Food Webs: Linkage, Interaction Strength and Community Infrastructure

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FOOD WEBS: LINKAGE, INTERACTION STRENGTH AND COMMUNITY INFRASTRUCTURE

THE THIRD TANSLEY LECTURE

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INTRODUCTION

It seems particularly opportune to discuss food webs and evolving views on their structure here for both their genesis and first modern treatment (Elton 1927) and much of their later development (May 1973; Pimm & Lawton 1978) has a decidedly British accent to it. The central significance of webs is derived from the fact that the links between species are often easily identified and the resultant trophic scaffolding provides a tempting descriptor of community structure. If this structure is in any fashion related to the persistence of natural communities or their stability, however defined, then we are dealing with issues of vital ecological importance.

Elton's views have admirably withstood the tests of time. They were especially useful to field biologists, and encouraged the assembly and organization of feeding data into networks of trophically bonded species or higher taxa. The early emphasis was on connectedness *per se*. Perhaps the first significant deviation from this theme was the development of the trophic dynamic viewpoint of Lindeman (1942) and all subsequent efforts to describe energy transfer and material flow through communities. A second departure, and one I believe to be conceptually richer, was the formalization of the view that web structure and community stability were related (MacArthur 1955). May (1973) in another landmark publication questioned this relationship and called attention to four primary web features: the number of species involved, the nature of their interconnections, the number of connections per species, and the intensity of interaction between web members. This focus has stimulated application to agroecosystems (Southwood & Way 1970), new interpretations of the number of trophic levels (Pimm & Lawton 1977), and a resurgence of interest in the significance of mutualism (Vance 1978). It has not been characterized by stunning breakthroughs, ecological stability remains a frustrating issue, and to a field ecologist, the ties between model and reality at times appear remote. All but ignored in these recent developments is an insightful recognition that trophic pathways might contribute little to ecosystem stability, and that the answers lie in the spatial patterning of the environment (Smith 1972). I wish to return to the basic observations on food webs as a naturalist and experimentalist, and employing an approach advocated by Sir Arthur Tansley (Godwin 1977), ask whether we are modelling their correct properties, and if not, what modifications might be made.

TERMINOLOGY

The assumed importance of predator-prey or consumer-resource relationships, their relative ease of observation, and an attractive, simple graphical format have accelerated the interest of ecologist and mathematician alike on web structure and organization

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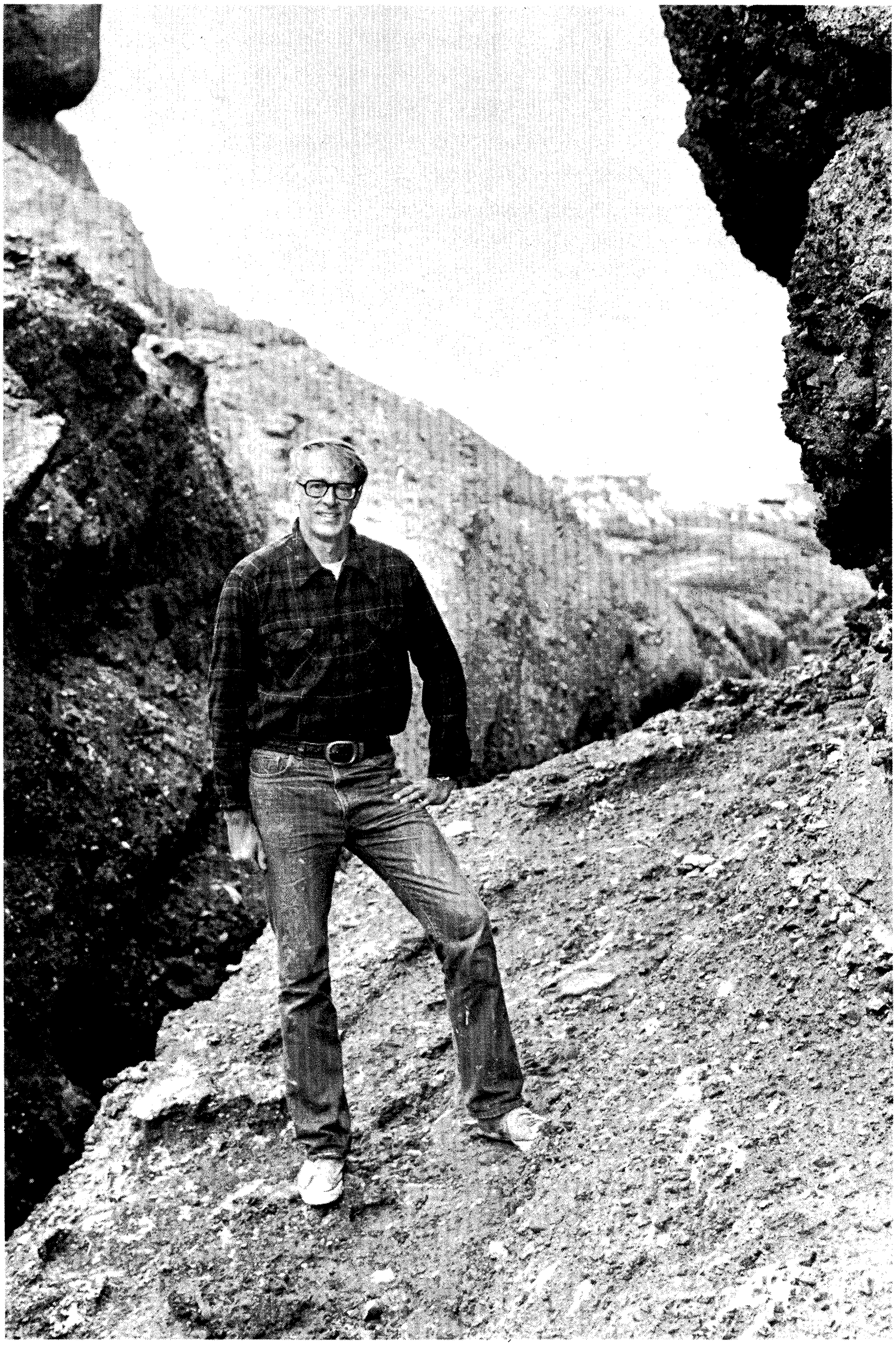

Professor R. T. Paine

(Cohen 1978; MacDonald 1979). I have found the following terms useful, and apply most of them in their common-sense, conventional ways.

Food chains and webs. The concept was apparently Elton's (1927). A hierarchy of monophagous consumers would constitute a chain: collection of these into broader units incorporating polyphagous consumers generates a web (or food cycle). In many respects, these differ little from Darwin's (1859, p. 59) view that plants and animals 'are bound together by a web of complex relations.' Interacting species may be related through trophic links, and the number of such links per consumer measures its connectedness or connectance (May 1973). Unfortunately, there is currently no prescription for how much grouping by taxa or guild might be permissible when determining trophic connections. Cohen (1978) has discussed the point and his and other analyses (for instance, MacDonald 1979; Pimm & Lawton 1978) suggested that some taxonomic lumping introduces little apparent bias.

Trophic levels. The term is one of convenience but assignment to a level often cannot be made. Elton (1927) both recognized and paid particular attention to the obscuring influences of body size, and gave numerous examples of omnivores. Lindeman (1942) identified specific levels, but clearly stated that they became less precise as one moves up the food chain. Darnell (1961), amongst many, has argued for the prevalence of rampant trophic opportunism: consumer nutrition is often derived from numerous prey categories which themselves cannot be assigned to any single level. Although many species are more eclectic in their dietary choices, nonetheless it is impossible to defend the sanctity of the trophic level concept.

Cross-linkage. Alteration of a predator's density bears immediate potential significance for its prey. If space or other resources are limiting, changes resulting from competitive interactions are apt to be induced within the prey guild. I refer to these lateral connections between competitors within the community nexus as cross-links. I believe it essential that they be distinguished from trophic links.

Linkage strength. The strength or importance of a trophic relationship cannot be assumed equivalent for all web members. A consumer will be a strong interactor if, in its absence, pronounced changes ensue (MacArthur 1972). Removal of a weakly interacting species will yield no or slight change. The emphasis is on the functional role occupied by species within food webs as determined by experimental alterations of their abundances. The relative strength of interaction is in part due to the consumer's density, in part to limitation to the predation process imposed by prey size (Paine 1976). Predator food preference is an essential ingredient, and an effect is especially likely when the prey is competitively superior (Harper 1969; Paine 1969). In some senses 'strength' is an abstraction, for under some circumstances a potentially significant interaction may not be realized. Conversely, it is difficult to envision conditions which would reveal the outcome of a fundamentally weak interation. A graphical description of linkage strength and other symbolisms are shown in Fig. 1.

Modules. Strong trophic interactions can produce predictable, persistent patterns in the resource guilds. Species that seem dependent on these resources, give evidence for evolved modification for use of, or association with, these resources, and that disappear upon the removal of a strongly interacting species (or appear with its addition) will be said to belong to a module. A module thus includes both a resource set and their specific

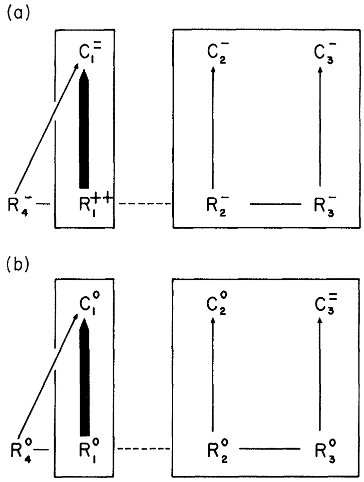

FIG. 1. A graphical model of interaction strength. (a) Strong interaction (b) weak interaction. The topological position of three consumers (C) and four resource states (R) are identical. The superscript identifies the proposed direction of change (−, decrease; + +, major increase; 0, no change) following removal (=) of a species. The heavy line indicates a strong interaction; the four species C_2, R_2, C_3, R_3 comprise a module (see text); the dashed line signifies the dependency of the module on the C_1–R_1 relationship.

consumers which, under conditions favouring maximal coevolution, will behave as a functional unit. May (1973) alludes to these as subsystems; Gilbert (1977) refers to them as coevolved food webs. In the engineering terminology of dynamical systems they may be components or subsets. Whichever term is applied, they are obviously important within food webs both because of the unit nature of their response and for the large number of species, and therefore potential number of links, involved. A module involving four species and linked to a strong interaction is shown in Fig. 1. Removal of C_1 produces an immediate increase in R_1 and initiates the disappearance of the modular components C_2, R_2, C_3 and R_3.

VARIATIONS IN LINKAGE

Food webs are idealized pictures of complex trophic patterns that change seasonally and geographically. When emphasis is placed on the linkage arrangements per se, perspective is lost on the extent of their variability and responses to local environmental change. Because connectedness in natural webs can be observed directly, and forms the basis for most mathematical exploration of web properties (Cohen 1978; Gallopin 1972; Levins 1975; May 1973) I present here two webs constructed from observations at Cape Flattery, Washington state, and Torch Bay, Alaska (Fig. 2). I have ignored tradition and not attempted to cast the participants into trophic levels. The arrows point towards the predator. Further, the symbolism of Fig. 1 is used to identify strongly interacting pairs and dashed lines and brackets suggest modules or interaction dependent subgroups.

