greater than reported by Bishop and Culbertson (1976). Within the Medora Ranger District, prairie dogs declined from 5,512 ha in 1939-42 to 404 ha in 1970-72. During this period they documented a 89% decline in the number of prairie dog colonies and a 93% decline in the area occupied by prairie dogs. A recent mapping effort in 2002 found about 1,400 ha and 107 colonies in the same area (Knowles 2002). In 1939, prairie dogs were primarily distributed along the Little Missouri River and the lower portions of some of its tributaries, and all that remained of the large colony complex between Belfield and Amidon were 3 small colonies. In 2002, only six prairie dog colonies remained along the Little Missouri River while the area encompassed by the large historic Belfield/Amidon colony complex, 31 small to medium colonies were located (Knowles 2002). We updated the prairie dog population trend reported by Bishop and Culbertson (1976) with current information of prairie dogs within the Medora Ranger District (Table 3).

In Montana, densities of prairie dog colonies have also declined. For example, Flath and Clark (1986) reported that 2.8% of the sections that they examined were occupied by prairie dog colonies. They used this information to estimate prairie dog abundances across Montana, and they estimated 595,300 ha of prairie dog colonies occurred at the time of settlement. However, their survey area did not include north-central Montana, the Crow Indian Reservation and the Northern Cheyenne Indian Reservation which all contain areas of excellent prairie dog habitat, and probably contained significantly more prairie dogs than estimated by Flath and Clark (1986). Thus, a statewide comprehensive estimate of presettlement prairie dog abundance in Montana would be considerably higher than 600,000 ha. As of the mid 1980s, Flath and Clark (1986) reported that prairie dogs in Montana only occupied about 50,600 ha and represented a 90% + decline from presettlement populations. A mid-1990s survey of prairie dogs in Montana produced a minimum estimate of about 26,720 ha of prairie dogs (FaunaWest 1998). In most areas within the geographic range distribution of prairie dogs in Montana, the percent of the landscape occupied by prairie dogs was less than 0.5% (Figure 3) (FaunaWest 1998).

Prairie dog distributional range contractions are apparent in both North Dakota and Montana. In North Dakota, Bailey (1926) noted that black-tailed prairie dogs occurred along the Missouri River bottomlands from the Standing Rock Reservation to the confluence of the Yellowstone River near Montana. This same area today does not have any prairie dogs (Knowles 2002). Moreover, prairie dogs have been virtually eliminated from a large agricultural area in the central portion of their range distribution in North Dakota. Prairie dog distribution in North Dakota is now limited to the Little Missouri River corridor, and the Standing Rock Indian Reservation and adjacent areas north of the Reservation.

In Montana prairie dogs have been greatly reduced on the northern and western portions of their range. For example, Coues (1875) described the prairie dog as common when crossing northern Montana between the Milk River and the Canadian border. This same area today contains only about a dozen colonies. A similar situation exists in the western range distribution of prairie dogs in Montana. From Shelby south to Whitehall, less than 20 prairie dog colonies remain. Cooper (1868 and 1869) described prairie dog colonies along the Missouri River from Fort Benton to the Dearborn River, while the Lewis and Clark Expedition reported prairie dogs along the Jefferson River near Whitehall (DeVoto 1953). Now prairie dogs are entirely gone from these areas of the Missouri River and Jefferson Rivers. Additionally, Stuart (1902) on his trip down the Yellowstone River to the Bighorn River used the words "many" and "plenty" to describe prairie dogs. Today there are only 5 known colonies in this same reach of the River, and another 5 colonies are known to exist on the Yellowstone River bottomlands from the Bighorn River to the Missouri River (FaunaWest 1998). As in North Dakota, the best prairie dog habitat in Montana is now used for agricultural croplands. There can be little question that Flath and Clark's (1986) estimate of 90%+ reduction in prairie dogs is accurate.

OBLIGATE AND COMMENSAL SPECIES

Finally, perhaps some of the strongest evidence of biological ubiquity for prairie dogs is seen in the black-footed ferret (*Mustela nigripes*), a specialized prairie dog predator, and the mountain plover (*Charadrius montanus*), a shorebird adapted to dryland areas with extremely short vegetation and an abundance of bareground. To have an obligate predator (Hillman and Clark 1980) and commensal bird species (Knowles et al. 1982) associated with a rodent community is truly remarkable. The test for dependence of these two species on prairie dogs has already been performed: remove the prairie dogs and see what happens. The black-footed ferret was taken to the brink of extinction (Clark 1989) and the mountain plover was reduced from a common (Coues 1878, Silloway 1903, Saunders 1911) to a rare (Leachman and Osmundson

1990) grassland bird species . Moreover, ferrets require large prairie dog complexes (>4,500 ha) to maintain viable populations (Forest et al. 1988, Harris et al. 1989). Specimens of ferrets have been collected throughout the range of the black-tailed prairie dog (Anderson et al. 1986), indicating that areas surrounding these collection sites at one time supported large prairie dog complexes. Nearly a quarter of the counties within the range of the black-tailed prairie dog has one or more recorded ferret specimens (Table 4). This represents a minimum estimate of black-footed ferret distribution by county since the presence of this species was not easily detected and no systematic effort was made to document its distribution prior to widespread extirpation. We consider specialization to prairie dogs as prey and specialization to unique habitat provided by prairie dog colonies as additional evidence supporting early estimates of prairie dog abundance made by Merriam (1902), Burnett (1918), Nelson (1919), Flath and Clark (1986).

DISCUSSION

Virchow and Hyngstrom (2002) mis-characterize the existing evidence to paint an inaccurate picture of what prairie dog distribution and abundance might have been prior to European settlement of the Great Plains. The assertion by Virchow and Hyngstrom (2002) that lack of historical accounts of prairie dog abundance together with only a few accounts of large colonies can be taken as evidence that prairie dogs were not abundant prior to settlement of the Great Plains is not accurate. They have focused on a limited number of early accounts of prairie dog abundance, and have ignored a much wider range of other available information that clearly shows that prairie dogs were a widespread and common species on the Great Plains.

There is nothing about early explorations that can be represented as systematic surveys for prairie dogs. Virchow and Hyngstrom (2002) state that Lewis and Clark, Maximilian, and Hayden took meticulous notes and would not have failed to record prairie dog colonies. However, it is apparent that these naturalists encountered many prairie dog colonies and failed to note their existence once the novelty of the species wore off. Moreover, there are sufficient accounts of large colonies throughout the range of the black-tailed prairie dog prior to or at the time of settlement to conclude that prairie dog colonies had the potential to grow to expansive sizes given the appropriate habitat.

There is little evidence to suggest that prairie dogs increased with the settlement process since cattle only replaced large herds of native ungulates which by numerous historic accounts created over-grazed conditions at least as extensive as those produced later by cattle (Hart 2001). Prairie dog control with poisons was already in practice by the 1880s before much of the range

had been settled. Merriam's (1902) interview of a few ranchers claiming a dramatic increase of prairie dogs and hearsay evidence of an increase of prairie dogs in one location in Kansas falls far short of a range-wide systematic survey of prairie dogs that could reliably estimate prairie dog populations and trend following settlement of the Great Plains. The Fort Belknap Indian Reservation represents a large block of prairie habitat not influenced by homesteading and the 1921 accounting of prairie dogs showed 8% of the rangelands occupied by prairie dogs. Similarly, land surveys immediately prior to homesteading in southeastern Montana (Flath and Clark 1986) documented that prairie dogs were widespread and occurred in extensive colonies. Government records of prairie dog poisoning during the early 1900s provide at least some quantitative estimate of the abundance of prairie dogs at the time of settlement. These records are consistent with other estimates of prairie dog abundance. In some areas of the northern Great Plains, physical evidence of expansive prairie dog colonies remains visible on the landscape, and remnant prairie dog colonies outline what were once much larger colonies.

Our knowledge of prairie dog ecology suggests that in the absence of poisoning and plague prairie dog colonies will expand to fill suitable habitat, that dispersing individuals can colonize suitable sites up to 10 km from existing colonies, and that small colonies can merge into larger colonies. Prior to the introduction of plague in black-tailed prairie dogs on the Great Plains in 1946 (Cully 1989), we are unaware of any disease pathogen in prairie dogs that would have significantly limited prairie dog populations over a broad area, and prior to the 1880s prairie dog poisoning was not significant. Prairie dogs had thousands of years to seek out and fill suitable habitats in the Great Plains, and they eventually developed an extensive geographic range distribution covering over 160,000,000 ha. In combination with the other prairie dog species, black-tailed prairie dogs provided sufficient habitat for development of an obligatory mammal predator and a commensal bird species.

Three conspicuous North American wildlife species were originally characterized by extreme biological success and abundance. These were the passenger pigeon (*Ectopistes migratorius*), the bison (*Bison bison*) and the black-tailed prairie dog (*Cynomys ludovicianus*). The passenger pigeon was hunted to extinction by 1914 (Terres 1991), the bison was reduced to less than 1,000 individuals by the late 1800s (McHugh 1972) and the black-tailed prairie dog was reduced to a fraction of its former range by the mid 1900s (Koford 1958, Clark 1989). Each of these species was biologically highly successful, and the collapse of their populations was related to unregulated take. Like the bison, the black-tailed prairie dog was specifically targeted for extinction by the Federal government. The effort to exterminate prairie dogs is well documented, and despite serious efforts through most of the 20th century, the prairie dog remains

a widespread and locally common species in some areas. The presettlement abundance and distribution of prairie dogs will never be known precisely because the people who had opportunity to observe prairie dogs prior to settlement of the Great Plains did not have the means nor the interest to do so quantitatively. However, multiple levels of evidence make it clear that prairie dog numbers are significantly below those of the late 1800s, and it is apparent that the failure to re-establish multiple large prairie dog complexes has left at least two associated species facing a real threat of extinction and other more broadly adapted associated species such as the burrowing owl (*Athene cunicularia*) and ferruginous hawk (*Buteo regalis*) with greatly depleted populations on the Great Plains. These obligates and associates could not have evolved and thrived over the course of several thousand years without abundant prairie dogs as hosts. Their declines are testimony to the fact that prairie dogs no longer occur in numbers that function on an ecosystem level as they once did. The question now is not how far prairie dogs have fallen, but how we should restore them to numbers that will conserve this important ecosystem role in the future.

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Table 1. Summary of reported prairie dog early poisoning efforts by state.

State	Area Poisoned (ha)	Time Period	Source
Colorado	17,750,000*	1912-1923,	Clark 1986
Montana	2,832,860**	1920	Bell 1921
Phillips Co.	72,479	1924-1939	BLM 1982
New Mexico	4,514,170***	1917-1932	Hubbard and Schmitt 1984
North Dakota	2,428,166****	1920	Bell 1921
South Dakota	400,000	1923-1939,	Linder et al. 1972
9 counties	161,133	1920,	Hanson 1988
5 counties	60,729	1922	Hanson 1988
Pine Ridge Res.	56,680	1922	Hanson 1988
Wyoming	>400,000	1915-1927	Clark and Campbell 1981
	1,120,290	1915-1923,	Martley 1954

* includes ground squirrels, Gunnison's and white-tailed prairie dogs.

** includes ground squirrels, and white-tailed prairie dogs.

*** includes Gunnison's prairie dogs.

**** includes ground squirrels.

Table 2. Annual prairie dog colony growth rates for Theodore Roosevelt National Park in western North Dakota and for four areas of Montana.

Area	Time period	Annual rate of change	Source
Roosevelt NP western ND	1947-53	51%	Theodore Roosevelt National Park files
	1953-56	-21%	
	1956-57	-26%	
	1957-63	29%	
	1963-65	1%	
	1965-73	-7%	
	1973-77	-1%	
	1977-82	2%	
	1982-85	12%	
	1985-88	-5%	
	1988-91	20%	
	1991-92	9%	
	1992-95	-3%	
	1995-97	3%	
C.M. Russell NWR north-central MT	1961-70	71%	Knowles 1982 & Charles M. Russell National Wildlife Refuge files
	1970-74	15%	
	1974-79	2%	
	1979-84	7%	
	1984-88	5%	
	1988-94	-5%	
	1994-95	-20%	
	1995-97	0%	
Phillips County north-central MT	1981-84	15%	Reading et al. 1989 and Stoneberg 1993 John Grensten (pers. comm.)
	1984-88	3%	
	1988-92	-10%	
	1992-93	-3%	
	1993-98	1%	
Northern Cheyenne Reservation, south-central MT	1984-90	12%	FaunaWest 1994 Steve Fourstar (pers. comm.)
	1990-94	-23%	
	1994-95	-36%	
	1995-97	25%	
	1997-98	39%	
	1998-99	63%	
	1999-00	37%	
Fort Belknap Reservation, north-central MT	1978-90	12%	FaunaWest 1991 Bureau of Indian Affairs Files Tim Vosburgh (pers. comm.)
	1990-94	-4%	
	1994-96	-23%	
	1996-97	22%	
	1997-98	11%	
	1998-99	-5%	
	1999-00	-9%	

Table 3. Summary of black-tailed prairie dog colonies within the exterior boundaries of the

Medora Ranger District in western North Dakota from 1939 to 2002. Data from 1939 through 1972 are from Bishop and Culbertson (1976), subsequent data collected by the authors.

<u>Time Period</u>	<u>Number of Colonies</u>	<u>Area (ha)</u>	<u>% of Area Occupied</u>	
			1939-42	392
1957-65	91	3,006	0.23	
1970-72	44	997	0.07	
2002	107	3,500	0.28	

Table 4. Number of counties by state within the range of black-tailed prairie dogs and the number of counties with documented black-footed ferret specimens (data from Anderson et al. 1986).

State	Number of counties within the black-tailed prairie dog range	Number of counties with ferret specimens	Percentage
Arizona	2	0	0
Colorado	29	10	34
Kansas	66	12	18
Montana	39	16	41
Nebraska	79	17	22
New Mexico	22	3	14
Oklahoma	38	4	11
South Dakota	32	20	63
Texas	107	7	7
Wyoming	14	8	57
Total	428	97	23

Figure 1. Map showing the current distribution of prairie dog colonies in Phillips and Blaine Counties, Montana. The current distribution can be used to estimate the location of large historic prairie dog colonies reported in this area by Messiter (1890) and homesteaders. (Map prepared by the Charles M. Russell National Wildlife Refuge.)

Figure 2. Map of the Fort Belknap Indian Reservation showing the location of prairie dog colonies mapped in 1921. The 1921 distribution map is courtesy U.S. National Archives, Washington, D.C.

Figure 3. Map of Montana showing the quarter latilong (area encompassed by a half degree of latitude and a half degree of longitude) distribution of the percent land area occupied by prairie dogs (data from FaunaWest 1998). (T = less than 0.1%, other figures represent percent land area occupied rounded to nearest tenth percent.)

Recovery of the Black-footed Ferret: Progress and Continuing Challenges

**Proceedings of the Symposium on the Status of the
Black-footed Ferret and Its Habitat, Fort Collins, Colorado,
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Edited by James E. Roelle, Brian J. Miller, Jerry L. Godbey, and Dean E. Biggins

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Areas Where Habitat Characteristics Could Be Evaluated To Identify Potential Black-footed Ferret Reintroduction Sites and Develop Conservation Partnerships

By Robert J. Luce¹

Abstract

This paper is an attempt to develop a new, broad list of potential black-footed ferret (*Mustela nigripes*) reintroduction sites across its historical range. I reviewed reports and publications that identified active, inactive, and potential reintroduction sites, including unpublished reports generated by State wildlife agencies and universities. I contacted local experts and reviewed the published and unpublished literature describing colony locations of three species of prairie dogs (*Cynomys* spp.). I list active reintroduction sites and others already planned and identify 70 other sites in the historical range of the black-footed ferret that might meet the biological and habitat suitability requirements for reintroduction of the species within 3–10 years, contingent upon directed management emphasis, State and Federal agency management priority, and, if on private land, landowner concurrence through agreements or incentives. I present this conceptual effort in the hope that identification of sites at this level will prompt discussion, revisions, additions, and deletions and will result in the formation of conservation partnerships that will contribute to black-footed ferret recovery.

Keywords: black-footed ferret, conservation, *Cynomys*, endangered species, *Mustela nigripes*, prairie dog, reintroduction

Introduction

Although many known, large prairie dog (*Cynomys* spp.) complexes have previously been identified, I believe that this paper is the first serious attempt to develop a new, broader list of potential reintroduction sites across the historical range of the black-footed ferret (*Mustela nigripes*). Some of these sites have been considered before, but many have not, or at least not in the same context as in the current effort. I present this conceptual effort in the hope that identification of the sites at this level will prompt discussion, revisions, additions, and deletions, and result in the formation of conservation partnerships that will contribute to black-footed ferret recovery.

Past efforts to identify sites have been constrained by the need to immediately take into account land ownership, plague history, and other factors that do not constrain the current conceptual effort. I hope that this paper prompts many who have not considered contributing to black-footed ferret recovery to get involved with a site in their locality. Several States that have not been involved in black-footed ferret recovery in the past have not previously participated in site identification.

I recognize that there are issues other than ecological ones that must be addressed when identifying potential reintroduction sites; however, I believe that recovery of the black-footed ferret depends first and foremost upon identifying and conserving areas that meet or have the potential to meet the biological parameters for establishment and long-term survival of viable populations. I believe that social and economic issues, including private land rights, economic concerns related to forage competition between livestock and prairie dogs, and others, are vitally important. I also believe, however, that a start must be made. Changes in Federal land management priorities, cooperative management planning on Federal lands, and financial incentives or regulatory assurances for private landowners or tribal governments must logically follow after habitat suitability has been established.

Recovery efforts for the endangered black-footed ferret have faced numerous and significant challenges, including extirpation of the species in the wild, development of captive breeding techniques and reintroduction methods, lack of adequate financial resources, and organizational inefficiencies (Forrest and others, 1985; Clark, 1986; U.S. Fish and Wildlife Service, 1988; Miller and others, 1996). Much work has been accomplished, and much remains to be done in these areas and others, but at present I believe that the most fundamental obstacle to meaningful recovery of the black-footed ferret in the wild is the availability of suitable habitat, both in quantity and quality; that is, prairie dog colonies of sufficient size and proximity to other colonies (Chaplin and others, 1996; Lomolino and others, 2002; Luce, 2003). There is a critical need to identify suitable sites and begin management of those sites for reintroduction and recovery. In fact, this may be the ultimate challenge to black-footed ferret recovery because it involves the greatest potential conflict with other land-use interests. Political and social barriers often surpass in difficulty those in the biological arena.

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In the late 1980s, spurred by the need to utilize animals produced by captive breeding, biologists identified several potential reintroduction sites. In 1988–89, R. Luce (written commun., 1995) developed a list of 18 potential reintroduction sites in Wyoming by using data from a variety of sources. Conway (1989) evaluated six of those sites and concluded that only two had prairie dog numbers suitable for black-footed ferret reintroduction. Closer examination of other sites in Wyoming, as well as sites in Arizona, Colorado, South Dakota, and Utah, revealed that many were more or less unsuitable at the time of evaluation for various reasons, principally because prairie dogs did not occupy the sites to the extent that earlier evaluations had recorded or assumed (M. Lockhart, written commun., 1999–2003). Ranking of sites suitable for black-footed ferret reintroduction and recovery has emphasized the importance of large complexes of prairie dog colonies and identification of multiple sites. Additionally, it has been assumed that more densely occupied black-tailed prairie dog (*C. ludovicianus*) colonies are preferable to less dense white-tailed (*C. leucurus*) or Gunnison's (*C. gunnisoni*) prairie dog colonies and that a plague-free environment is preferable. New data documenting maintenance and/or growth of both prairie dog and black-footed ferret populations at reintroduction sites on Gunnison's and white-tailed prairie dog complexes where plague is present in Arizona (B. Van Pelt, oral commun., 2004) and Wyoming (M. Grenier, oral commun., 2004) indicate that these assumptions warrant further investigation.

A revision of the current Black-footed Ferret Recovery Plan (U.S. Fish and Wildlife Service, 1988) is underway, so it is important to note that I do not intend to supersede the site selection process that will be a part of the revised plan. The revised plan may include new downlisting and delisting goals for number of black-footed ferrets and number or location of reintroduction sites, but in either case a large number of potential reintroduction sites must be identified. I offer a new baseline list that includes contributions from all portions of the species' historical range, both previously overlooked sites and recently identified sites. I do not attempt to identify long-term black-footed ferret recovery needs for various areas of the species range because a rangewide delisting goal has not been identified and because a related method for apportioning recovery responsibilities among political jurisdictions has not been formalized to date (see Ernst and others, this volume).