The Cape Flattery web encompasses earlier research at mainland sites (Paine 1966; Paine & Vadas 1969) and more recent material from Waadah and Tatoosh Islands (Paine 1976, 1977). Although fourty-four taxa are given, this remains but a small portion of over 300 possible (Suchanek 1979). Nonetheless, I believe that all the major components

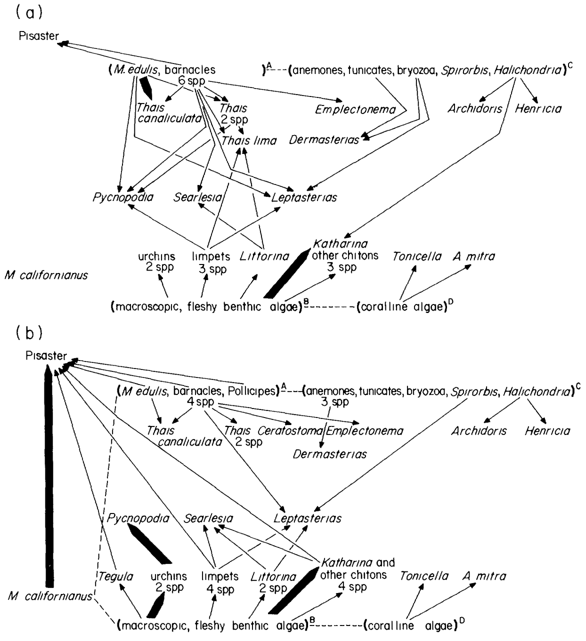

FIG. 2. Two eastern Pacific rocky intertidal food webs. (a) Torch Bay, Alaska (b) Cape Flattery area, Washington. The topological positions of species common to both is identical. Symbolism is the same as in Fig. 1.

have been identified with the exception of the anemone *Anthopleura xanthogrammica* (Brandt), two uncommon gastropod species (*Thais lamellosa* (Gmelin) and *Onchidoris bilamellata* (Linnaeus)) and five species of crab. This intertidal community is also subject to avian predation by oystercatchers (*Haematopus bachmani* Audubon), black turnstones (*Arenaria melanocephala* (Vigors)), surfbirds (*Apriza virgata* (Gmelin)), and glaucous-winged gulls (*Larus glaucescens* Naumann). None of these omissions is thought to be functionally significant, although the anemone is clearly partially coupled to the foraging activities of starfish (Dayton 1973) and both gastropods join a complex of others primarily if not solely exploiting barnacles. Other studies supplementing these trophic patterns are Mauzey (1966); Mauzey, Birkeland & Dayton (1968); Connell (1970); Dayton (1971); Menge (1972a, 1972b); Menge & Menge (1974); Nicotri (1977) and Louda (1979). Hewatt (1937) and Menge & Sutherland (1976) present more abbreviated summaries of the same food web.

The Torch Bay web is not as well known primarily because of the remoteness of the site. The community has most of the same taxa as that at Cape Flattery although *Mytilus californianus* Conrad is rare, occurring mainly in tide pools. Experiments and strong inference indicate the distribution of its smaller and thinner-shelled congener, *M. edulis* Linnaeus, is controlled by the predatory gastropod *Thais canaliculata.* (Duclos). The intertidal algal community appears controlled by the herbivore *Katharina tunicata* (Wood).

The topological placement of the taxa in both webs (Fig. 2) has been maintained to emphasize the regional changes in connectedness despite the great similarity of the species complements. At Torch Bay, *Pisaster ochraceus* (Brandt) is probably 'just another starfish,' in part because *M. californianus* is a minor community component. Rather than

TABLE 1. Between region shifts in diet of three major invertebrate predators. C.F. refers to Cape Flattery region, Washington and T.B. to Torch Bay, Alaska. Data are given as numbers of prey individuals consumed

Predator	Pisaster		Leptasterias		Pycnopodia	
Location	C.F.	T.B.	C.F.	T.B.	C.F.	T.B.
N. observations	20749	922	221	131	110	108
Prey taxa						
Barnacles						
Balanus glandula	8592		24			
Balanus spp.	2699	182	64	85		8
Chthamalus dalli	2141		23		4	
Pollicipes polymerus	691		1			
Mussels						
Mytilus edulis	1602	733		21		43
M. californianus	2084		7		7	
Chitons						
Katharina tunicata	132	1				1
Tonicella lineata	46					
Mopalia spp.	101		1			1
Herbivorous gastropods	10		4	1	3	5
Tegula funebralis	2184					
limpets	220		14	18		21
Littorina spp.	27		9			
Carnivorous gastropods	75	6	4	1		9
Echinoderms						
Strongylocentrotus spp.	1				93	2
Cucumaria				1		11
starfish					2	1
Annelids (Spirorbis)			57			
Crabs	21		3			1
N. species	41	4	19	11	5	23
H′	1·90	0·24	0·96	0·65	0·26	0·94
Other	123	0	10	4	1	5

being linked to forty-one species, it only connects to four at Torch Bay (Table 1). Sea urchins, though abundant, are not functionally significant *in the lower intertidal* at Torch Bay. On the Washington coast they predominated in the diet of the starfish *Pycnopodia helianthoides* (Brandt) whereas in Alaska they are a minor component. The number of interactions directly involving *Pycnopodia* changes by a factor of 4·6 between regions (Table 1). Conversely, the diet of *Leptasterias hexactis* (Stimpson) seems moderately constant, an observation that might be related to its small body size. There are other major changes in the pattern of connectedness. *Dermasterias* switches its prey entirely between regions, and at Torch Bay *Katharina* is a major sponge consumer and another species of *Thais* has been added. These changes may be due, in part, to regional changes in the character of the exploited resource. For instance, on the Washington coastline, the sponge *Halichondria* occupies about 5% of the available substratum (Paine 1974). At Torch Bay, where I have estimated 20% coverage, this species is heavily consumed by *Katharina* and the starfish *Henricia*. On the other hand, *Katharina* is consistently abundant at both sites (Cape Flattery; $\overline{X}$ = 27·2 m^{-2}, S.D. = 17·7, n = 76; Torch Bay: 24·8, 15·9, 8), lives at comparable tide levels, yet is connected differently to both its prey and predators (Fig. 2).

Although factors underlying these switches cannot be interpreted presently, they surely are not minor. They represent major changes in the pattern of connectedness and therefore of material and energy transfer. Evidence for regional lability in structure is obvious and includes two important web traits: the number and pattern of linkage connections of the higher order consumers and a measure of the diversity (H′; Pielou 1975) of this linkage (Table 1).

Two further sources of variation in trophic pattern can be examined. Table 2 shows the geographic variability of *Pisaster*'s diet over 30 degrees of latitude. Although the intertidal community retains its essential composition (Ricketts, Calvin & Hedgpeth 1968), *Pisaster*'s diet changes substantially, especially in terms of the number of links. Table 3 gives an indication of variation by habitat. The data set encompasses 7633 *Pisaster* observed between June 1963 and August 1971 in four portions of a mosaic environment. Although the total number of prey links is roughly similar, the major connections are highly variable, especially if barnacles are excluded from the comparison. Further, these within-habitat differences seem constant through time. I have shown that in the boulder field, the herbivorous gastropod *Tegula* is consistently the major source of food energy for *Pisaster* (Paine 1969). On mid-intertidal rock platforms, trophic conditions vary little from year to year (Paine 1974) when *Pisaster* is present, and barnacles and mussels are the main dietary items. On low intertidal benches most of the nutrition is derived from chitons. I believe these variations, be they geographic or within habitat, provide little insight into community organization.

STRONG INTERACTIONS: REALITY AND IMPLICATIONS

One of the continuing triumphs of experimental ecology has been in identifying species native to marine benthic and small freshwater ecosystems that play major roles in community organization. The results nicely complement comparisons of natural communities either with or without some major native species, or before or after its reintroduction or exclusion. I believe this body of literature is overwhelmingly convincing, and because its primary message is that nature is complex, subtle and interactive, I will discuss the evidence for strong interactions and some of their consequences as a unit. I exclude from

TABLE 2. Latitudinal variation in the primary diet of *Pisaster ochraceus*

Source	Paine	Feder 1959	Paine	Mauzey 1966	Quinn 1979	Paine
Location	Punta Baja, Mexico	Monterey Bay, California	Outer Coast, Washington	Friday Harbor, Washington	Torch Bay, Alaska	Torch Bay, Alaska
Latitude (°N)	29°54′	36°36′	48°19′	48°37′	58°27′	58°27′
N. Observation	97	633	20749	1554	592	336
Major prey taxa; proportion of total						
Mytilus spp.	0·30	0·17	0·18	0·12	0·80	0·77
Balanus spp.		0·30	0·54	0·51	0·18	0·23
Tetraclita	0·45	0·26				
Chthamalus			0·10			
Pollicipes	0·10	0·04	0·03			
Carnivorous gastropods		0·02	< 0·01	0·04	0·02	
Herbivorous gastropods	0·10	0·11	0·12	0·25		
Chitons	0·03	0·04	0·01	0·07		
Number of links	7	33	41	25	4	2
Diversity (H′) of links	1·40	2·08	1·90	1·99	0·54	0·53

TABLE 3. Major dietary components of *Pisaster ochraceus*, by habitat. Data taken at Mukkaw Bay, Washington, June 1963–August 1971

	Habitat			
	Mid-intertidal rock platforms	Dissected rock platforms	low intertidal rock platforms	Boulder field
Total *Pisaster* examined	1866	1588	1253	2926
Number of censuses	66	45	36	99
Prey taxa				
Barnacles				
Balanus glandula	3025	2512	904	1871
B. cariosus	863	603	87	113
Chthamalus dalli	316	1004	68	639
Pollicipes polymerus	39	47	28	
Mussels				
Mytilus spp.	1453	608	629	40
Chitons				
Katharina tunicata	3	3	108	1
Tonicella lineata		1	43	
Mopalia spp.	1	6	8	81
Herbivorous gastropods				
Tegula funebralis	5	208		1761
Acmaea scutum	14	21	76	39
Acmaea digitalis	26	26	4	3
Other limpets	8		15	5
Littorina scutulata	9	17		1
Carnivorous gastropods				
Thais emarginata	17	14	1	24
Other {total individuals	11	10	53	49
Other {species	9	6	13	12

consideration below the many dramatic examples of major change subsequent to the introduction or exclusion of exotic species (Darwin 1859; Elton 1958; Zaret & Paine 1974), primarily because these impose an influence beyond the evolutionary experience of the assemblage.

The eastern Pacific near-shore community previously mentioned is both biotically rich and roughly comparable from Baja California to the western Aleutian Islands. The experimental exclusion of *Pisaster* in Washington leads to the competitive elimination of all the bracketed categories (Fig. 2) by *M. californianus* (Paine 1966, 1974, and unpublished) despite the presence of numerous other predators. The results obtain because the competitively-dominant mussels become large too rapidly to be controlled effectively by other potential consumers. *Pisaster* consumes most mussel size categories and therefore escapes are relatively scarce in its presence. The experimental exclusion of the sea urchin *Strongylocentrotus purpuratus* (Stimpson) in the same community yields a comparable impact for identical reasons: this urchin controls the growth and distribution of competitively superior benthic algae and it is capable of destroying them at all body sizes. Thus sea urchin removal produces a lush plant community where none had existed previously; urchin addition causes a reversion to a seemingly barren, herbivore resistant flora (Paine & Vadas 1969; Paine 1977). An associated species-rich complex of other herbivores seems to have little influence on the outcome of such manipulations. These modular species are described later. Comparable results obtain when urchin populations elsewhere are manipulated or exploited, as a rich literature attests (Kitching & Ebling 1961; Ogden, Brown & Selesky 1973; for instance).

Human activities have provided useful though ecologically discouraging insights on the significance of linkage patterns within this same community. At one time sea otters were patchily abundant. Their removal has generated a well documented cascade of effects (Estes & Palmisano 1975). Sea otters, although consuming a wide variety of prey, effectively control the abundance of urchins which, in turn, control the algal community. Islands with and without otters are conspicuously different because destabilizations at the highest trophic level induce structural changes which cascade through the community, transmitted by a chain of strongly interacting links. Despite limited opportunity for experimentation, two lines of evidence extend the latter conclusion: the impact of otter reintroduction can be predicted with accuracy (Duggins 1980), and examination of stratified Aleut middens shows that otter remains are inversely correlated with those of urchins (Simenstad, Estes & Kenyon 1978). Although there is as yet no evidence for modules, the cascading influences generate major interisland differences in gull foraging activity (Trapp 1979), and one can argue that the now extinct, enormous, Stellar's sea cow was dependent on the lush algal community maintained by effective suppression of urchins (Haley 1978). A highly comparable cascade is known from the Canadian maritime provinces in which lobsters play an ecologically equivalent role to otters (Mann & Breen 1972; Mann 1977).

I have removed a starfish, *Stichaster australis* Verrill, from an intertidal shoreline in New Zealand, producing rapid domination by a mussel (*Perna*) at the expense of other resident-space-requiring species (Paine 1971). Although no modules were identified specifically, the competitive dominant had monopolized virtually all the space within 15 months, with the elimination of nineteen other species. Not only was a strong interaction demonstrated, but the influence of *Stichaster* was independent of the variety of prey consumed. I have now collected 365 feeding observations on this starfish: 76% of them are on mussels and, further, there is little tendency towards dietary breadth despite the local abundance of phyletically diverse, potentially suitable, alternative prey. The contrast with the trophic generalist *Pisaster* is sharp, and yet the experiments yielded similar results for similar reasons. The top predator's influence is due to the strong, competitively asymmetric, cross-linkages which translate changes in either *Pisaster* or *Stichaster* abundance into changes in allocation of the limiting requisite, space.

Birkeland (1974) has detailed a food web with only nine major constituents characterizing a subtidal sandy bottom community in Puget Sound, Washington. The web is unusual in that a single prey, the sea pen *Ptilosarcus guerneyi* (Gray), provides the primary trophic base for a complex of at least eight consumers. In one sense, then, sea pens are key industry (Elton 1927) organisms. Birkeland established connectedness patterns and rates of prey consumption through hundreds of hours of scuba diving. Figure 3 is slightly modified from Birkeland, and gives the essence of the relationships. All species consume *Ptilosarcus*, and three of them (*Hippasteria*, *Tritonia* and *Armina*) exclusively so. There is a single top predator, the starfish *Solaster dawsoni* Verrill, and Birkeland was able to calculate that if it was removed, *Mediaster* would increase and eventually outcompete the module of specialists. All other species would persist, albeit at greatly reduced densities. In sum, not only were a strong interaction and a dependent module comprising 3/8th of the species identified, but the study also indicates the potential fragility of the ensemble to perturbation of a single resident species.

The studies just discussed reveal the significance of certain key predators, the importance of cross-links and the reasons underlying cascading alterations in structure. They suggest patterns that can be extended with some caution to many other benthic and aquatic communities.

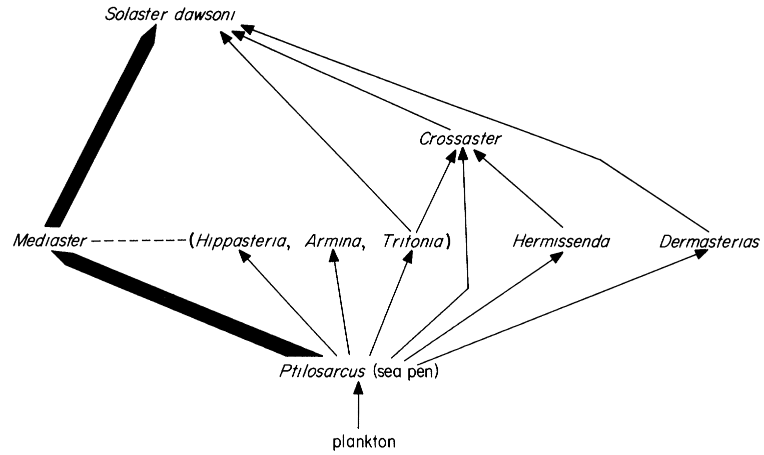

FIG. 3. A shallow subtidal food web of Puget Sound, Washington. Redrawn from Birkeland (1974), employing the symbolism of Fig. 1.

Lubchenco & Menge (1978) and Menge (1979) have studied a low, rocky intertidal community along the western Atlantic shore. Starfish (*Asterias*) are strong interactors: their removal produces monocultures of mussels at the competitive expense of barnacles and algae. However, starfish influence occurs sporadically, not chronically, and is ecologically unpredictable. No associated modules appear to have evolved. In addition, other experiments suggest that *Thais lapillus* (Linnaeus) is almost as strong an interactor: its removal (Menge 1976) leads to a mussel dominance not attained in its presence. Apparently, in communities subject to extensive physical disturbances, competitive dominants can evolve which in turn generates strong interactions. However, because the dominant is essentially a fugitive, superior defensive attributes have not evolved. Thus, such a species remains susceptible to many consumers which may regulate its distribution and abundance. The Torch Bay intertidal community (Fig. 2) could be similar, and the pattern of multiple key consumers reappears in the work of Kitching, Sloane & Ebling (1959) and Peterson (1979), in which *M. edulis*, though clearly competitively superior under most conditions, never achieves the body stature to escape from all predators.

The influence of event predictability, in the sense that organisms can adapt and evolve responses to it, is further revealed by studies on the destruction wrought by *Acanthaster planci* (Linnaeus) on Into-Pacific coral reefs (Endean 1976). Starfish plagues occur sporadically in space and time. When they do occur there is a substantial impact on community composition exerted by a single native species of high trophic status. *Acanthaster* is obviously a strong interactor. However, it is also unpredictable, and it is probably not coincidental that no modules seem associated with its activities. Its destructive influence is clearly related to the competitive status of its prey (corals) again emphasizing the significance of cross-linkages in community organizational schemes. There are no signs that the awesome trophic complexity of such communities, glimpses of which can be seen in Hiatt & Strasberg (1960) or Kohn & Nybakken (1975), exerts any ameliorating influence during outbreaks.

Finally there is convincing evidence that aquatic webs show many of the same organizational features as benthic ones. Hrbáček (1958) and Brooks & Dodson (1965) demonstrated that the presence of certain fish species results in substantially different plankton communities. Dodson (1970) suggested, and Giguère (1979) has experimentally proven, that the presence or absence of salamander larvae lead to one, or another, set of zooplankton. Recently, Dodson (1979) has extended this body of literature. I conclude that in these plankton webs vertebrate predators, be they fish, amphibia or birds (under appropriate circumstances), have the potential to interact strongly with certain prey and to mould community structure in a generally predictable fashion. Further, modules may be present: what Dodson (1970) terms 'complementary feeding niches' represent, from the community viewpoint, a predictable supplementation of the species list associated with a strongly interacting predator. However, little evidence on within module coevolution is available, unless one interprets the predictable development of rotifer swarms in the presence of major vertebrate predators and the well-documented chemical signalling between them (Gilbert 1966) in this fashion.

Three final examples can be given to document events in aquatic food webs. Power & Gregoire (1978) have examined a land-locked seal → fish relationship in which lakes with seals have significantly altered fish communities as compared with those without these effective predators. Fraser (1970) and Swanberg (1974) have re-examined the complex ctenophore → ctenophore → herring and cod web. Although the relationships are primarily inferential, all are realistic, and support the notion of a trophic cascade associated with a series of nested strong interactions. Similar conclusions can be drawn from the fascinating analysis of May *et al.* (1979) of the baleen whale → Antarctic krill situation: alteration of a dominant consumer set has instituted major changes within the community nexus. Augmentation of populations of supplementary species (penguins, crabeater seals) is associated with the demise of whale stocks. Modules were not observed in the sense that whale dependent species went locally extinct, but perhaps this is seeking too much in a system this remote and difficult to study except on an immense spatial scale.

WEAK INTERACTIONS

The ideal weakly interacting species in some respects is experimentally unsatisfactory: its addition or deletion causes no detectable change. Furthermore, such results are highly likely in natural communities in which the experimenter must contend with high levels of 'noise'. I record here the basic data on three experiments that reveal some of the nuances and difficulty of examining weak interactions.

The chiton *Katharina* is a large, abundant herbivore on mid and low intertidal rock platforms. Preliminary observations had suggested that it cannot suppress the brown alga *Hedophyllum sessile* Setchell. To test this view *Hedophyllum* was removed from large (17–27 m^2) rock platforms but with all other organisms retained. Unaltered controls were adjacent. Experiment 1 was initiated 8 May 1978. By December the area was 50% covered, as determined by replicated quadrat samples, by *Hedophyllum*; by late April 1979 the value was 95%. Experiment 2 was identical in design. A second area was cleared 15 May 1979. By August *Hedophyllum* accounted for 35% of the canopy, by September 80%, and by December 1979 had decreased to 36%. Chiton density remained relatively constant throughout the study (Table 4); *Hedophyllum* exhibited normal seasonal changes in % cover in all areas (Table 5). Clearly, judged by an ability to control development of a dominant alga, *Katharina* is a weak interactor. On the other hand it exerts a major influence on associated benthic algae and is a functionally dominant grazer in Alaska. I have thus identified it as a strong interactor in Fig. 2, although this could be questioned.

TABLE 4. Effects of removing the chiton *Katharina tunicata* on the associated herbivores. C = control; E = experimental site. Data are given as number per m². An asterisk indicates a significant ($P < 0.05$) difference in specific grazer density between control and experimental sites

		Date						
Grazer	Treatment	8 May '78	18 Aug '78	28 Dec. '78	28 April '79	15 May '79	24 July '79	20 Sept. '79
Katharina	C	20	24	25	22	34	21	42
Tonicella lineata	C	9	7	4	11	14*	6	7
	E	7	4	–	–	7	3	2
Acmaea mitra	C	7	4	3	1	4	3	4
	E	4	4	–	–	0	0	0
Acmaea pelta	C	13	11	6	9*	19*	13*	4*
	E	13	7	3	17	26	16	27

Table 4 shows that *Katharina* exerts an influence on at least one of the associated grazers and perhaps others, based on results in the second year of experiment 1. The control for this manipulation was a site from which both *Hedophyllum* and *Katharina* had been removed and, since *Hedophyllum* recovers equally with or without *Katharina*, potential variations in algal primary cover are not a factor. The limpet *Acmaea pelta* (Rathke) increased significantly in abundance in the experimental area (Mann-Whitney U, Siegel 1956), due to competitive release. Conversely, both other grazers (Table 4) tended to decrease, probably because of changes in the quality of their resource. Although these species are dynamically coupled, none seem capable of controlling the dominant alga even when grazer density is increased by factors of 2–3. They, therefore, are weak interactors.

I further tested the hypothesis of weak interaction in a removal experiment on *A. mitra* Rathke, a species feeding exclusively on coralline algae (but certainly also ingesting any attached microscopic flora or spores of macrophytes). The species is moderately abundant at low tide levels on the Washington outer coast: cave mouths ($N = 18$, $\bar{X} = 1{\cdot}23\ m^{-2}$ s.d. $= 1{\cdot}23$), rock platforms (20, $2{\cdot}22\ m^{-2}$, 4·6), or underneath sea urchins (44, $6{\cdot}05\ m^{-2}$, 7·37). It becomes more abundant in the shallow subtidal.

Acmaea mitra was initially removed from a 15 m² *Hedophyllum* covered platform at the 1·0′ level on Tatoosh Is. in June 1979. Since the species is not overly vagile, and many individuals remain within limited areas for long intervals (months), reinvasion does not pose a problem. An unmanipulated control area was adjacent. The coralline algal community initially showed no differences between control and experimental sites in the percent cover of five major types (Mann-Whitney U-test), so the data were pooled. Re-examination of the site 6 months later revealed no re-entry of *A. mitra*, no apparent compensatory changes in the abundances of other grazers, no differences in the cover of *Hedophyllum* other than normal seasonal changes, and two shifts in the relative abundance of the coralline algae (Table 5). These changes are probably causally related with one crust category (*Lithophyllum* spp.) tending to overgrow another in the absence of grazing pressure. Although the evaluation is made difficult by problems with coralline alga taxonomy and their patchy distribution (suggested by the generally great range in value of percent cover) I believe the conclusion of no or slight change to be sound. *Acmaea mitra* clearly is a weakly interacting species, at least at the level of population density manipulated and within the time frame of observation.

TABLE 5. Response of the coralline algal complex following removal of *Acmaea mitra*. Data are given as mean percentage cover and (range). An asterisk indicates a significant ($P < 0{\cdot}05$) deviation from the control condition. N = number of quadrat samples

					Coralline algal understorey				
Date		*N*	Hedophyllum canopy	*N*	Corallina spp.	Bossiella spp.	Lithothamnium type 'A'	Lithothamnium type 'B'	Lithophyllum spp.
10 June 1979	Initial Composition	20	100	8	32·9 (10–65)	4·5 (0–10)	30·0 (10–55)	19·2 (5–35)	13·5 (0–35)
2 Dec. 1979	Control	5	38*	12	31·7 (0–80)	4·6 (0–20)	29·2 (10–90)	28·5 (0–80)	6·3 (0–20)
	Experimental	5	36*	12	31·3 (0–70)	2·5 (0–5)	30·8 (0–70)	14·6* (0–100)	20·8* (0–60)

RELATIONSHIPS WITHIN THE MODULE

Competitive relationships within this coralline algal-specific grazer module appear to be as weak as the consumer-resource ones, although the conclusion is entirely inferential. The grazers *A. mitra* and *Tonicella* coexist peacefully, often within a few cm of one another for extended intervals (months). It is not clear how they react to the presence of *Katharina*. However, they may respond to the urchin, *S. purpuratus*; densities are often higher under urchins than on the rock platform itself (*Tonicella*, 14 m^{-2}, *A. mitra* 6·1 m^{-2}) implying that this relationship is a facilitating one. That is, urchin feeding biases the composition of the algal community in favour of species requiring coralline algae, and their spines might afford protection as well.