The most promising recovery sites already have active reintroduction programs in place. I believe that several new sites with potential for adequate occupied habitat to be present within 3–10 years should be identified for each of the political jurisdictions within the historical range of the black-footed ferret. It is not appropriate to wait for a definitive answer as to the number of black-footed ferrets necessary for delisting or the amount of actual habitat that will be needed. Many more sites must be evaluated than are currently being considered because environmental unknowns, especially plague and drought, affect the viability of individual sites; therefore, longevity cannot be predicted or guaranteed. In addition,

political and social attitudes may change, resulting in loss of support for maintaining adequate occupied prairie dog habitat at a given site. I identify a large number of sites so that no one site will be under pressure for rapid development, but yet the presence of the sites on the list will allow agencies to begin planning toward management of those sites, potentially allowing a significant number of them to be available for black-footed ferret reintroduction in 3–10 years.

Methods

I reviewed previous efforts that identified active, inactive, and potential black-footed ferret reintroduction sites, including the U.S. Fish and Wildlife Service (FWS) reintroduction site list (Conway, 1989; M. Lockhart, written commun., 1999–2003; fig. 1). I also reviewed published literature, including Lair and Mecham (1991), Vanderhoof and Robel (1994), Ernst (2001), and Johnson and others (2003). In addition, I reviewed available information regarding other potential sites, including unpublished reports generated by State wildlife agencies

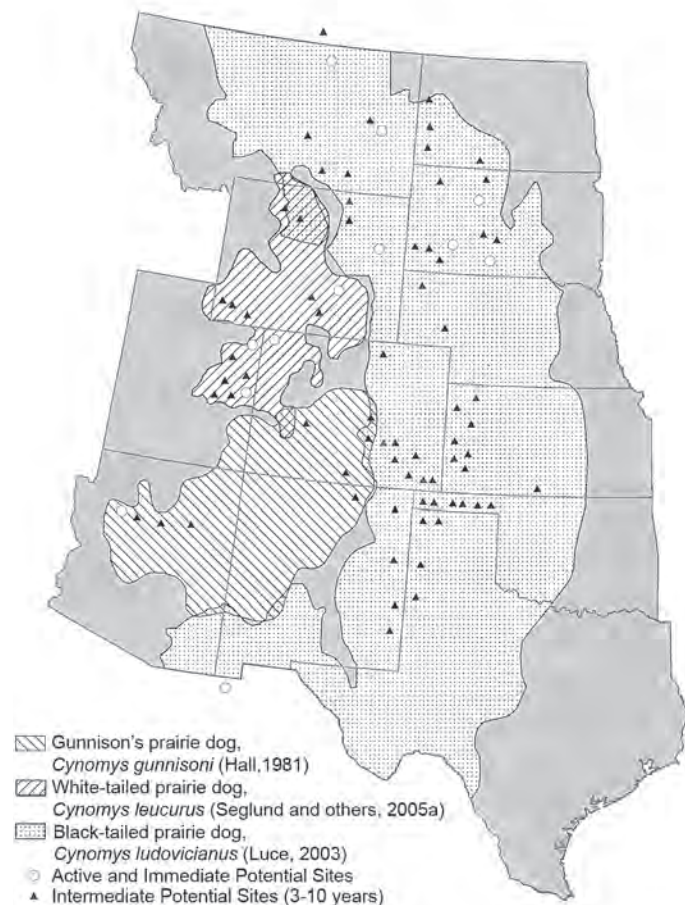


Figure 1. Location of eight active black-footed ferret (*Mustela nigripes*) reintroduction sites (1990–2004); three Immediate Potential Sites (1–3 years); and 70 Intermediate Potential Sites, at which, pending further evaluation, opportunities for reintroducing ferrets may exist in 3–10 years.

and universities, and contacted local experts. I had personal communication with Steve Whiteman, Southern Ute Tribe; Craig Knowles, FaunaWest Wildlife Consultants; Derrick Holdstock and Heather Whitlaw, Texas Parks and Wildlife Department; Julianne Hoagland, Oklahoma Department of Wildlife Conservation; Pamela Schnurr, Colorado Division of Wildlife; Dave Wagner, Northern Arizona University; Bill Woodson, U.S. Army; Mike Albee, U.S. Bureau of Land Management; Tim Byer and Dave Augustine, U.S. Forest Service; Joe Truett, Turner Endangered Species Fund; Allison Puchniak, Montana Department of Fish, Wildlife and Parks; Terry Enk, New Mexico Department of Game and Fish; Pete Gober, Randy Matchett, Scott Larson, John Nysted, and Lou Hanebury, U.S. Fish and Wildlife Service; Mark Lomolino, State University of New York, College of Environmental Science and Forestry; Amy Seglund and Craig McLaughlin, Utah Division of Wildlife Resources; Pat Fargey, Grasslands National Park, Canada; Martin Grenier, Wyoming Game and Fish Department; Tim Vosburgh, Intertribal Black-tailed Prairie Dog Coordinator; Bill Van Pelt, Arizona Game and Fish Department; Rurik List, Instituto de Ecologia, Ciudad Universitaria Coyoacan, Mexico; Travis Livieri, Prairie Wildlife Research; Mike Fritz, Nebraska Game and Parks Commission; and Sandy Hagen, North Dakota Game and Fish Department.

Information was acquired for 12 States within the historical range of the black-footed ferret, five Native American reservations, two States in Mexico, and one Canadian Province. The foundation for this effort was provided by intensive and extensive inventories and preparation of management plans for black-tailed prairie dogs, as summarized in Luce (2003); white-tailed prairie dog survey data, as summarized in Seglund and others (2005a); and Gunnison's prairie dog survey data, as summarized in Seglund and others (2005b).

I use the following terminology. Active Sites are those at which black-footed ferrets have been previously released and are being actively managed. Immediate Potential Sites are those already identified by the Black-footed Ferret Recovery Implementation Team and upon which reintroduction work has begun. Intermediate Potential Sites are those at which opportunities may exist in the 3- to 10-year time frame.

Planning efforts conducted by recovery partners require a queue of potential sites. I provide a locally specific list of all potential black-footed ferret reintroduction sites across the species' historical range but focus on Intermediate Potential Sites since these provide the next step in black-footed ferret reintroduction beyond management of Active Sites. Reintroduction efforts could begin at an Intermediate Potential Site before the minimum occupied habitat identified was available if expansion could be reasonably anticipated within a decade. Therefore, sites that are now below the minimum threshold for occupied habitat are also listed in this paper, anticipating that they have potential to meet or exceed the minimum within 10 years. Although I surmise that long-term potential sites may exist, I do not list those here.

At existing black-footed ferret reintroduction sites, as well as in State black-tailed prairie dog management plans,

contiguous habitat is defined as a complex of colonies in which no colony is farther than 7 km from another colony (Biggins and others, 1993). A colony is defined as a concentration of black-tailed prairie dogs with an average density of at least 4.05 individuals/ha (Luce, 2003) or as a concentration of white-tailed prairie dogs with a minimum of 20 burrow openings/ha on 5-ha parcels (Biggins and others, 1993; Seglund and others, 2005a). Colony has not yet been defined for Gunnison's prairie dogs, but the species is biologically similar to the white-tailed prairie dog. Although this rigorous definition was not used to identify the Intermediate Potential Sites in this paper, it must be assumed that sites will be required to meet a similar standard eventually before their full potential for maintenance of a long-term, viable black-footed ferret population can be achieved.

Based on bioenergetic (Biggins and others, 1993) and behavioral considerations (R. Matchett and T. Livieri, oral commun., 2003) and known densities of the respective species, I began with the premise that the minimum adult population of 30 individuals identified in the 1988 recovery plan (U.S. Fish and Wildlife Service, 1988) might require 1,215 ha of contiguous, occupied black-tailed prairie dog habitat; 1,823 ha of contiguous, occupied Gunnison's prairie dog habitat; or 2,430 ha of contiguous, occupied white-tailed prairie dog habitat. I recognize that prairie dog densities vary between sites and at individual sites on an annual basis, but I found it necessary to use averages in this evaluation process.

I also worked from the premise that the amount of extant, occupied habitat noted above may not be necessary to identify potential reintroduction sites and perhaps begin black-footed ferret releases. I suggest that 607.5 ha of contiguous, occupied black-tailed prairie dog habitat; 911.3 ha of contiguous, occupied Gunnison's prairie dog habitat, or 1,215.0 ha of contiguous, occupied white-tailed prairie dog habitat may be sufficient to begin management planning or possible experimental release of black-footed ferrets. The choice of 50 percent was arbitrary and assumes that prairie dog colonies will grow. Of course, many other factors may affect suitability of a reintroduction site, but I believe that these rough measures may allow preliminary identification of a queue of sites that can be further evaluated.

I characterized sites in regard to the species of prairie dog present, the amount of occupied prairie dog habitat, and disease status in a manner similar to that used by M. Lockhart (written commun., 1999–2003). Many of these sites have been recently identified as a result of ongoing inventories of prairie dog habitat.

Results

Current and potential black-footed ferret reintroduction sites are listed below for U.S. States and some Native American tribal lands, Canadian Provinces, and Mexican States having historical prairie dog habitat. Each is preceded by background information related to prairie dog popula-

tions. Many sites are in the early stages of identification and mapping; some may not yet be fully mapped, and some have no data on the amount of occupied prairie dog habitat or density of prairie dogs. Sites are summarized in table 1 (Active and Immediate Potential Sites) and table 2 (Intermediate Potential Sites), and locations are illustrated in figure 1.

Arizona

Black-tailed and Gunnison’s prairie dogs occurred in Arizona historically. The black-tailed prairie dog was extirpated from Arizona in the 1930s; therefore, reintroduction of black-tailed prairie dogs would be necessary before their colonies could serve as reintroduction sites for black-footed ferrets. In 2002, Wagner and Drickamer (2002) collected data from all potential sources and identified 400 locations with Gunnison’s prairie dog colonies. They revisited 293 colonies in 2000 and 2001 and found that 270 were active. Gunnison’s prairie dogs are located in northern Arizona from the Colorado River to Flagstaff and eastward along the Little Colorado River. No survey data are available for the Navajo Indian Reservation, which may comprise as much as one-third of the potential range.