There seems little doubt that coralline algae, probably the most geographically ubiquitous group of macroalgae, require grazing for their establishment and persistence (Paine & Vadas 1969; Vine 1974). This proposition was examined experimentally in two ways. A strip 4m × 0·5 m was scraped down to the algal basal system or bedrock within a dense forest of *Corallina vancouveriensis* Yendo. Squares roughly 0·3 m × 0·3 m in dimension were painted around their perimeter with a 10 cm band of anti-fouling paint which effectively reduces entry by benthic grazers. Four squares served as experimental, herbivore-free arenas. Five immediately adjacent scraped areas but with unimpeded herbivore access were the controls. The null hypothesis tested is that coralline recovery is independent of an herbivore presence. Figure 4 indicates this clearly to be not so: in the controls recovery to 80% cover occurred within 11 months, and to > 90% coralline cover within 21 months. Three of the herbivore-free sites failed to converge on the controls and have remained significantly different since the fourth month. The remaining experimental site behaved as though it was grazed, and was excluded. Re-establishment of *C. vancouveriensis*, at least from a basal system comparable to what would remain if the area had been severely grazed, is significantly facilitated by and requires grazers.

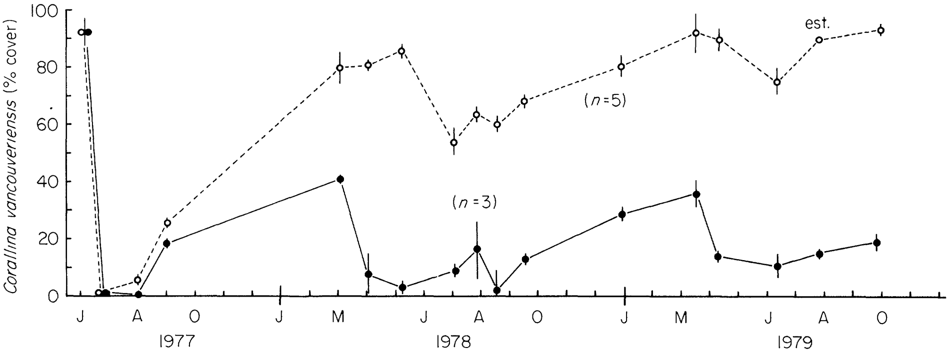

FIG. 4. Change in percentage cover of *Corallina* in experimental, grazer-free, plots (● --- ●) and control areas (○—○) with the normal grazer compliment. Vertical lines are ±1 standard deviation, based on arcsine transformed data.

The second experiment examined the proposition that persistence of established coralline algae is enhanced by grazers. The manipulation takes advantage of the fact that *A. mitra* is often encrusted with corallines in the genera *Corallina*, *Bossiella*, *Lithothamnium*, *Lithophyllum* and *Mesophyllum*. Living *A. mitra* were collected, cleaned of their

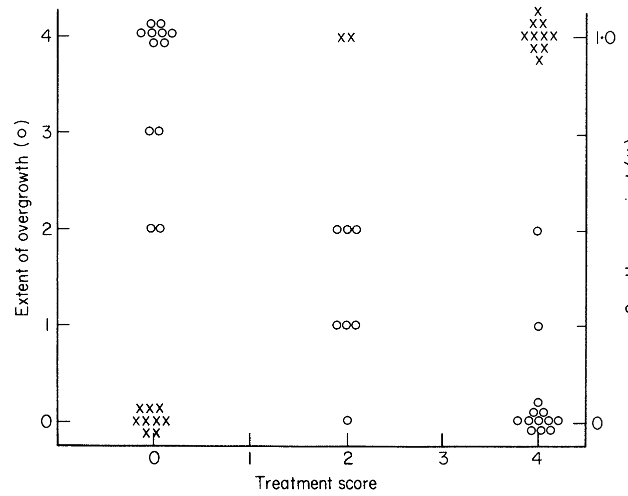

FIG. 5. The inverse relation between extent of overgrowth and coralline algal survival along a compound gradient of increasing herbivore pressure and increasing *Hedophyllum* cover.

flesh, and then bonded to the intertidal with Sea Goin′ poxy putty, a non-toxic epoxy cement. The shells were placed in areas with and without *Katharina* and/or *Hedophyllum*, since this large alga both shades and whiplashes smaller, fleshy algae and diatoms, and the chiton consumes them. The results (Fig. 5) are clear. There is an inverse relation between extent of algal overgrowth on the limpet shells, and the combined influence of grazing pressure and *Hedophyllum*. This influence is positively related to crustose coralline algal survival after 3 months, scored on an all or nothing basis. In the absence of grazing pressure the crustose corallines become overgrown, predominantly by chain-forming diatoms, *Ulva* and *Halosaccion* (a red alga), and die. Erect, articulated coralline algal genera appear more immune to this mortality source.

Perhaps the most convincing, independently derived evidence of the tightness of modular bonding comes from work on settlement cues released by the algae, specifically attracting grazers. Barnes & Gonor (1973) showed that competent larvae of *Tonicella* settled almost exclusively on coralline algae and that the response was elicited by a water soluble algal extract. Morse *et al.* (1979) have chemically identified a well-known vertebrate neurotransmitter, γ-aminobutyric acid, from crustose coralline algae and demonstrated that it induces settlement by a grazer. Steneck (1977) has described morphological adjustments by corallines to obligate grazers that reduce the consumer's impact. The overall implication assembled from diverse sources is one of a mutualism characterized by loose but nonetheless positive interdependence and benefit to all participants. It can only exist in the presence of strongly dominating grazers which are minimally involved in the module's interactions and which protect the corallines from overgrowth by fleshy algae. The adaptive pathways seem to represent varying levels of transition from grazer-resistant to grazer-dependent status.

CONCLUSIONS

I began with the observation that the quest for a satisfactory solution to the diversity-stability relationship has been profitably frustrating. The answers remain remote but not for lack of attention, since the issue bears both enormous theoretical and practical implications. The focus has swung, rightly I believe, toward attempts to understand the design of natural webs. Two previous viewpoints are especially prominent here, and I have attempted to oppose them with mine in Fig. 6. I have used as a setting the interactions between some of the invertebrate grazers and their algal prey. Although my preoccupation with aquatic webs may introduce some bias, it can be justified as follows. Rate processes seem generally faster than in terrestrially-based systems and therefore induced changes are more observable. Strong links tend to characterize some of the plant-herbivore relationships, and thus the cascade of change is more pervasive.

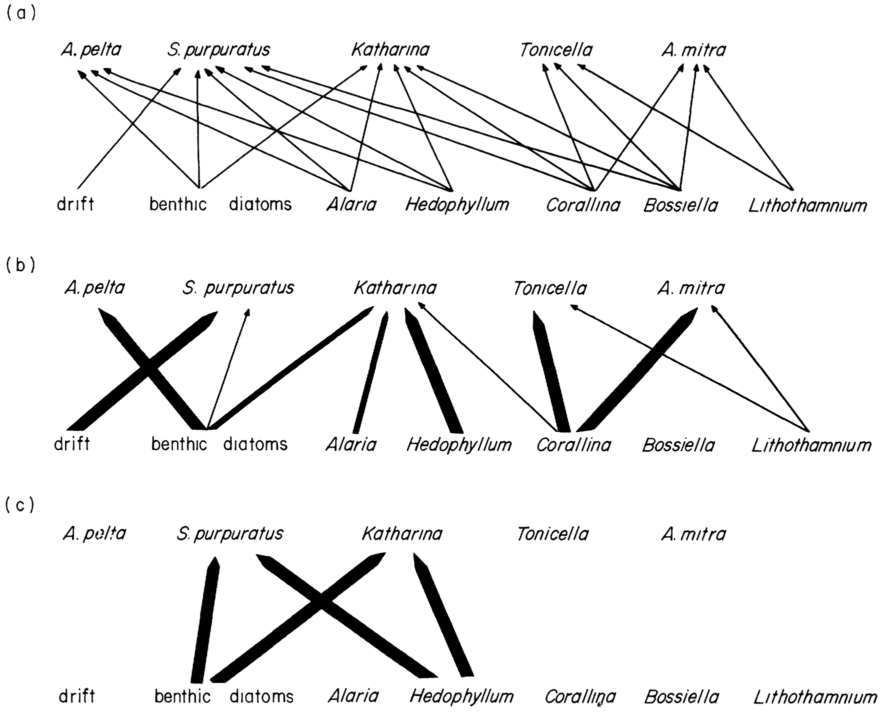

FIG. 6. Three conceptually and historically different approaches to depicting trophic relationships, illustrated for the same set of species. The connectedness web (a) is based on observation, the energy flow one (b) on some measurement and literature values, and the functional web (c) on controlled manipulation.

Connectedness webs have the most tradition behind them. They have served as the intellectual cornerstone for most if not all modern theoretical treatment because web membership and trophic interrelations can be generated by observation alone. Although some models (May 1973; DeAngelis 1975) consider interaction strength, others do not (Cohen 1978; MacDonald 1979; Rejmanek & Stary 1979), and the notion that randomly connected model ecosystems are a useful caricature of the real world has increasingly come into question (Lawlor 1978; Roberts 1974). The merit of the connectedness models is that they have maintained a lively and constructive debate which has identified certain significant food web attributes.

Less can be said about the relation between flow webs and community organization. They require substantially more information, much of it physiological, to construct. They are statically descriptive at best and, further, assume importance is measured by the rate of material or energy flux through nodes in the web. This is hardly true. The approach is often remote from intimate biological detail, pays little heed to competitive cross-links, and has generated few or no insights into ecological processes.

I have spent most of my hour discussing a web in which what I call functional significance is emphasized. Unfortunately, it requires experimental manipulation for verification of the linkage strengths. However, as Fig. 6 notes, it can be adequately described by fewer interspecific relationships than the others, much in the fashion that Gilbert (1977) suggests for a tropical, terrestrial community. My approach places no weight on major energy flow pathways that have no bearing on community organization, for instance, a *S. purpuratus*—drift algal connection. It is immune to the observational artifact that often functionally significant prey are rare because of a strong, controlling interaction. Thus, *M. californianus* is hardly the most frequent item in *Pisaster*'s diet (Tables 1, 2). The approach finds both strength and reality in the following.

(1) Enumerating links through direct observation provides little information on a particular species' importance and the connectedness component of food webs is susceptible to enormous geographic and within-habitat variations. What counts is the competitive stature of the preferred prey, implying that cross-links will be as important as trophic ones.

(2) Trophic links are unequal in strength, and most benthic and aquatic communities seem to be characterized by high variance in this measure. Strong links are easily demonstrated experimentally, and their presence readily explains the cascading changes that characterize certain altered ecosystems, changes that may involve as many as four distinct 'trophic levels.' Further, predictable strong linkage can generate trophically different but persistent, alternative resource bases. These latter appear not to develop when the strong interaction is unpredictable in space or time.

(3) Finally, predictable strong interactions can encourage the development of modules or subsystems embedded within the community nexus. The individuals comprising these may be co-adapted to one another and exhibit sophisticated mutualisms. Many members are probably extremely specialized, and the module itself may be dependent on events biologically external to itself for continuity. Modules add much richness to ecological systems and many develop their own infrastructure but most members are probably not functionally significant and therefore are weakly-interacting species.

I wish to close with a final observation: pattern is generated by process. One embodies static description, the other more subtle and dynamical events. Food webs along with their associated cross-links provide a realistic framework for understanding complex, highly interactive, multispecies relationships. I believe the next generation of models must be more sensitive to interaction strength, less so to trophic complexity, for the answers to questions on the stability properties of complex, natural communities increasingly violated by mankind are vital, and our time is short.