Active Sites

Aubrey Valley

Arizona has one active black-footed ferret reintroduction site on a Gunnison’s prairie dog complex in Aubrey Valley (Coconino, Yavapai, and Mojave Counties) in the northwest-

ern part of the State (fig. 1). Reintroduction efforts began in 1996. The site is designated a black-footed ferret nonessential experimental population, and releases of captive black-footed ferrets are ongoing. Approximately 25 black-footed ferrets occur in the wild there at present. Total occupied prairie dog habitat is approximately 12,039 ha on a mixture of private, State, and Hualapai Indian Reservation lands. Monitoring at this site has not documented plague during the last 20 years, although it has been noted in the region. Prairie dog populations can be severely affected by drought at this site (M. Lockhart, written commun., 1999–2003).

Intermediate Potential Sites

East of Seligman

Approximately 2,502 ha of active Gunnison’s prairie dog colonies were present on-site in 1992. The site is a large open grassland bisected by I-40. Occupied habitat was reduced considerably in 1996 because of a plague epizootic, but recovery began in 2001. This area is <10 km from Aubrey Valley (Wagner and Drickamer, 2002; D. Wagner, oral commun., 2003).

West of Dilkon, Navajo Indian Reservation

The Navajo Natural Heritage Program surveyed Gunnison’s prairie dogs in this area to investigate its potential as a black-footed ferret reintroduction site. The survey documented approximately 3,200 ha of occupied habitat. This area was affected by plague in 1996, and there has been little recovery to date (Wagner and Drickamer, 2002; D. Wagner, oral commun., 2003).

Table 1. Sites at which black-footed ferrets (*Mustela nigripes*) have been reintroduced and are being managed (Active Sites), and sites identified by the Black-footed Ferret Recovery Implementation Team where some work preparatory to reintroduction has been done (Immediate Potential Sites).

State	Site name	Nearest town	Plague status
Active Sites			
Arizona	Aubrey Valley	Seligman	Not present
Colorado	Colorado/Utah	Dinosaur	Present
Montana	North-central Phillips County	Malta	Present
South Dakota	Cheyenne River Indian Reservation		
	Conata Basin/Badlands National Park	Wall	Not present
	Rosebud Indian Reservation	Winner	Not present
Utah	Colorado/Utah	Dinosaur, Colo.	Present
Wyoming	Shirley Basin	Medicine Bow	Present
Chihuahua, Mexico	Janos	Janos	Not present
Immediate Potential Sites			
Montana	Custer Creek	Miles City	Unknown
Utah	Cisco Desert	Green River	Present
Wyoming	Thunder Basin National Grassland	Bill	Present

Table 2. Sites at which, pending further evaluation, opportunities for reintroducing black-footed ferrets (*Mustela nigripes*) may exist in 3–10 years (Intermediate Potential Sites; $n = 70$).

State or Province	Site name	Nearest town	Plague status
Arizona	East of Seligman	Seligman	Present
	West of Dilkon, Navajo Indian Reservation	Dilkon	Present
	West of Wupatki National Monument	Flagstaff	Present
Colorado	Pueblo County	Pueblo	Present
	Weld County	Greeley	Present
	Bent County	Lamar	Present
	Baca County	Springfield	Present
	Crowley County	Rocky Ford	Present
	Pueblo Army Depot	Pueblo	Present
	Fort Carson	Colorado Springs	Present
	Comanche National Grassland, Carrizo Unit	Pritchett	Present
	Comanche National Grassland, Timpas Unit, and Pinon Canyon Maneuver Site	La Junta	Present
	Cimarron National Grassland	Springfield	Present
	BLM Twin Lakes Allotment	Alamosa	Present
	Parlin	Gunnison	Present
Kansas	Z-Bar Ranch	Medicine Lodge	Plague free
	Logan County	Colby	Plague free
	Northern Kearny County	Garden City	Plague free
	Greeley County	Horace	Plague free
	Rawlins County	Atwood	Plague free
	Hamilton County	Syracuse	Plague free
	Southern Kearny County	Garden City	Plague free
	Sherman County	Colby	Plague free
Montana	Leachman complex	Billings	Present
	Northern Cheyenne Indian Reservation	Colstrip	Present
	Miles City BLM District	Miles City	Present
	Fort Benton-Roundup-Harlowton area	Roundup	Present
Nebraska	Blue Creek Ranch	Oshkosh	Plague free
	Oglala National Grassland	Chadron	Plague free
New Mexico	Vermejo Park Ranch	Raton	Unknown
	Quay/Curry County interface	Tucumcari	Unknown
	Roosevelt County/Grulla National Wildlife Refuge	Portales	Unknown
	Lea County	Lovington	Unknown
	Union County	Clayton	Unknown
North Dakota	Horse Creek area, Little Missouri National Grassland	Williston	Unknown
	Standing Rock Indian Reservation	North Lemmon	Unknown
	South Unit, Theodore Roosevelt National Park	Dickinson	Plague free
	Little Missouri River	Bowman	Plague free

Table 2. Sites at which, pending further evaluation, opportunities for reintroducing black-footed ferrets (*Mustela nigripes*) may exist in 3–10 years (Intermediate Potential Sites; $n = 70$)—Concluded.

State or province	Site name	Nearest town	Plague status
Oklahoma	Southwest Cimarron County	Boise City	Plague free
	Texas County No. 1	Guymon	Plague free
	Texas County No. 2	Guymon	Plague free
	Beaver County No. 1	Beaver	Plague free
	Beaver County No. 2	Beaver	Plague free
South Dakota	Pine Ridge Indian Reservation	Pine Ridge	Plague free
	Standing Rock Indian Reservation	Lemmon	Plague free
	Lower Brule Indian Reservation	Pierre	Plague free
	Wind Cave National Park	Hot Springs	Plague free
	Grand River National Grassland	Lodgepole	Plague free
	Bad River Ranches	Pierre	Plague free
Texas	Smithwick area, Buffalo Gap National Grassland	Hot Springs	Plague free
	Rita Blanca National Grassland	Dalhart	Unknown
	Muleshoe National Wildlife Refuge	Lubbock	Present
	Sherman County	Dumas	Unknown
	Deaf Smith County	Amarillo	Unknown
Utah	Buckhorn and Crescent Junction	Price	Present
	Twelvemile Flat	Green River	Present
	Eightmile Flat (Myton Bench)	Green River	Present
	Sunshine Bench/Brush Creek	Green River	Present
	Buckhorn Flat	Price	Present
Wyoming	Meeteetse	Meeteetse	Present
	Bolton Ranch	Saratoga	Present
	Carter	Kemmerer	Present
	Cumberland	Kemmerer	Present
	Fifteenmile	Worland	Present
	Flaming Gorge	Green River	Present
	Shamrock Hills	Rawlins	Present
	Kaycee	Kaycee	Unknown
Saskatchewan, Canada	Sheridan Local Training Center	Sheridan	Unknown
	Grasslands National Park	Swift Current	Unknown

West of Wupatki National Monument

Gunnison's prairie dogs are present at this site north of Flagstaff. A complex of 950 ha was mapped in 2001. Plague has occurred, but the extent has not been quantified (Wagner and Drickamer, 2002; D. Wagner, oral commun., 2003).

Colorado

Black-tailed prairie dogs, white-tailed prairie dogs, and Gunnison's prairie dogs occur in Colorado. Complete location data are not available for Gunnison's prairie dogs since some potential habitat in southwestern Colorado has not been surveyed. White-tailed prairie dogs are also currently being surveyed in northwestern Colorado. Black-tailed prairie dogs occur in all counties in the historical range in the eastern one-third of the State, and recent surveys indicate 255,596 ha of occupied habitat (Colorado Division of Wildlife, 2003). Location data from that survey are not available to the author at this time, however. EDAW, Inc. (2000) identified the 10 counties with the largest amount of active, occupied habitat in the State: Pueblo (8,989 ha), Weld (8,146 ha), Bent (6,914 ha), Baca (5,816 ha), Crowley (5,475 ha), Adams (5,372 ha), Prowers (5,161 ha), Boulder (4,668 ha), Cheyenne (3,717 ha), and Kiowa (3,629 ha). EDAW, Inc. (2000) identified 17 colonies >405 ha and 45 colonies from 203 to 405 ha in the black-tailed prairie dog range in Colorado.

Active Sites

Colorado/Utah

White-tailed prairie dogs occupy the only active black-footed ferret reintroduction site in Colorado. The site is located in northwestern Colorado in Moffat and Rio Blanco Counties and extends into Utah (Uintah County) and Wyoming (Sweetwater County). The Wyoming portion of the site, called Kinney Rim, has virtually no active colonies at the current time. Reintroduction efforts began in 1998. The site is designated a black-footed ferret nonessential, experimental population, and releases of captive black-footed ferrets are ongoing. A small population of black-footed ferrets occurs in the wild there at present. Total occupied prairie dog habitat is approximately 20,250 ha, primarily on U.S. Bureau of Land Management (BLM) land, and plague is present. Potential habitat present in the Colorado portion of this site is estimated at 45,553 ha (M. Lockhart, written commun., 1999–2003).

Intermediate Potential Sites

Pueblo County

Black-tailed prairie dogs occupy this site. The northern half of the county, north of the City of Pueblo, has the largest concentration of colonies and the majority of the 8,989 ha of colonies identified in the county (EDAW, Inc., 2000). This county is primarily private land; therefore, development of

black-footed ferret reintroduction sites would require participation by private landowners.

Weld County

Black-tailed prairie dogs occupy this site. The northeastern half of the county, northeast of the City of Greeley, has the largest concentration of colonies and the majority of the 8,146 ha of colonies identified in the county (EDAW, Inc., 2000). This county is primarily private land; therefore, development of black-footed ferret reintroduction sites would require participation by private landowners.

Bent County

Large black-tailed prairie dog colonies occur in the northern and western parts of the county, encompassing the majority of the 6,914 ha identified (EDAW, Inc., 2000). This county is primarily private land; therefore, development of black-footed ferret reintroduction sites would require participation by private landowners.

Baca County

The western one-half of the county, centered on the town of Pritchett, has the largest concentration of black-tailed prairie dog colonies and has the majority of the 5,816 ha identified in the county (EDAW, Inc., 2000). This county is primarily private land; therefore, development of black-footed ferret reintroduction sites would require participation by private landowners.

Crowley County

Large black-tailed prairie dog colonies occur in several places in the county, encompassing 5,475 ha (EDAW, Inc., 2000). This county is primarily private land; therefore, development of black-footed ferret reintroduction sites would require participation by private landowners.

Pueblo Army Depot

Black-tailed prairie dogs occupy this site, which is on a U.S. Army installation. Approximately 1,066 ha of occupied habitat were present before a plague outbreak in 2003. The site is managed by the military and is protected from shooting and poisoning except where black-tailed prairie dogs may constitute a human health hazard (B. Woodson, oral commun., 2003). A large area of occupied habitat also occurs on private lands adjacent to Pueblo Army Depot in El Paso County (EDAW, Inc., 2000).

Fort Carson

Black-tailed prairie dogs occupy this site, which is on a U.S. Army installation. Approximately 1,418 ha of occupied habitat were present before a plague outbreak occurred in 2002 or 2003. The site is managed by the military and is protected from shooting and poisoning except where black-tailed prairie

dogs may constitute a human health hazard (B. Woodson, oral commun., 2003). A large area of occupied habitat also occurs on private lands adjacent to Fort Carson, particularly along the southern boundary in Pueblo County (EDAW, Inc., 2000).

Comanche National Grassland, Carrizo Unit

Recent GIS analyses identified 46,395 ha of potential black-tailed prairie dog habitat on this site in Baca County. Potential habitat was defined as land with clay or loamy soil and <5 percent slope. Of this potential habitat, 1,622 ha are currently occupied, with an additional 450 ha occupied outside of potential habitat (primarily on lands mapped as sandy soils, most likely because of inaccurate generalities in the soil map). The Carrizo Unit has extremely fragmented land ownership. Intermingled private lands have even higher densities of colonies (due to higher grazing intensity), but landowners have strongly negative attitudes toward black-tailed prairie dogs. Approximately 2,076 ha of occupied black-tailed prairie dog habitat occurs on National Forest lands, and the amount of occupied habitat on intermingled private lands is unknown (D. Augustine, written commun., 2003).

Comanche National Grassland, Timpas Unit, and Pinon Canyon Maneuver Site

Black-tailed prairie dogs occupy this site, which is on the Timpas Unit and the adjoining U.S. Army Pinon Canyon Maneuver Site. Together these areas provide a large block of land in public ownership with little fragmentation. The Timpas Unit includes a number of private inholdings but is far less fragmented than the Carrizo Unit (above). The amount of occupied habitat in the Timpas Unit is lower than in the past because of plague. A total of 35,917 ha of potential habitat exists, of which 192 ha are currently occupied. An additional 41 ha are outside the area mapped as suitable habitat, for a total of 233 ha on the Timpas Unit. Occupied habitat on the Pinon Canyon Maneuver Site totaled 143 ha when last mapped (D. Augustine, written commun., 2003).

Cimarron National Grassland

Black-tailed prairie dogs occupy this site, which has approximately 16,200 ha of potential habitat, 1,296 ha of which were occupied in 2003. The area is bounded on the north by cropland and on the south by riparian/sand sagebrush (*Artemisia filifolia*) habitat. The Cimarron is separated from the Comanche by sand sagebrush habitat unsuitable for black-tailed prairie dog expansion (D. Augustine, written commun., 2003).

Bureau of Land Management Twin Lakes Allotment

Gunnison's prairie dogs occur at this site on public land in Conejos County, approximately 32 km south of Alamosa. The area supports a large complex of colonies dating back

to the 1970s, many of which are old or inactive. Existing occupied habitat is approximately 512 ha (M. Albee, oral commun., 2003).

Parlin

Gunnison's prairie dogs occur at this site, which is on public land 19 km southeast of Gunnison in Gunnison County. The amount of occupied habitat in 1980 was 497 ha (M. Albee, oral commun., 2003).

Kansas

Only black-tailed prairie dogs occur in Kansas. Recent surveys estimate 52,861 ha of occupied habitat in western Kansas (Kansas Black-tailed Prairie Dog Working Group, 2002). The estimate of suitable habitat in Kansas based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 60,181 ha.

Intermediate Sites

Z-Bar Ranch

Black-tailed prairie dogs occupy this site, which is on property owned by Turner Enterprises, Inc., approximately 40 km southwest of Medicine Lodge in Barber County. The site currently supports 101 ha of occupied habitat and is growing steadily. Grassland conservation and black-tailed prairie dog expansion are high priority management objectives (J. Truett, oral commun., 2003).

Logan County

This county contained the largest complex (3,522 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Northern Kearny County

The northern part of this county contained the second largest complex (1,104 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Greeley County

This county contained the third largest complex (826 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Rawlins County

This county contained the fourth largest complex (448 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Hamilton County

This county contained the fifth largest complex (423 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Southern Kearny County

The southern part of this county contained the sixth largest complex (400 ha) of black-tailed prairie dogs in Kansas in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Sherman County

This county had the highest number of colonies and highest occupied area in the 1990–92 survey: 60 colonies and 1,420 ha (Vanderhoof and Robel, 1992, 1994). It also had significant occupied black-tailed prairie dog habitat in 2001 (Kansas Black-tailed Prairie Dog Working Group, 2002).

Montana

Both black-tailed and white-tailed prairie dogs occur in Montana. White-tailed prairie dogs are confined to a very small area near the border with Wyoming and occupy roughly 40 ha of habitat at the present time; therefore, no black-footed ferret reintroduction potential exists for the foreseeable future. Black-tailed prairie dogs occur in the eastern part of the State, and the best estimate of occupied area is 36,450 ha (Montana Prairie Dog Working Group, 2002). The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 97,349 ha.

Active Sites

North-central Phillips County

Black-tailed prairie dogs occupy this site. Black-footed ferret releases have occurred since 1994. Occupied prairie dog habitat was 12,014 ha in the mid-1990s, with 5,457 ha occurring on Fort Belknap Indian Reservation, 4,472 ha on BLM lands, and 2,085 ha on Charles M. Russell National Wildlife Refuge. The area was heavily affected by plague in the late 1990s. The black-footed ferret population is very low at the current time. Land ownership is mixed private, Federal, and tribal (M. Lockhart, written commun., 1999–2003).

Immediate Potential Sites

Custer Creek

Black-tailed prairie dogs occupy this site in Prairie and Custer Counties, which contains >100 colonies and 1,705 ha of occupied habitat on a mixture of State, private, and BLM lands. Plague has not been documented since 1996. Since this

site is in an area of checkerboard land status, private interests control the site potential (M. Lockhart, written commun., 1999–2003).

Intermediate Potential Sites

The following locations were identified in the Conservation Plan for Black-tailed and White-tailed Prairie Dogs in Montana (Montana Prairie Dog Working Group, 2002) as 4 of the 10 largest known prairie dog complexes in Montana in 2000.

Leachman Complex

This site is entirely on tribal land in the northwest portion of the Crow Indian Reservation in Yellowstone and Big Horn Counties, and once supported an estimated 4,050–4,860 ha of occupied prairie dog habitat (L. Hanebury, oral commun., 2003). The site included >2,835 ha of occupied prairie dog habitat in recent times but suffered a plague outbreak prior to 2003. Approximately 2,430 ha remained in two colonies in the southwest and central portions of the area in 2003. With translocations, this complex could be viable within a few years (L. Hanebury, oral commun., 2003). Since surveys of suitable habitat on the Crow Indian Reservation have not been completed, sites other than the Leachman site may also exist (L. Hanebury, oral commun., 2003).

Northern Cheyenne Indian Reservation

Suitable habitat exists on the Reservation along the upper Tongue River in Big Horn and Rosebud Counties as well as on adjacent U.S. Forest Service and private lands. Occupied habitat exceeded 5,265 ha prior to a recent plague outbreak. With the help of translocations, this site grew to approximately 2,025 ha in 2003 (L. Hanebury, oral commun., 2003).

Miles City Bureau of Land Management District

Potential habitat exists in Custer and Prairie Counties. This site is mixed private and BLM lands and supported approximately 2,430 ha of prairie dogs in 2000; however, recent plague outbreaks have reduced the size of this complex to approximately 1,337 ha. A change in land ownership resulted in reduced access for mapping, which may have exaggerated the apparent decline in occupied habitat (L. Hanebury, oral commun., 2003).

Fort Benton-Roundup-Harlowton Area

Suitable habitat exists along the upper Musselshell River in Yellowstone, Stillwater, Musselshell, Golden Valley, Wheatland, and Petroleum Counties. The area is mixed private, BLM, and FWS lands and supported >2,430 ha of prairie dogs in 2000 (L. Hanebury, oral commun., 2003).

Nebraska

Only black-tailed prairie dogs occur in Nebraska. Recent surveys estimate 32,400 ha of occupied habitat (M. Fritz, oral

commun., 2003) in western Nebraska. The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 55,588 ha.

Intermediate Potential Sites

Blue Creek Ranch

This site, which is owned by Turner Enterprises, Inc., is 16 km northeast of Oshkosh and currently has 8 ha of occupied habitat, which is expanding. Grassland conservation and black-tailed prairie dog expansion are high management priorities (J. Truett, oral commun., 2003).

Oglala National Grassland

This site is located in Sioux and Dawes Counties and currently has 284 ha of occupied black-tailed prairie dog habitat. The Oglala National Grassland will require time to expand existing prairie dog habitat and to consolidate the land base to improve the management potential (S. Larson, written commun., 2003).

New Mexico

Black-tailed and Gunnison's prairie dogs occur in New Mexico. Recent black-tailed prairie dog surveys estimate 24,300 ha of occupied habitat (Johnson and others, 2003) in eastern New Mexico. The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 35,288 ha. Surveys are ongoing for Gunnison's prairie dog, but there is no estimate of current occupied habitat.

Intermediate Potential Sites

Vermejo Park Ranch

This site, which is owned by Turner Enterprises, Inc., is located 40 km southwest of Raton and currently has 689 ha of occupied habitat, which is expanding rapidly. Grassland conservation and black-tailed prairie dog expansion are high priorities (J. Truett, oral commun., 2003).