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A fuzzy-neural system for identification of species-specific alarm calls of Gunnison's prairie dogs

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Abstract

In this study we describe the design and application of an automated classification system that utilizes artificial intelligence to corroborate the finding that Gunnison's prairie dogs have different alarm calls for different species of predators. This corroboration is strong because it utilizes an entirely different analysis technique than that used in the original research by Slobodchikoff et al. [Slobodchikoff, C.N., Fischer, C., Shapiro, J., 1986. Predator-specific alarm calls of prairie dogs. Am. Zool. 26, 557] or in subsequent study done by Slobodchikoff et al. [Slobodchikoff, C.N., Kiriazis, J., Fischer, C., Creef, E., 1991. Semantic information distinguishing individual predators in the alarm calls of Gunnison's prairie dogs. Anim. Behav. 42, 713–719]. The study described here also is more completely automated than earlier study in this area. This automation allowed a large volume of field data to be processed where all measurements of relevant parameters were performed through software control. Previous study processed a smaller data set and utilized manual measurement techniques. The new classification system, which combines fuzzy logic and an artificial neural network, classified alarm calls correctly according to the eliciting predator species, achieving accuracy levels ranging from 78.6 to 96.3% on raw field data digitized with low quality audio equipment. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Acoustic; Alarm calls; Fuzzy logic; Neural nets; Prairie dogs

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1. Introduction

An increasing body of evidence shows that the alarm calls of some animals contain meaningful information of a semantic nature. Semantic content in predator-specific alarm calls has been found in the vocalizations of some ground squirrels (Owings and Virginia, 1978) and in vervet monkeys (Seyfarth et al., 1980). The California ground squirrel has a different call for aerial predators than it does for terrestrial predators. Vervet monkeys have different alarm calls for several species of predators, such as the leopard, martial eagle, and python. Semantic information has also been found in the alarm vocalizations of dwarf mongooses (Beynon and Rasa, 1989), and in the alarm calls of chickens (Gyger et al., 1987), lemurs (Pereira and Macedonia, 1991), and red squirrels (Greene and Meagher, 1998).

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A diversity of information of a semantic nature has been associated with Gunnison's prairie dog alarm calls. This includes, (1) different alarm calls for different species of predators (Slobodchikoff et al., 1986; Kiriazis, 1991); (2) information about the size, shape, and color of different individuals within a predator species (Slobodchikoff et al., 1991); (3) information related to the direction and speed of approach of a predator (Kiriazis, 1991); (4) and dialects in alarm calls between colonies (Slobodchikoff and Coast, 1980; Slobodchikoff et al., 1998).

In this study we describe the design and application of an automated system of analysis that is used to corroborate the finding that Gunnison's prairie dogs have different alarm calls for different species of predators. Earlier techniques that demonstrated the existence of these predator-specific alarm calls were subject to various limitations. For example, using observational techniques, Kiriazis (1991) demonstrated that alarm calls, recorded in the presence of predators of various types, elicit predator-specific behaviors in prairie dogs that hear the recordings played back in the absence of any predators. Such observational techniques strongly suggest that there exist different alarm calls for different species of predators. However, these techniques do not provide quantitative or structural insights into the nature of the alarm calls under investigation.

Evidence for predator-specific alarm calls was also demonstrated by Slobodchikoff using a technique that relies on the analysis of audio waveforms (sonograms) generated by sophisticated signal processing programs (Slobodchikoff et al., 1991). In this methodology, a number of attributes of sonograms made from the prairie dog alarm calls were measured manually. These hand measurements were analyzed using multivariate statistics in order to demonstrate the existence of predator-specific alarm calls. Manual measurement techniques are time consuming and they tend to make the analysis of large numbers of alarm calls impractical. This limitation invites criticisms related to any statistical analysis that is tied to the measurements. Manual measurements are also imprecise and open the possibility that human bias is introduced into the measurements. Both of these weaknesses of manual measurement techniques can be overcome by enhanced automation of the experimental procedure. However, even if the methodology used by Slobodchikoff was more completely automated, the analysis technique of multivariate statistics itself presents some limitations that must be addressed. Although capable of identifying important alarm call parameters and, to some degree, their relative importance, multivariate statistics cannot easily be used to ascertain the manner in which these factors encode information in animal vocalizations. Since ultimate proof of the actual level of complexity of animal communications must rely on some exposition of the manner in which these communications encode information, this is a serious limitation that must be overcome.

The automated classification system described in this study addresses all of the limitations just discussed. Using a sophisticated numeric-processing environment, the new system of analysis is implemented as a fully automated software package where all measurements are made under software control. In addition to this, the power of fuzzy logic and artificial neural networks is used to analyze and classify the prairie dog alarm calls with high accuracy into predator-specific classes. Furthermore, the new system promises to support more sophisticated future research into the manner in which information is encoded in alarm calls. Fuzzy logic is a system of mathematics that allows the vagueness of linguistic concepts to be represented by sets with imprecise boundaries (Zadeh, 1965; Ross, 1995). In fuzzy logic, the membership of an element in a set does not always signify complete inclusion or complete exclusion but can assume values between these two extremes. Working with the degrees of membership allows the imprecision inherent in natural language to be represented and it supports a form of approximate reasoning that attempts to model the way human beings reason. Artificial neural networks refer to computer programs and also to actual hardware devices that have been designed to emulate some of the functionality and attributes of human neural networks (McCulloch and Pitts, 1943; Rumelhart et al., 1986). In artificial neural networks the information is distributed among the many links that connect the simple processing units contained in the network. A network gains information (i.e. trained) by example as data sets are repeatedly presented to it. During this training period the network itself adjusts the network's links in order to retain information gained from the inputs. A network continues to be trained in this manner until it is able to function at an acceptable level of performance.

2. Materials and methods

The research described in this study used tape recordings of Gunnison's prairie dog alarm calls obtained over a period of 10 years (1988–1997) at two separate prairie dog colonies, both described in Slobodchikoff et al. (1991). Recordings were made using a Sennheiser ME-88 directional microphone and two different models of cassette tape recorders, an Uher model 160 recorder and a Sony TC-D5PRO II recorder. For the purposes of this analysis, we used calls from 25 individual prairie dogs for each of the following predators: humans, represented by seven different individuals; red-tailed hawks, represented by 16 different individuals; domestic dogs, represented by eight different individuals; and coyotes, represented by five different individuals. Because the alarm call data were obtained over a 10-year period, we sampled calls from multiple generations of prairie dogs.

Copies of these data recordings were digitized using a generic sound card and software package in an IBM compatible PC with an Intel 486 processor. The sound card had 16-bit resolution and sampled data at 44 100 Hz. Following the digitization process a standard 'cut and paste' sound editor that was part of the package was used to manually extract the individual prairie dog 'barks' and save them in separate files. These files of single alarm call barks formed the library of files that was used for all of the classification tests described in this study. The files associated with a given recording session and species of predator were all given the same root name; each individual file with the same root name was given a unique index value. For example, one series of files that contain alarm call barks issued in the presence of a dog named Moby are named moby1, moby2, moby3, etc. while another series of calls recorded in the presence of a hawk are named aerial1, aerial2, aerial3, and so on. After completing this manual process of creating separate files, with each file containing an individual alarm call bark, all subsequent data manipulation was performed using a system of computer programs created by one of the authors. These programs were implemented using the high-performance numeric computation software called MATLAB and the neural network toolbox associated with MATLAB. Classification tests were run on all combinations of the different predator species associated with the alarm calls. In other words, all six combinations of two different species were tested, all four combinations of three different predator species were tested, and data associated with all four species was tested.

The automated classification system first preprocesses each of the prairie dog alarm calls and then trains and tests a neural network. In the preprocessing stage, the frequency ratios contained in each alarm call bark are determined and then vectors of fuzzy values are created that characterize each alarm call bark. These vectors are used as input for the training and testing of the neural network. A block diagram of the automated classification system is given in Fig. 1. The main functional units of the automated classification system are described in detail below.

2.1. Determination of the frequency ratios contained in each alarm call bark

When an experiment was to be run that attempted to classify a targeted combination of predator-specific alarm calls, each file used in that experiment was converted from a simple time domain recording of an alarm call bark into a matrix of sound frequencies contained within that bark. This conversion process was implemented in the following way. Each digitized data file representing an alarm call bark was divided into partitions of 256 data points each. Since alarm calls were recorded at a rate of 44 100 samples per s, each bark was effectively divided into a number of time periods of 0.0058 s each. The fast fourier transform algorithm was then used to transform each partition of data points (i.e. each time period) into a normalized power spectrum of the sound frequencies that were expressed during that time period. Thus, each alarm call bark was transformed into a matrix of values representing sound frequencies where each column in the matrix represented a different time period in the bark and recorded all of the frequencies that were expressed within that time period.

Once the matrix of frequencies was obtained, a complete collection of frequency ratios was computed in the following way. For each time period (matrix column) the set of frequency ratios was computed by dividing each frequency expressed in that time period into all other smaller frequencies expressed within that period. Thus, every time period was represented by a set of frequency ratios, all of which lay within the range of values 0–1. The frequency ratios computed in this manner for each time period were then combined into one total set of values that represented the entire alarm call bark that was being analyzed. Fig. 2 gives a simplified illustration of this process.

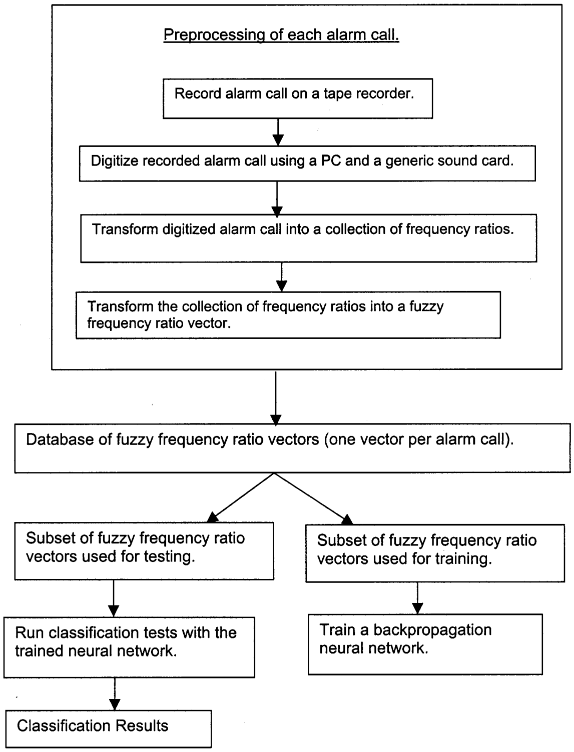
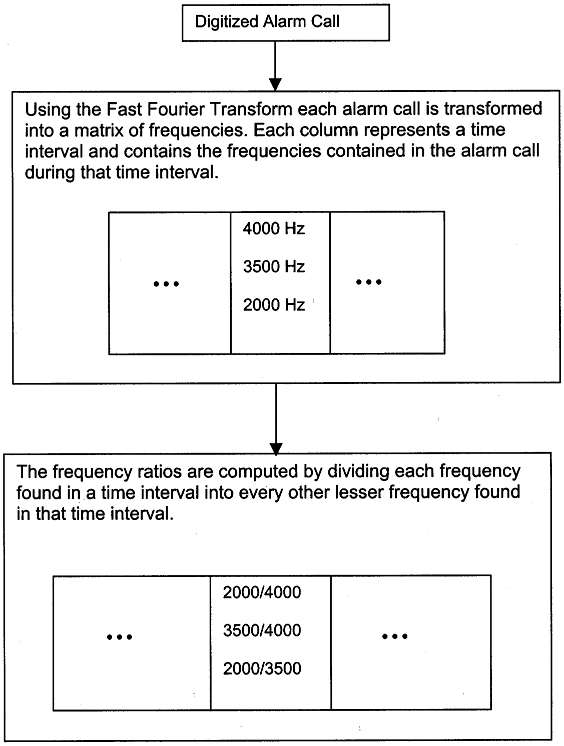


Fig. 1. Diagram of the automated classification system, showing the steps involved in processing and classifying alarm calls. Each alarm call becomes a component or vector of the database of fuzzy frequency ratio vectors. A part of this database is used for training a backpropagation neural network, and another part of the database is used for the classification tests with the trained neural network.



Using the Fast Fourier Transform each alarm call is transformed into a matrix of frequencies. Each column represents a time interval and contains the frequencies contained in the alarm call during that time interval.

The frequency ratios are computed by dividing each frequency found in a time interval into every other lesser frequency found in that time interval.

Fig. 2. Steps involved in transforming an alarm call into a collection of frequency ratios. In the time interval shown in the figure, there are three frequencies contained within the interval. To obtain the frequency ratios, each frequency within that time interval is divided into every other lesser frequency.

2.2. Creation of vectors of fuzzy values that characterize alarm call barks

Traditional or 'crisp' logic only allows for the elements of a given universe to belong to sets within that universe completely or not at all. An element x either belongs to set S completely and is said to have membership value 1 in that set, or it does not belong to set S at all and is said to have membership value 0 in that set. Unlike crisp logic, fuzzy logic allows for elements to possess partial membership in sets. One could think of such membership as being represented by a number in the range of values 0–1. At first this might seem strange, but in fact everyday logic is often more fuzzy than crisp. For example, a person that is 6 ft tall might be considered to have complete membership (i.e. have membership value 1) in the set of tall persons. Another person that is 5 ft 11 in. tall is smaller but still possesses the attribute of tallness and might be given a membership value of 0.95 in the set of tall persons. In other words, the second person has the attribute of tallness to degree 0.95. This example helps one to see that fuzzy sets are useful for characterizing the degree to which something possesses an attribute of interest. In the classification system being described in this study, fuzzy logic was used to characterize the degree to which different ranges of frequency ratios existed in each alarm call bark.

In order to characterize the collection of frequency ratios computed for each alarm call in a meaningful way, each collection was divided into 21 sub-ranges of ratios. Once this division was made, a vector of 21 fuzzy membership values was computed. Each membership value in the vector represented the degree to which a corresponding sub-range of frequency ratios approximated a particular fuzzy frequency ratio.

To make this more explicit, consider that the frequency ratios computed for a given bark lie in the range of values 0–1. These ratios were divided into 21 sub-ranges as indicated in Fig. 3. If the entire spectrum of sub-ranges was shown in Fig. 3, there would be 19 of the larger overlapping triangles (B–T) and two of the smaller right triangles, one on each end of the diagram (A and U). Each of these triangles encompasses a particular sub-range of frequency ratios and represents a membership function for a fuzzy set. For example, triangle C in Fig. 3 represents the fuzzy membership function ‘approximately 0.10’. Similarly, each of the other membership functions represents a fuzzy frequency ratio. The fuzzy value corresponding to frequency ratio interval i was computed using the following formula:

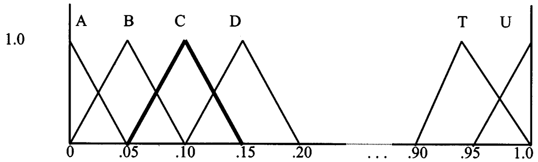


Fig. 3. Graph of fuzzy sets (triangles shown on graph) that partition the range of frequency ratios (given on the x-axis) into subsets. A line extended vertically from a particular frequency ratio found along the x-axis intersects a fuzzy set. The corresponding value of this point of intersection on the y-axis represents the membership value (μ) of that frequency ratio in that fuzzy set.

$$\mu_i = g_i^* \vee (\mu_{1i}, \mu_{2i}, \mu_{Ni})$$

where, μ_i, the fuzzy membership value for fuzzy frequency ratio interval i; μ_{1i}, the fuzzy membership value for the first frequency ratio in interval i; μ_{Ni}, the fuzzy membership value for the last frequency ratio in interval i; $\vee$, the maximum function (the standard fuzzy union operator) g_i, (number of frequency ratios in interval i)/10.

A number of different formulations of the equation given above were investigated. The equation given produced the best results.

Each vector of fuzzy membership values computed represented a distribution of fuzzy frequency ratios that was used to represent an individual bark in a prairie dog alarm call; these were the values that were provided as input to the neural network. Each fuzzy frequency ratio distribution formed a particular signature that represented the presence of a specific combination of fuzzy frequency ratios. Therefore, the overall classification system created is a fuzzy-neural classifier because the input to the neural network was a vector of fuzzy values.

2.3. Training and testing of a neural network using the computed vectors of fuzzy values

After the set of alarm call barks selected for a given classification test were transformed into vectors of membership values for fuzzy frequency ratios as described earlier, the barks were divided into two roughly equal-sized sets of vectors. One set was used to train a neural network how to identify which predator was associated with each

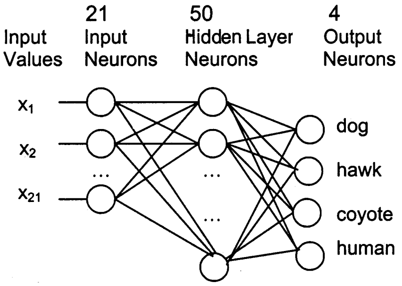


Fig. 4. A simplified diagram of the neural network used to classify alarm calls associated with all four species of predators.

alarm call bark. This data set was called the training set. The other data set was used to test the trained network for its ability to correctly guess which predator was associated with each alarm call bark. This second set was called the testing set. The two sets were disjoint which means that none of the vectors used to test the accuracy of the neural network were used to train the network. The complete data set consisted of a total of 359 alarm calls associated with humans, 171 associated with dogs, 275 associated with coyotes, and 213 associated with hawks. Recall that every alarm call bark was saved in a file whose name had a unique index that was appended to a common prefix used to represent each specific predator. The training set was composed of alarm call barks in files with odd numbered indices. The testing set came from files with even numbered indices.

The neural networks used to classify alarm call barks were feedforward networks. A feedforward network allows signals (values) to travel only in one direction in the network from the input layer to the output layer, no feedback is allowed. All of the tests described in this study were executed with neural networks that used 21 neurons in the input layer and 50 neurons in the hidden layer. The hidden layer size of 50 neurons gave the optimum combination of shortest training time and best accuracy. The number of different species-specific classes being investigated in a given test determined the number of neurons in the output layer of the network used in that test. For example, three neurons were used in the output layer of networks that classified alarm call barks vocalized in the presence of three different species of predators.

The input layer received the 21 fuzzy values that represented the ranges of frequency ratios as explained earlier. The values placed on the input nodes were passed on weighted connections to the neurons in the hidden layer. Each of the input nodes was connected to each node in the hidden layer and each hidden layer node was connected to each node in the output layer. Each hidden layer node applied its sigmoid transfer function to the weighted sum of the values sent to it by the input nodes. This resulted in the generation of new values at the output connection of the hidden layer nodes. The values generated by the hidden layer nodes were sent directly to the output nodes. Similarly, each output node applied its linear transfer function to the weighted sum of the input values it received from the hidden layer neurons. This generated a new set of values at the outputs of the output layer neurons. The output layer nodes were used to classify alarm call barks into different predator species. Each output node represented a particular species; the output node with the largest value for a given input vector named the species associated with that input. A simplified diagram of the neural network used to classify alarm calls associated with all four species of predators is given in Fig. 4.

In the neural networks, the information that linked input alarm calls to predator species was maintained in a distributed fashion in the weights that were associated with the connections in the network. A training algorithm was used to adjust the weights associated with each of the connections in the network. Each training cycle of the network caused the connection weights to be altered in such a way that the sum of squared errors of the network neurons were minimized. The changes in the weights were computed using the derivative of the square of the error at each neuron where the error was the difference between the expected output of the neuron and the actual output. This training algorithm is called the back-propagation gradient descent technique (Rumelhart et al., 1986) An adjustment of the connection weights represents a modification of the informa-

Table 1
Summary information for all combinations of the different predator species

Species classified	Accuracy (%)	Training sessions
Humans, dogs	87	2000
Humans, coyotes	89	1500
Humans, hawks	95	1500
Dogs, coyotes	88	2000
Dogs, hawks	96	2000
Coyotes, hawks	90	2500
Humans, dogs, coyotes	79	3000
Humans, dogs, hawks	85	3500
Humans, coyotes, hawks	86	2500
Dogs, coyotes, hawks	85	3500
Humans, dogs, coyotes, hawks	79	5000

tion embodied in the network. Weight adjustment was scheduled to continue iteratively until either no error occurred when classifying input vectors or until the training algorithm no longer improved the classification accuracy of the network. In none of the classification experiments did the network reach 100% accuracy. Therefore, in each test the iterative training regime stopped itself when no further improvement was seen in three consecutive training sessions.

3. Results

Table 1 provides a summary of information for all the classification tests run. Each row represents a classification experiment for a specific combination of target species. For example, the second row of Table 1 represents the classification test that trained a backpropagation neural network to distinguish between alarm call barks issued in the presence of humans and alarm call barks issued in the presence of coyotes. The network was able to distinguish between the alarm calls with an accuracy of 89%. Furthermore, it took 1500 training sessions to achieve this accuracy.

A contingency table showing the results of the classification of alarm calls associated with all four species of predators is given in Table 2. The column labels represent the species that were ‘guessed’ by the neural network to be associated with the alarm calls tested. The row labels represent the actual species associated with the alarm calls tested. For example, the cell associated with row ‘dog’ and column ‘hawk’ gives data related to the number of times the neural network incorrectly associated a hawk with alarm calls vocalized in the presence of a dog. The diagonal cell in row ‘human’ and column ‘human’ gives data related to the number of times the neural network correctly associated a human with alarm calls vocalized in the presence of a human. Each cell in Table 2 contains two values. The first value gives the observed count for that cell and the parenthesized value gives the expected count for that cell if the neural network had been selecting randomly among the four species. The values show that the classification results are highly significant ($\chi^2 = 793$, df $= 9$, $P < 0.005$).

Table 2
Contingency table for classification of alarm calls for all the four predator species[a]

Actual species associated with alarm calls	Species associated by neural network with alarm calls			
	Human	Dog	Coyote	Hawk
Human	154 (70)	12 (31)	10 (41)	2 (36)
Dog	18 (34)	62 (15)	4 (20)	3 (18)
Coyote	14 (54)	14 (24)	99 (32)	10 (28)
Hawk	13 (42)	1 (19)	4 (24)	88 (21)

[a] Each cell contains the observed value and the expected value in parentheses. These results are highly significant ($\chi^2 = 793$, df $= 9$, $P < 0.005$).

4. Discussion

The results presented above show highly accurate classifications of species-specific alarm calls. The highest classification accuracy of 96% was obtained between dog and hawk calls. The lowest accuracy of 79% was obtained when classifying all four species together and when classifying humans, dogs, and coyotes. All other classification tests were between 85 and 95% accurate.

The classification system described in this study provides strong corroboration that Gunnison's prairie dogs have different alarm calls for different species of predators. The corroboration is strong because it comes through the use of an entirely different analysis technique than that used in the original research by Slobodchikoff et al. (1986) or in subsequent study done by Slobodchikoff et al. (1991). The study described here also is more completely automated than earlier study in this area. This automation allowed a large volume of field data to be processed where all measurements of relevant parameters were performed through software control. Previous study processed a smaller data set and utilized manual measurement techniques. A further advantage of the new system of analysis is that it utilizes powerful tools of artificial intelligence: fuzzy logic and neural networks. Neural networks in particular help to establish a plausible link between what prairie dogs are actually experiencing or capable of experiencing, and what the research tool (a neural net) is demonstrating. If a simple primitive artificial neural network can distinguish, with high accuracy, alarm calls issued in the presence of different species of predators, it seems to be reasonable to assume that the organic neural networks of Gunnison's prairie dogs are capable of making the same discrimination.

It is surprising that the experimental results presented in this study demonstrated such high accuracy. The original alarm call field recordings were made over a period of years in outside locations at two different prairie dog colonies. There were various sources of noise (including wind, trains, etc.) encountered during the taping sessions which resulted in recordings of varying quality. Additional degradation in sound quality came from the fact that the digitized alarm calls were made from copies of the original field recordings and these copies were played into a PC using a low-quality tape recorder. Thus, no extraordinary measures were taken to assure high fidelity sound reproduction. In addition to using noisy field data digitized with low quality audio equipment, it should be pointed out that no data filtering was done. The automated classification system utilized all the individual alarm call barks that were selected for a given classification test; no data was thrown out. Not only can one assume that some of the alarm call barks were of poor quality due to noise etc. but it is entirely possible that not all alarm call barks were intended primarily to specify the species-specific information. For example, it was mentioned earlier that prairie dog alarm calls have been shown to possess other types of information such as size, shape, and color of individual predators as well as direction and approach of a predator.