Quay/Curry County Interface

This site is south of Tucumcari and contains >3,848 ha of occupied habitat, with >2,025 ha contiguous. The mean size of colonies is 19 ha, and the maximum area of a single colony is 152 ha (Johnson and others, 2003).

Roosevelt County/Grulla National Wildlife Refuge

This site is south of Portales and contains >5,265 ha of occupied habitat, with >2,025 ha contiguous. The mean size of colonies is 35 ha, and the maximum size of a single colony is 339 ha (Johnson and others, 2003).

Lea County

This site is northeast of Lovington and contains approximately 9,720 ha of occupied habitat, with >2,025 ha contiguous. The mean size of colonies is 60 ha, and the maximum area of a single colony is 956 ha (Johnson and others, 2003). Plague has recently been active in this area, but impacts have not been quantified (P. Gober, oral commun., 2003).

Union County

This site is southwest of Clayton and contains approximately 3,240 ha of occupied habitat. The mean size of colonies is 41 ha, and the maximum area of a single colony is 292 ha (Johnson and others, 2003).

North Dakota

Only black-tailed prairie dogs occur in North Dakota. Recent surveys estimate 8,303 ha of occupied habitat (Knowles, 2003) in western North Dakota. The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 40,723 ha.

Intermediate Potential Sites

Horse Creek Area, Little Missouri National Grassland

Black-tailed prairie dogs occupy 162 ha at this site in McKenzie County in western North Dakota. The site has strong potential to reach biological readiness for black-footed ferret reintroduction within 10 years, but local support cannot be predicted at this time. The site is included in the most recent land management plans for Little Missouri National Grassland and is plague free (S. Larson, written commun., 2003).

Standing Rock Indian Reservation

Black-tailed prairie dogs occupy 1,215 ha at this site in Sioux County. Colonies are scattered over a large area, and the land base is a checkerboard of private and tribal lands. The area is plague free (S. Larson, written commun., 2003).

South Unit, Theodore Roosevelt National Park

Black-tailed prairie dogs occupy 729 ha at this site in Billings County. In 2002, 61 active colonies were mapped (Knowles, 2003). Knowles (2003) predicted that the site potential on the national park is >2,633 occupied ha based on the amount of suitable habitat present. Additional suitable habitat occurs on adjacent private land, and the area is plague free (Knowles, 2003).

Little Missouri River

Black-tailed prairie dogs occupy this site in Slope County. The site had 345 ha of occupied habitat in 2002. Significant biological potential exists if private land issues can be addressed. The area is plague free (Knowles, 2003).

Oklahoma

Only black-tailed prairie dogs occur in Oklahoma. Recent surveys estimate 26,007 ha of occupied habitat (J. Hoagland, oral commun., 2003) in western Oklahoma. The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 27,806 ha.

Intermediate Potential Sites

Sites in Oklahoma have previously been described as clusters of colonies (M. Lomolino, written commun., 2003).

Cimarron County

This site is in the southwestern corner of the county. Cluster A had 12 colonies totaling 345 ha, and Cluster B had 6 colonies with a total of 652 ha when mapped in 1996–98 (Lomolino and Smith, 2001; M. Lomolino, written commun., 2003).

Texas County No. 1

This site is in the north-central part of the county. Cluster C had 12 colonies with a total of 332 ha when mapped in 1996–98 (Lomolino and Smith, 2001; M. Lomolino, written commun., 2003).

Texas County No. 2

This site is in the east-central part of the county. Cluster D had 18 colonies with a total of 302 ha when mapped in 1996–98 (Lomolino and Smith, 2001; M. Lomolino, written commun., 2003).

Beaver County No. 1

This site is in the east-central part of the county. Cluster E had 10 colonies with a total of 93 ha when mapped in 1996–98 (Lomolino and Smith, 2001; M. Lomolino, written commun., 2003).

Beaver County No. 2

This site is in the south-central part of the county. Cluster F had 34 colonies with a total of 319 ha when mapped in 1996–98 (Lomolino and Smith, 2001; M. Lomolino, written commun., 2003).

South Dakota

Only black-tailed prairie dogs occur in South Dakota. A 2001 survey estimated 64,800 ha of occupied habitat (South Dakota Prairie Dog Work Group, 2001) in western South Dakota. The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 80,786 ha.

Active Sites

Cheyenne River Indian Reservation

Black-tailed prairie dogs occupy this site in Dewey and Ziebach Counties. Total occupied habitat is 17,861 ha in three separate complexes, one of which is 8,424 ha. An operational prairie management program is currently pursuing black-footed ferret reintroduction. There is no history of plague in the area (M. Lockhart, written commun., 1999–2003).

Conata Basin/Badlands National Park

Black-tailed prairie dogs occupy this site in Pennington, Shannon, and Jackson Counties. Total occupied habitat is 6,116 ha, with 4,779 ha on U.S. Forest Service lands and 1,337 ha on National Park Service lands. The estimated potential for the area based on suitable habitat is 7,128 ha. There is no history of plague in the area (M. Lockhart, written commun., 1999–2003).

Rosebud Indian Reservation

Black-tailed prairie dogs occupy 28,350 ha at this site in Todd and Mellette Counties, 18,225 ha of which is on tribal trust lands. There is no history of plague in the area (M. Lockhart, written commun., 1999–2003).

Intermediate Potential Sites

Pine Ridge Indian Reservation

Black-tailed prairie dogs occupy 20,250–40,500 ha on tribal lands at this site in Shannon County. The site has the biological capacity to support a large black-footed ferret population but may be constrained by social, cultural, and political factors (S. Larson, written commun., 2003).

Standing Rock Indian Reservation

Black-tailed prairie dogs occupy 2,835 ha at this site in Corson County. Black-tailed prairie dogs are scattered over a large area, and the land base is a mixture of private and tribal. There is no history of plague in the area (S. Larson, written commun., 2003).

Lower Brule Indian Reservation

Black-tailed prairie dogs occupy 11,745 ha at this site in Stanley and Lyman Counties. There is no history of plague in the area (S. Larson, written commun., 2003).

Wind Cave National Park

Black-tailed prairie dogs occupy 689 ha at this site in Custer County. Biologically, this site could be ready for black-footed ferret reintroduction within a few years, and the National Park Service is supportive. There is no history of plague in the area (S. Larson, written commun., 2003).

Grand River National Grassland

Black-tailed prairie dogs occupy 648 ha at this site in Perkins and Corson Counties. Biologically, this site is not ready for black-footed ferret reintroduction, as it needs time for black-tailed prairie dogs to expand occupied habitat. The U.S. Forest Service needs to consolidate its land base; however, it has identified the site for prairie dog expansion in the most recent land management plan. There is no history of plague in the area (S. Larson, written commun., 2003).

Bad River Ranches

Black-tailed prairie dogs occupy this site on lands owned by Turner Enterprises, Inc., in Stanley and Jones Counties, 16 km southwest of Pierre. The site currently has 506 ha of occupied habitat and is growing steadily. Grassland conservation and black-tailed prairie dog expansion are high priorities. There is no history of plague in the area (J. Truett, oral commun., 2003).

Smithwick Area, Buffalo Gap National Grassland, Fall River Ranger District

Black-tailed prairie dogs occupy 405 ha at this site in Custer County. From a biological standpoint, the site could be ready for black-footed ferret reintroduction within 5 years. The site was included in the most recent land management plan for Buffalo Gap National Grassland. There is no history of plague in the area (S. Larson, written commun., 2003).

Texas

Only black-tailed prairie dogs occur in Texas. Ongoing surveys currently estimate 79,785 ha of occupied habitat in western Texas (D. Holdstock, oral commun., 2003). The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 118,717 ha.

Intermediate Potential Sites

Rita Blanca National Grassland

Black-tailed prairie dogs occupy this site north of Dalhart in Dallam County. The site was identified by Lair and Mecham (1991) as having >4,050 ha of occupied habitat, with 49 colonies >41 ha in size and >1.0 percent of the land area in prairie dog colonies (Lair and Mecham, 1991; Ernst, 2001).

Muleshoe National Wildlife Refuge

Black-tailed prairie dogs occupy this site northwest of Lubbock in Bailey County. It was identified by Lair and Mecham (1991) as having >2,835 ha of occupied habitat, with 25 colonies >41 ha in size and >1.0 percent of the land area in prairie dog colonies (Lair and Mecham, 1991; Ernst, 2001).

Sherman County

Black-tailed prairie dogs occupy this site north of Dumas. It was identified by Lair and Mecham (1991) as having >3,240 ha of occupied habitat, with 32 colonies >41 ha in size and 1.5 percent of the land area in prairie dog colonies (Lair and Mecham, 1991; Ernst, 2001).

Deaf Smith County

Black-tailed prairie dogs occupy this site southwest of Amarillo. It was identified in Lair and Mecham (1991) as having >5,670 ha of occupied habitat, with 55 colonies >41 ha in size and 1.5 percent of the land area in prairie dog colonies (Lair and Mecham, 1991; Ernst, 2001).

Utah

Gunnison's prairie dogs and white-tailed prairie dogs occur in Utah. Data on locations and occupied area are still being developed for both species.

Active Sites

There is one active black-footed ferret reintroduction site in Utah (see discussion under Colorado).

Immediate Potential Sites

Cisco Desert

White-tailed prairie dogs occur at this potential site identified by the Black-footed Ferret Recovery Program. The site was mapped in 1986 (Boschen, 1986) and again in 2002 (Seglund and others, 2005a). The site is on public land in Grand County in east-central Utah along I-70 from east of Green River to the Colorado border. Land ownership is mixed private, State, and Federal (M. Lockhart, written commun., 1999–2003).

Intermediate Potential Sites

Buckhorn and Crescent Junction

White-tailed prairie dogs occupy this site in Emery and Grand Counties in south-central Utah. According to C. McLaughlin (oral commun., 2003), Cedar Creek Associates mapped 7,644 ha, including both active and inactive colonies, in this complex on public lands in 1985. The area mapped extended south of Huntington to I-70 along State Highway 10, east to State Highway 6, and along I-70 to Thompson Springs. In 2002, mapping within the same area recorded 7,881 ha, including active and inactive colonies, approximately a 3 percent increase from 1985 (C. McLaughlin, written commun., 2003).