The use of a large number of alarm call barks recorded over a period of several years in varying conditions at two separate prairie dog colonies helped to guard against training the neural network to recognize something other than species specific information. For example, if the same external sounds or noise were present each time alarm call barks were recorded in the presence of dogs, the neural network might be recognizing that external noise and not be identifying predator specific information related to dogs. Another possible source of non-species specific information could be the characteristics of the vocalizations of specific prairie dog individuals. Reby et al. (1997) showed this capability of neural networks when they trained them to recognize the individual vocalizations of four fallow deer. Given the data set used for the work described in this study, it is unlikely that recognition of individual prairie dog vocalizations could explain the high accuracy of the classification results.

It is interesting, and not entirely surprising, that frequency ratios have been found to be an important factor in classifying predator-specific prairie dog alarm calls as described in this study. In music, the ratio of the frequencies of musical notes is highly significant because it defines a relationship between those notes that is immediately recognizable when one hears the notes. Striking examples of this are the notes of the same name, which differ in frequency by powers of two. Consider also that two chords, for example, the sixth and seventh chords of a given key, can contain several identical notes but differ only in one specific note and yet still produce clearly distinct harmonies. It seems quite possible that certain combinations of frequency ratios might form patterns that could be used to identify the distinguishable units or phonemes of an acoustic communication system.

The work presented in this study strongly suggests that frequency ratios are related in some way to the manner in which information is encoded in Gunnison's prairie dog alarm calls. Establishing the importance of this parameter was one of the major outcomes of the work described here. However, the exact way in which the information is encoded in Gunnison's prairie dog alarm calls and the level of linguistic complexity of these calls are clearly not addressed in this study. Additional work is needed to address these difficult issues. Nonetheless, part of the significance of the classification system presented in this study is that, it provides a system of analysis that can be used to investigate these more difficult questions. This system draws on powerful techniques of artificial intelligence that can be expanded to examine the issue of how and at what level of complexity information is encoded in animal alarm calls.

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Habitat Use and Time Budgeting by Wintering Ferruginous Hawks

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HABITAT USE AND TIME BUDGETING BY WINTERING FERRUGINOUS HAWKS[1]

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Abstract: From 1992–1995 we studied the winter ecology of Ferruginous Hawks (*Buteo regalis*) in Colorado. Hawks spent 84% of the daylight interval perching. Time-budgets indicated that on average hawks perched 18 times day^{-1} (range 3–50), with perches averaging 30 min in duration. Diurnal perching was in trees, on poles, and on the ground. Utility poles and other human-made structures were used more than ground and deciduous tree perches. Tree perches were used for the longest mean duration. The mean daily Minimum Convex Polygon (MCP) home range of 36 hawks was 3.53 km^2. The black-tailed prairie dog (*Cynomys ludovicianus*) was the most important prey species, and extant prairie dog colonies characterized winter habitat for Ferruginous Hawks.

Key words: *activity, black-tailed prairie dog,* Buteo regalis, Cynomys ludovicianus, *Ferruginous Hawk, time budget.*

INTRODUCTION

Although much is known about the biology of Ferruginous Hawks (*Buteo regalis*) during the breeding season, little is known about the species during winter (Steenhof 1984). Banding studies have elucidated migration timing, routes, endpoints, and mortality of Ferruginous Hawks banded in Alberta (Schmutz and Fyfe 1987), Colorado (Harmata 1981), and North Dakota (Gilmer et al. 1985). Winter population estimates and geographic distribution have been derived from Christmas Bird Counts (Warkentin and James 1988). However, few published accounts have detailed habitat use, time-budgeting, or diets of Ferruginous Hawks in winter. Nesting Ferruginous Hawks are thought to be highly intolerant of human presence (Schmutz 1984, White and Thurow 1985). In contrast, wintering Ferruginous Hawks concentrate on prey-rich locations such as black-tailed prairie dog (*Cynomys ludovicianus*) colonies, regardless of human use of surrounding areas (Schmutz and Fyfe 1987, Plumpton and Andersen, unpubl. data). However, the future of such prey populations is in question (Miller et al. 1994), underscoring the importance of detailing species-specific requirements of Ferruginous Hawks during winter.

Successfully formulating management plans or understanding the biology of a species necessitates studying that species' requirements in all seasons. Our goal is to provide information on a well-studied raptor in a poorly-studied portion of its annual cycle.

METHODS

STUDY AREA

Fieldwork was conducted in portions of Adams, Denver, and Weld Counties, Colorado. In undeveloped areas, vegetation was characterized by shortgrass prairie. In locations where they had not been extirpated, black-tailed prairie dogs maintained vegetation at disclimax.

Hawks were captured for radio attachment using the Lockhart method (Harmata 1984) and with weakened and padded leg-hold traps baited with live mice and placed in sight of perched hawks along roadsides (Plumpton et al. 1995). Body mass was measured to the nearest 25 g using a spring scale. Visual identification legbands (VID) engraved with unique alphanumeric codes (Acraft Sign and Nameplate Co., Ltd., Edmonton, Alberta, Canada) were used to aid individual recognition

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within and among winters. Radio transmitters were attached to the rachis of the central rectrix or to two center rectrices with epoxy and cable ties.

Radio-tagged hawks were selected for observation at random without replacement. The selected hawk was located via telemetry before daylight and its behavior continuously recorded (Martin and Bateson 1986) throughout the daylight hours. Recording began when daylight permitted visual identification of the target hawk and ended when darkness precluded such discrimination. Triangulation was not used; we used telemetry only as needed to follow and maintain visual contact with study hawks. When hawks occupied a new perch, the time to the nearest minute and perch substrate were recorded, and location was estimated. At the termination of each perch, time again was recorded to allow calculation of perch duration. Hawks were observed from vehicles, from the farthest distance (about 1 km) that provided adequate viewing with a spotting scope. Daily Minimum Convex Polygon (MCP) home range areas were calculated using the program MCPAAL (Stuwe and Blohowiak 1985). The present analysis considers data from complete daily observations only. Upon successfully tracking all members of the radio-marked cohort for a complete day, and with each addition of an individual into the marked cohort, selection of hawks for observation again was randomized.

Diurnal time budgets were reconstructed for each hawk, for each complete day of data collection. Time budgets and daily MCPs incorporated perched locations only, because flight represented a small portion of the daily time budget during winter. Additionally, locations of flying hawks could not be accurately estimated nor attributed to a particular behavior with certainty. Feeding behavior of radio-tagged hawks was monitored to the extent possible, concurrent with continuous observations.

DATA ANALYSIS

General linear models were used (PROC GLM; SAS Institute 1988) to test for differences among years. The Shapiro/Wilk test was used to test for normality of the data. Homogeneity of error variances was evaluated with a folded-form *F*-statistic (PROC TTEST).

When data satisfied parametric statistical assumptions, *t*-tests and product-moment correlations were used. When data failed to satisfy the assumption of normal distribution, logarithmic transformations or nonparametric equivalents were used. Count data were tested using frequency-table analysis. Repeated measures from an individual hawk were averaged (Martin and Bateson 1986); thus, sample sizes (*n*) are based on the number of hawks from which data were collected unless otherwise indicated. All statistical tests were conducted at $\alpha = 0.05$. Values presented are means ± SE. Ranges presented are extremes of daily observations, and are not the range in observed means.

RESULTS

Seventy-one Ferruginous Hawks were trapped 84 times from 1 October 1992 through 19 February 1995. Thirty-six hawks were equipped with telemetry transmitters and observed for 1,325 hr, during 148 complete winter days.

TIME BUDGETING

Wintering hawks predominantly perched, and little of each day was devoted to active flight or soaring. On average, hawks perched for 84 ± 1% of the daylight interval (range: 45–99%) and flew or soared for 16 ± 1% of the day (range: 0–55%).

The mean number of perches occupied daily was 18 (range: 3–50), and the mean duration of individual perch events was 30 ± 0.8 min (range: 1–482 min). Ferruginous Hawks used 2,603 diurnal perches in 3 categories of substrate: (1) deciduous trees ($n = 777$), (2) utility poles, fenceposts, and other human-made objects ($n = 1{,}042$), and (3) bare ground ($n = 781$). Three perches were undetermined because the hawks were in view-obstructed habitats, and perch was indicated by a stationary transmitter signal. One-way frequency table analysis indicated that perch substrates were not used equally ($\chi^2_2 = 53.2$, $P < 0.001$). The mean duration of perches also differed ($P < 0.001$) by substrate (ground mean = 24.5 ± 1.1 min, pole mean = 25.8 ± 1.1 min, tree mean = 42.8 ± 2.0 min). Of the time devoted to diurnal perching, 33 ± 2% was spent on poles, 25 ± 2% on ground perches, and 42 ± 3% in deciduous trees.

HOME RANGE

The mean daily MCP home range was 3.53 ± 0.44 km^2 (range: 0.01–40.0 km^2, $n = 148$).

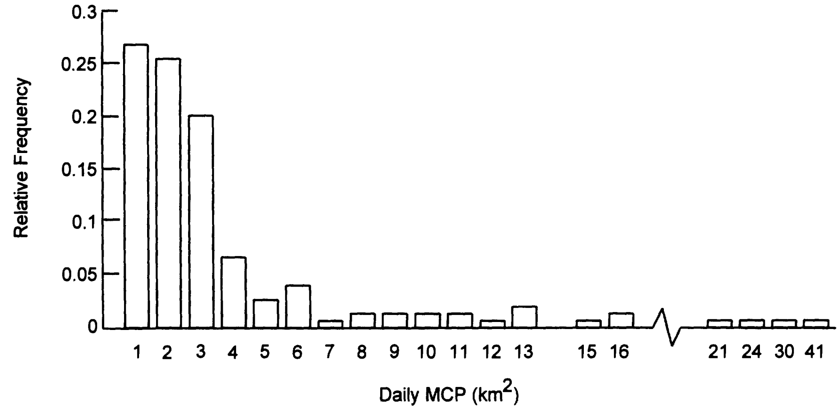

FIGURE 1. Daily Minimum Convex Polygon home range areas (n = 148 days) occupied by 36 radio-tagged Ferruginous Hawks wintering in Colorado, 1992–1995.

Ninety percent of daily MCPs were < 9 km^2 (Fig. 1).

DAILY MOVEMENT PATTERNS

We collected > 1 daily MCP for 30 of the 36 hawks. Individual hawks often exhibited daily (within-winter) and annual (among-winter) reuse of specific areas and habitats, resulting in spatial overlap within hawks and among successive days. Twenty-seven of 30 hawks (90%) had daily MCPs that spatially overlapped both within and among winters.

FORAGING

Ferruginous Hawks were observed eating cottontail rabbits (*Sylvilagus* spp.) or black-tailed jackrabbits (*Lepus californicus*) (n = 4), black-tailed prairie dogs (n = 11), and unidentified small rodents (n = 1). Hawks occasionally kleptoparasitized prey from other raptors (2%). However, hawks secured prey most often by scavenging an unattended carcass (36%, n = 16), but often had their scavenged prey items stolen (18%, n = 8). Hawks made few kills that they consumed undisturbed (5%, n = 2). All of the kills we witnessed were prairie dogs, and most of the kills made by Ferruginous Hawks (75%, n = 8) were stolen by Bald Eagles (*Haliaeetus leucocephalus*) or Golden Eagles (*Aquila chrysaetos*). Prey acquisitions often occurred with such speed that the source of prey was not determined with certainty (25%, n = 11). Most (95%) of the successful prey acquisitions of any type were initiated from a perch. Prey acquisition was initiated from pole perches 20 times (44%), ground perches 14 times (31%), and tree perches 9 times (20%). In only one instance (2%) was a prey item acquired following extended soaring.