Twelvemile Flat

White-tailed prairie dogs occur at this site on public lands in the BLM Diamond Mountain Resource Area west and north of Green River in northeastern Utah. Twelvemile Flat contained 363 ha of occupied habitat in 1985. The site was resurveyed in 1992–93 (Cranney and Day, 1994) and found to have 771 ha of occupied habitat, slightly over double the amount present in 1985. In 2002, mapping located 365 ha of occupied habitat (C. McLaughlin, written commun., 2003).

Eightmile Flat (Myton Bench)

White-tailed prairie dogs occur at this site on public lands in the BLM Diamond Mountain Resource Area west and north of Green River in northeastern Utah. Eightmile Flat contained 2,673 ha of occupied habitat in 1985. The site was resurveyed in 1999 and found to have increased by 9 percent, to 2,936 ha of occupied habitat (C. McLaughlin, written commun., 2003).

Sunshine Bench/Brush Creek

White-tailed prairie dogs occur at these sites on public lands in the BLM Diamond Mountain Resource Area west and north of Green River in northeastern Utah. The sites were mapped to evaluate their suitability for black-footed ferret reintroduction in 1992–93 (Cranney and Day, 1994). The Sunshine Bench complex contained 2,085 ha of occupied habitat in 1992–93, while the adjacent Brush Creek area contained 145 ha of occupied habitat. The combined occupied area of Sunshine Bench and Brush Creek was 7,837 ha in 2002 (C. McLaughlin, written commun., 2003).

Buckhorn Flat

White-tailed prairie dogs occur at this site on public lands 56 km south of Price. The estimated occupied habitat at the site is 2,412 ha (A. Seglund, written commun., 2003).

Wyoming

Black-tailed and white-tailed prairie dogs occur in Wyoming. Black-tailed prairie dogs occur in the eastern one-third of the State. Recent occupied habitat estimates range widely, but the current estimate is 50,625 ha (M. Grenier, written commun., 2003). The estimate of suitable habitat based on the Bailey Ecoregion habitat model (Luce, 2003) is a minimum of 64,059 ha. White-tailed prairie dogs occur in the west-central part of the State, and surveys are underway to estimate occupied habitat.

Active Sites

Shirley Basin

Shirley Basin/Medicine Bow is the only active black-footed ferret reintroduction site in Wyoming and occurs in the white-tailed prairie dog range. The site was fully mapped in 1989 (Conway, 1989) and again in 1990 by using a combination of aerial transects and ground verification (Hnilicka and Luce, 1992). In 1990, intensive mapping showed the complex to contain 59,726 ha (Parrish and Luce, 1990). Captive-bred

black-footed ferrets were released from 1991 to 1994, and the highest number of black-footed ferrets found on subsequent surveys was in 2004, when 85 individuals were located during spotlight surveys (Grenier and others, 2004) of less than 20 percent of the occupied habitat (based on 1990 mapping data). Therefore, considerable potential exists for a large, contiguous population of black-footed ferrets or several subpopulations. It is important to note that both prairie dogs and black-footed ferrets have persisted with plague present since at least 1987 (Orabona-Cerovski, 1991).

Immediate Potential Sites

Thunder Basin National Grassland

Black-tailed prairie dogs occur at this site in Campbell, Converse, and Weston Counties. The site is identified as a black-footed ferret reintroduction site in the current Forest Plan for the Medicine Bow National Forest/Thunder Basin National Grassland. There was no history of plague before 2001 when an extensive die-off occurred, reducing occupied habitat by over 4,050 ha. Recovery is occurring. Prior to the plague outbreak, occupied black-tailed prairie dog habitat was 8,079 ha, including 7,290 ha on U.S. Forest Service land and 789 ha on State land. The U.S. Forest Service estimates that there are 193,590 ha of potential habitat on its lands in this area of Wyoming (T. Byer, written commun., 2003).

Intermediate Potential Sites

Meeteetse

White-tailed prairie dogs occupy this site west of Meeteetse in Park County. This site, from which all of the black-footed ferret captive breeding stock was taken, had 4,930 ha of occupied habitat in 1982, just after black-footed ferrets were first discovered, and a high population of 129 black-footed ferrets (43 adults, 25 litters) in 1984. Because of plague in white-tailed prairie dogs, occupied habitat was reduced to roughly 2,029 ha by 1989, 2 years after all extant black-footed ferrets were captured for captive breeding (Black-footed Ferret Advisory Team, 1990). The site has not shown significant recovery of prairie dogs since 1989 (Biggins, 2003). The habitat capability of the site remains, including old burrow systems, so the potential exists for recovery to sufficient occupied habitat for black-footed ferret reintroduction within 10 years.

Bolton Ranch

White-tailed prairie dogs occupy this site west of Saratoga in Carbon County. Land ownership is a checkerboard of public and private lands. The site had 4,500 ha of occupied

habitat in 1989 when it was first surveyed (Conway, 1989). No surveys have been conducted since then (Grenier and others, 2003; R. Luce, written commun., 1995).

Carter

White-tailed prairie dogs occupy this site 32 km southeast of Kemmerer, on BLM lands in Lincoln County. The site has not been fully mapped or surveyed to determine prairie dog density. It contained more than 4,050 ha of occupied habitat when partially mapped in the 1980s (Grenier and others, 2003; R. Luce, written commun., 1995). The Carter site is potentially connected to another site (Moxa) which is 32 km north of Kemmerer, indicating that an extremely large complex may exist in this area. Moxa was identified in the mid-1990s when 17,415 ha of occupied habitat were mapped, and the site has not been resurveyed (Grenier and others, 2003; B. Luce, unpub. data, 1995).

Cumberland

White-tailed prairie dogs occupy this site southwest of Kemmerer in Lincoln County. Land ownership is a checkerboard of public and private lands. The site was fully mapped and preliminary density data were collected in the 1980s (Clark and Campbell, 1981). Occupied habitat was 4,293 ha. The site has not been remapped.

Fifteenmile

White-tailed prairie dogs occupy this site on BLM land 40 km west of Worland in Hot Springs County. The site contained 3,078 ha of occupied habitat when mapped in the 1980s and has not been remapped (Grenier and others, 2003; R. Luce, written commun., 1995).

Flaming Gorge

White-tailed prairie dogs occupy this site on BLM land 64 km south of Green River in Sweetwater County. The site was intensively mapped in 1989 and contained 3,049 ha of occupied habitat (Martin and Luce, 1990). It has not been remapped.

Shamrock Hills

White-tailed prairie dogs occupy this site on BLM land 16 km north of Rawlins in Carbon County. The site was mapped in the 1980s and had >4,050 ha of occupied habitat. The site has not been remapped (Grenier and others, 2003; R. Luce, written commun., 1995).

Kaycee

Black-tailed prairie dogs occupy this site west of the town of Kaycee in Johnson County, primarily on private land. This site was discovered recently and has not been mapped, but

it is estimated that >1,215 ha of occupied habitat are present (R. Luce, unpub. data, 2003).

Sheridan Local Training Center

Black-tailed prairie dogs occupy this site on a U.S. Army installation adjacent to Sheridan in Sheridan County. The site contained 284 ha of occupied habitat in 2001, and adjacent private and State lands had a substantial amount of additional occupied habitat (R. Luce, unpub. data, 2003).

Canada

Only black-tailed prairie dogs occur in Canada, which is the northern extent of the range of the species.

Intermediate Potential Sites

Grasslands National Park and Vicinity

Black-tailed prairie dogs occur at this site in Saskatchewan, 160 km south of Swift Current. The site has 25 colonies containing a minimum of 1,044 ha. It has been partially mapped since 1993 but was fully mapped for comparative purposes from 1998 to 2002 and had a stable occupied area for that time period (P. Fargey, written commun., 2003).

Mexico

Black-tailed prairie dogs occur in northern Mexico, the southern extent of the range, and are the only species of prairie dog in Mexico in the historical range of the black-footed ferret.

Active Sites

Janos

Black-tailed prairie dogs occur at this site north of Nuevo Casas Grandes in Chihuahua. Estimated occupied prairie dog habitat is 19,845 ha, and the potential suitable habitat is 55,080 ha. Land ownership is divided between Federal Ejidos and private ownership. This is a large prairie dog complex and may have the potential for one contiguous black-footed ferret population or several subpopulations. No management plan exists for the area (R. List, oral commun., 2003).

Intermediate Potential Sites

There are no Intermediate Potential Sites in Mexico.

Discussion

It is clear from past efforts that a “best and only” methodology for successful black-footed ferret reintroduction has not been unequivocally established. The 1988 recovery plan (U.S. Fish and Wildlife Service, 1988) encourages experimentation. It also emphasizes a management philosophy important for both establishing and maintaining reintroduced populations whereby the broadest possible distribution of black-footed ferrets might be achieved. This risk management approach is important to protect the species overall from adverse impacts that may occur locally, especially disease.

Preparation of this paper does not constitute a proposed State or Federal action at any of the proposed sites; it is merely a conceptual approach to aid in black-footed ferret recovery. Many steps will be required before any site can eventually receive ferrets; however, I do not believe that it is necessary or appropriate to wait for final biological, social, and political issues to be addressed at a given site in order for it to be considered for the list of potential reintroduction sites. This conceptual exercise identifies sites based entirely on either a minimum area of occupied prairie dog habitat or a small but increasing prairie dog population at a site that has the habitat characteristics necessary to support black-footed ferrets. I recognize that myriad actions would be necessary before black-footed ferrets could actually be released at a given site, especially where private lands are involved.

The general limitation of lack of habitat or habitat availability is shared with many other species. But in the case of the black-footed ferret, which is a highly specialized prey/habitat obligate of prairie dogs, dependence has proven to be especially catastrophic because of the dramatic reduction of its prey over the past century by adverse land-use practices such as prairie conversion to cropland, poisoning to reduce forage competition with domestic livestock, and sylvatic plague, an exotic disease catastrophic to prairie dogs (Cain and others, 1972; Hansen, 1988; Cully, 1993; Van Pelt, 1999; U.S. Fish and Wildlife Service, 2000; Cully and Williams, 2001; Antolin and others, 2002; Luce, 2003). Despite these potential conflicts and future challenges, identification of appropriate sites for black-footed ferret reintroduction has been ongoing for over two decades.

Although occupied prairie dog habitat has been significantly reduced since western settlement (Hoogland, 1995; Miller and Cully, 2001), it has been only in the last decade that the degree of both the quantity and quality of this loss relative to potential black-footed ferret recovery has been recognized. At present there may not be sufficient occupied prairie dog habitat in total in the historical ranges of the black-tailed prairie dog, white-tailed prairie dog, and Gunnison's prairie dog, either in quantity or quality, for the black-footed ferret to be

fully recovered, especially if black-footed ferret populations are to be broadly represented geographically as a precaution against depressant stochastic influences (M. Lockhart, written commun., 1999–2003).

The 1988 Black-footed Ferret Recovery Plan (U.S. Fish and Wildlife Service, 1988) set a downlisting goal for the species at 1,500 adults in 10 or more populations dispersed across its historical range, with no single population being less than 30 adults. Downlisting the species would move it from endangered to threatened status but would not represent complete recovery. Delisting the black-footed ferret through recovery sufficient to obviate its endangered status and permit its removal from the endangered species list (pursuant to the Endangered Species Act of 1973, as amended) would require even more recovery sites.

I suggest that it may be necessary to evaluate an order of magnitude more sites to achieve complete recovery and delisting, or 100 sites across the historical range of the species. These sites should be widely dispersed and represent the variety of habitats available, including different prairie dog species, ecological circumstances, disease prevalence, and the like. Since some sites may prove not to be usable for biological, social, or other reasons, or may not be successful, it will be necessary to consider many.

Plague is a confounding factor. Annual monitoring to document plague activity and the amount of habitat affected would assist prairie dog and black-footed ferret management. Continuing research on the mechanisms by which plague is spread, pretreatment of prairie dogs, and posttreatment of burrows to kill fleas and thus reduce the magnitude of an epizootic may allow practical management of the disease in the next 10 years. Meanwhile, maintaining spatial distribution of prairie dog complexes and isolated colonies over the entire range to act as reservoirs to replace prairie dogs lost to plague, as well as development of black-footed ferret reintroduction sites east of the plague line (in the plague-free area), will greatly assist in managing the impacts of the disease on prairie dogs.

In my opinion, data presented by Cully and Williams (2001) suggest that a fundamental change may be occurring in prairie dog ecology whereby some large colonies, especially those of black-tailed prairie dogs, may not persist when repeatedly challenged by plague. Persistence of only small colonies or complexes may have serious implications for black-footed ferret recovery. Extensive habitat will be necessary for reintroduction success, especially in the absence of management, and few large sites may persist at their full habitat capability in the face of repeated plague epizootics. On the other hand, recent surveys of white-tailed prairie dogs and black-footed ferrets in Shirley Basin, Wyo., indicate that these areas may have proportionately higher value than previously thought because both prairie dogs and black-footed ferrets have maintained significant populations in the presence of plague since monitoring was begun in 1991 (Luce, 2002;

Grenier and others, 2004). In fact, both white-tailed prairie dog and black-footed ferret numbers increased despite more than 10 years of active plague (Grenier and others, 2004).

Status of Prairie Dog Conservation

Since black-footed ferret recovery and prairie dog management issues are closely tied, the future of the black-footed ferret essentially depends on developing effective management of black-tailed, white-tailed, and Gunnison's prairie dogs. The Black-tailed Prairie Dog Conservation Team (later just the Prairie Dog Conservation Team), which includes representatives from 12 State wildlife agencies, has been working since 1998 to develop effective conservation for prairie dogs. The team first developed the Black-tailed Prairie Dog Conservation Assessment and Strategy (Van Pelt, 1999), which was followed by an addendum called the Black-tailed Prairie Dog Multi-State Conservation Plan (Luce, 2003), a guideline for development of State black-tailed prairie dog management plans. Black-tailed prairie dog management plans have been completed in Colorado, Kansas, Montana, New Mexico, North Dakota, Oklahoma, and Texas. Draft management plans are moving toward finalization in South Dakota and Wyoming. Arizona has a draft management plan and is currently evaluating black-tailed prairie dog reintroduction, while Nebraska does not expect to continue development of a management plan.

The Black-tailed Prairie Dog Multi-State Conservation Plan includes several provisions that are important to black-footed ferret recovery, two areas of which are of the greatest significance. First, the objectives for occupied area, shown in table 3, indicate a commitment on the part of a majority of the States with black-tailed prairie dogs to increase the occupied area from 631,127 ha to 685,946 ha by 2011 (Luce, 2003). Second, the Multi-State Conservation Plan sets other target objectives for the United States as follows:

1. Maintain at least the current occupied area of black-tailed prairie dog habitat in the two complexes greater than 2,025 ha that now occur on and adjacent to Conata Basin-Buffalo Gap National Grassland, S. Dak., and Thunder Basin National Grassland, Wyo.
2. Develop and maintain a minimum of nine additional complexes greater than 2,025 ha (with each State managing or contributing to at least one complex) by 2011. A State could contribute to a 2,025 ha complex along a State boundary by cooperating with the adjacent State to manage part of the complex. A similar agreement could be developed between a State and a Native American tribe.
3. Achieve and maintain at least 10 percent of total occupied habitat in colonies or complexes greater than 405 ha by 2011.

Table 3. Estimates of historical, current, gross, and suitable black-tailed prairie dog (*Cynomys ludovicianus*) habitat, and the 10-year minimum habitat objective (Luce, 2003). Native American tribes in Montana, South Dakota, and North Dakota will set an occupied-area objective independent of the States.

State	Historical potential habitat ¹ (ha)	Current occupied habitat ² (ha)	Gross habitat ³ (ha)	Suitable habitat ⁴ and minimum 10-year objective ⁵ (ha)
Arizona	2,854,090	0	2,854	1,861
Colorado	11,077,916	255,596	110,779	103,588
Kansas	14,513,206	52,861	61,039	60,181
Montana	24,479,316	36,450	120,401	97,349
Nebraska	14,594,350	32,400	59,430	55,588
New Mexico	15,803,686	24,300	39,148	35,288
North Dakota	4,473,334	8,303	44,733	40,723
Oklahoma	8,750,479	26,007	28,702	27,806
South Dakota	11,851,333	64,800	88,339	80,786
Texas	31,829,943	79,785	125,933	118,717
Wyoming	8,937,378	50,625	75,524	64,059
Total	149,165,031	631,127	756,882	685,946

¹Historical potential habitat = total potential habitat (not occupied habitat) encompassed within the range of the black-tailed prairie dog (as mapped by Hall, 1981). See Luce (2003) for further explanation.

²Current occupied habitat = estimates provided by the individual States.

³Gross habitat = total area of core range $\times 0.01$ + area of secondary range $\times 0.001$. Core range was defined as Bailey Ecoregions dominated by shortgrass prairie plants and having black-tailed prairie dogs on the list of native fauna. Secondary range was defined as Bailey Ecoregions dominated by plants not associated with shortgrass prairie, or having historically suitable habitat but a current sociopolitical climate unfavorable for prairie dog management. See Luce (2003) for additional details.

⁴Suitable habitat = gross habitat minus habitat with $>10\%$ slope and habitats such as large bodies of water, badlands, wetlands, forests, or other features not used by prairie dogs. Agricultural lands were included if they met the slope criterion.

⁵Minimum 10-year objective = objective for minimum area of occupied prairie dog habitat in each State, and total for the 11 States, by 2011.

- Maintain distribution across at least 75 percent of the counties in the historical range or at least 75 percent of the historical geographic distribution. Ten States currently meet this objective (Arizona does not since the black-tailed prairie dog was extirpated), and all but Nebraska and Arizona have black-tailed prairie dogs in 100 percent of the counties in the historical range. This objective addresses the need to maintain all prairie dog colonies, whatever the size or location, throughout the range. State management plans will deal directly with management of complexes and individual, isolated colonies.

Management strategies for black-tailed prairie dogs on tribal lands were prepared for the Intertribal Prairie Ecosystem Restoration Consortium in January 2002 (T. Vosburgh, oral commun., 2003). The goal is to develop and implement management programs for the conservation of prairie dog habitat. These management strategies were revised on February 4, 2002, following review and comment from participating

tribes, the U.S. Fish and Wildlife Service, and the Interstate Coordinator for the 12-State Prairie Dog Conservation Team. The consortium convened twice in 2002 and is working with other groups and agencies to move prairie dog management and conservation forward. The tribes have drafted plans to ensure that prairie dog populations and habitat are maintained. The Lower Brule and Fort Belknap Indian Reservations have final prairie dog management plans in place, and draft plans have been prepared for the Fort Berthold, Northern Cheyenne, Crow Creek, and Rosebud Indian Reservations.

The States of Wyoming, Colorado, Utah, and Montana developed a conservation assessment for the white-tailed prairie dog in 2005 (Seglund and others, 2005a), as did the States of Arizona, New Mexico, Colorado, and Utah for the Gunnison's prairie dog (Seglund and others, 2005b). When a conservation strategy is developed for the Gunnison's prairie dog, complexes of colonies will be identified, and other sites with black-footed ferret reintroduction potential may thus become apparent.

Summary and Recommendations

The black-footed ferret recovery program has faced and overcome several obstacles to reach the point where it is today. Foremost were capture of the wild population at Meeteetse, Wyo., captive breeding, development of release strategies, and release site identification based on habitat suitability and other factors. Given that those obstacles to success were overcome, I believe that, at the present time, continued progress on black-footed ferret recovery depends upon identification and active management of additional reintroduction sites. To that end, I identify 70 sites in the historical range of the black-footed ferret that might meet the biological and habitat suitability requirements for reintroduction of black-footed ferrets within 3–10 years, contingent upon directed management emphasis, State and Federal agency management priorities, and, if on private land, landowner concurrence based on agreements or incentives.

The Black-footed Ferret Recovery Implementation Team and Prairie Dog Conservation Team are encouraged to:

- Cooperate closely with State and Federal agencies and eight tribal governments to move toward the targets set in the Black-tailed Prairie Dog Multi-State Conservation Plan and State and tribal management plans.
- Assist the White-tailed and Gunnison's Prairie Dog Working Groups to develop management plans for both species.
- Cooperate to evaluate the sites presented in this paper and develop strategies to begin management of as many sites as possible for black-footed ferret reintroduction within 10 years.
- Support and advance the High Plains Partnership landowner incentive program and/or other programs designed to bring about landowner participation in grassland species management.

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