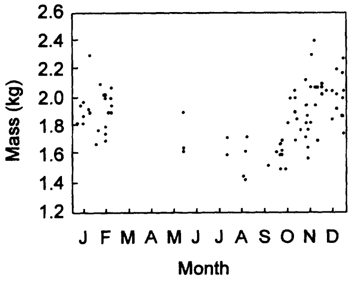

FIGURE 2. Body masses of Ferruginous Hawks trapped in Colorado (n = 84), 1992–1995.

CONDITION

Body masses of 71 hawks were taken at the time of original capture and remeasured for 9 hawks trapped twice and 2 hawks trapped three times. Mass averaged 1.88 ± 0.02 kg (n = 84). Mass varied through the year (Fig. 2) and was generally highest during mid-winter and lowest during late summer.

SITE FIDELITY

Two hawks were recaptured in all three winters and three were recaptured in two consecutive winters. We collected > 1 complete daily observation in consecutive winters for four of these five hawks. All four exhibited spatial overlap of daily MCPs, within and among winters. Most often hawks reused roost trees occupied in previous winters. One additional hawk was VID band-resighted, but not retrapped, in the area it had used and been captured in during the previous winter.

DISCUSSION

McAnnis (1990) reported that seven nesting male Ferruginous Hawks perched for 51% and flew for 49% of the diurnal time budget. Two males nesting in Idaho averaged 61% of the diurnal time budget perching and 39% flying (Wakeley 1978a). We observed that hawks were more sedentary during winter, and little soaring was attempted.

McAnnis (1990) estimated that seven male Ferruginous Hawks nesting in Idaho occupied a mean MCP nesting range of 9.9 km^2. Removing an outlier reduced the mean MCP to 7.6 km^2. Wakeley (1978b), observing for roughly the same time frame as McAnnis (1990), reported MCPs for two males nesting in Idaho of 17.2 and 21.7 km^2. Although the largest of the daily MCPs in our study exceeded those reported by McAnnis (1990) and Wakeley (1978b), the average MCPs for Ferruginous Hawks wintering in Colorado were smaller.

Bildstein (1978) discussed some of the problems in quantifying foraging behaviors (for example, what constitutes a foraging attempt?) and thus the difficulty of drawing reliable conclusions or relating findings to other studies. To minimize the effect that different possible interpretations of field behaviors would have on conclusions in the present study, we make no reference to attempted prey captures. Prey acquisition is the ultimate goal of foraging, but successfully acquiring prey could result from any number of methods including killing, kleptoparasitism, or scavenging unattended prey carcasses. Thus, the success rate of catching live prey is less relevant than is the rate at which any type of prey is secured.

Wakeley (1978c) identified four hunting methods used by nesting male Ferruginous Hawks: (1) from a perch, (2) from the ground, (3) from low-altitude, active flight, and (4) from high-altitude, soaring flight. Wakeley (1978c) found that nesting male Ferruginous Hawks often used wooden fence posts as hunting perches, and one occasionally used wooden utility poles. He reported that hunting from elevated perches was among the least successful techniques of nesting male Ferruginous Hawks, but one of the most used in terms of time budgeting and in the frequency of captures attempted. Likewise, the majority of perches that preceded both passive prey acquisition (kleptoparasitism and scavenging) and active prey acquisition (killing directly) in our study were utility poles. However, Wakeley made no mention of scavenging. It is likely that territorial, nesting hawks existing at low density have little opportunity to scavenge or kleptoparasitize kills made by other raptors, whether conspecific or heterospecific, as is clearly the case with nonterritorial wintering Ferruginous Hawks, existing at much higher density.

Black-tailed prairie dogs constituted only 1% of the number of prey items taken by nesting Ferruginous Hawks in South Dakota (Blair and Schitoskey 1982). In our study, prairie dogs were the only prey species that we observed Ferruginous Hawks killing directly, and the species most often scavenged and kleptoparasitized. Winter habitat for Ferruginous Hawks in our study area was characterized by active black-tailed prairie dog colonies.

Breeding adult European Kestrels (*Falco tinnunculus*) depleted body reserves as they provisioned young, expending energy catching food they did not eat, and losing mass (Village 1990). Postfledging juveniles depleted reserves quickly in the first few weeks of independence from adults. In the winter, activity of kestrels of both age classes decreased, and captured food was consumed, rather than provided to young, and energy intake exceeded energy outputs, so mass increased. We observed a similar annual pattern of mass gain and loss in Ferruginous Hawks. However, we cannot eliminate the alternative that mass differences may have represented distinct populations using our area at different times of the year. However, wintering hawks in this study occupied smaller ranges and remained sedentary more than did nesting hawks studied elsewhere; this energy savings could result in a mass gain as described by Village (1990) for European Kestrels.

Ferruginous Hawks can exhibit a high rate of philopatry to wintering areas. All of the hawks recaptured ($n = 5$) or band-resighted from previous years ($n = 1$) were observed in areas occupied in a previous winter or multiple previous winters. Our study was not designed, however, to follow the fates of Ferruginous Hawks among multiple winters. Thus, philopatry may have been much higher than we demonstrate from fortuitous recaptures alone. Harmata and Stahlecker (1993) report about 30% of inter-annual site fidelity by wintering Bald Eagles. Rough-legged Hawks (*B. lagopus*) also overwinter in previously used areas (Garrison and Bloom 1993).

Ferruginous Hawks are restricted to grassland and shrub-steppe habitats, and conversion of prairie to agriculture is considered a major cause of declines in nesting populations (Houston and Bechard 1984, Schmutz 1984, 1987). However, in winter, these hawks are behaviorally plastic and tolerant of human disturbance and alteration of landscapes, provided that adequate populations of prairie dogs remain (Plumpton and Andersen, unpubl. data). Clearly, wintering Ferruginous Hawks: (1) can remain sedentary for long intervals, and occupy small daily and seasonal home ranges, (2) will reoccupy geographic areas and specific habitats for long intervals within a winter, and may reoccupy former ranges in successive years, (3) rely on a narrow spectrum of prey species, chiefly black-tailed prairie dogs, and occur in greatest density where such colonial prey occur, and (4) will acquire prey by killing directly, kleptoparasitizing from conspecifics and heterospecifics, and scavenging. If survival of overwintering Ferruginous Hawks is jeopardized by loss of wintering habitats or prey populations, identification and preservation of suitable habitats and prey sources within the winter range emerges as an important conservation issue for Ferruginous Hawks.

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Anthropogenic Effects on Winter Behavior of Ferruginous Hawks

David L. Plumpton; David E. Andersen

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ANTHROPOGENIC EFFECTS ON WINTER BEHAVIOR OF FERRUGINOUS HAWKS

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Abstract: Little information is known about the ecology of ferruginous hawks (*Buteo regalis*) in winter versus the breeding season and less about how the species adapts to fragmented grassland habitats. Accordingly, we studied the behavior of 38 radiotagged ferruginous hawks during 3 winters from 1992 to 1995. We used 2 adjacent sites in Colorado that were characterized by low and high levels of anthropogenic influence and habitat fragmentation: the Rocky Mountain Arsenal National Wildlife Refuge (RMANWR; low-level influence), and several adjacent Denver suburbs (high-level influence). Relative abundance of ferruginous hawks differed by treatment area and year ($P < 0.001$); hawks were most numerous where black-tailed prairie dogs (*Cynomys ludovicianus*) were most plentiful. Daily Minimum Convex Polygon (MCP) home range areas did not differ ($P = 0.28$) for RMANWR ($\bar{x} = 4.71$ km^2, SE = 1.33, $n = 25$) and suburban hawks ($\bar{x} = 2.30$ km^2, SE = 0.50, $n = 13$). The number of perches occupied per day between the sites was not different ($P = 0.14$), but hawks at RMANWR used pole and ground perches more frequently and for a greater portion of the daily time budget ($P < 0.05$). Hawks at RMANWR spent less time roosting after sunrise ($\bar{x} = 61$ min) than did suburban hawks ($\bar{x} = 138$ min; $P = 0.004$) and spent less time roosting during the day (RMANWR = 100 min; suburb = 189 min; $P = 0.009$). Prey acquisition and associated intra- and interspecific interactions were not different ($P > 0.05$) at RMANWR and suburban sites. Ferruginous hawks appear to modify their behavior in fragmented, largely human-altered habitats, provided some foraging habitats with adequate populations of suitable prey species are present.

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Key words: anthropogenic, black-tailed prairie dog, *Buteo regalis*, *Cynomys ludovicianus*, ferruginous hawk, habitat loss, habitat use, radiotelemetry.

As habitats become fragmented, local extirpation becomes increasingly likely for species with specialized resource requirements (Harris 1984, Temple 1986, Robinson 1991; Morrison et al. 1992:70), predators (Temple 1986), species with large spatial requirements (Robinson 1991), and species with restricted or small geographic ranges (Simberloff 1994). However, how animals adapt to fragmented habitats is not well documented. Many birds possess adaptations for moving among habitat fragments, making use of newly created habitats, and occupying, avoiding, or vacating newly altered habitats (see review by Knopf 1986). Thus, birds are excellent subjects for the study of anthropogenic or human-related effects, particularly those bird species thought sensitive to such influences.

The ferruginous hawk is an ecological specialist that occupies a specific and narrow range of habitats and has specialized prey requirements (Schmutz 1987, 1989). We describe and contrast winter habitat use by ferruginous hawks between areas subjected to different degrees of human habitat alteration and attendant human activity. We selected ferruginous hawks for several reasons: (1) we know little about the effect of habitat fragmentation on this species, (2) we lack information about habitat requirements and behavior in winter, (3) ferruginous hawks were abundant in some suburban areas of Colorado and were apparently tolerant of human presence in these environments, and (4) they were highly conspicuous and sedentary in winter whereby foraging behavior was readily observed.

STUDY AREA

The study area spanned portions of Adams, Denver, and Weld counties, Colorado (Fig. 1). We conducted fieldwork in 2 adjacent sites: RMANWR and the Denver suburbs of Brighton, Broomfield, Eastlake, Northglenn, Thornton, and Westminster (collectively, the subur-

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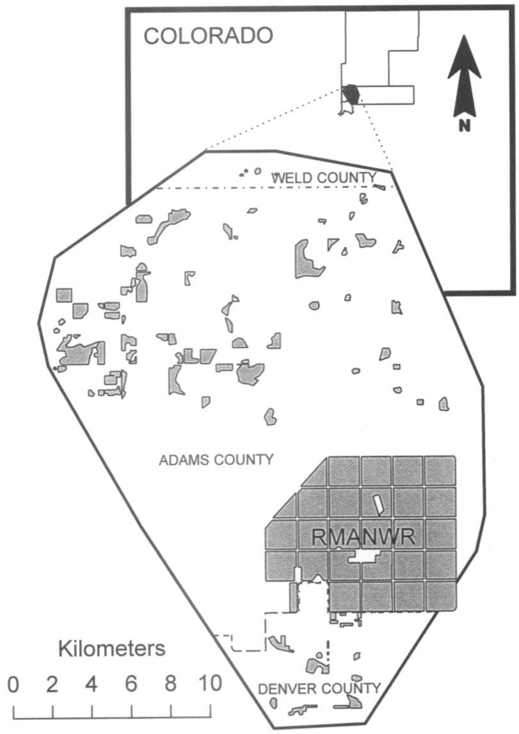

Fig. 1. Study area showing Rocky Mountain Arsenal National Wildlife Refuge and habitat patches composing the adjacent suburban study site, 1992–95. Remaining grassland fragments are shaded.

ban site). These sites differed principally in the extent of human alteration and degree of fragmentation and insularization of habitats. Elevation was about 1,500 m above mean sea level. In undeveloped areas of both sites, shortgrass prairie characterized vegetation and included weedy forbs, cheatgrass (*Bromus* spp.), and crested wheatgrass (*Agropyron cristatum*). Sand sagebrush (*Artemisia filifolia*), rubber rabbitbrush (*Chrysothamnus nauseosus*), and yucca (*Yucca* spp.) occurred throughout the study area; plains cottonwood (*Populus sargentii*) and willow (*Salix* spp.) dominated in riparian areas and where planted in some upland areas. In locations where humans have not extirpated them, black-tailed prairie dogs maintained vegetation at disclimax. Deciduous trees and utility poles used as roosts and perches by ferruginous hawks were plentiful in both sites.

RMANWR

The RMANWR was the largest contiguous block of undeveloped habitat within the area (70 km^2). Anthropogenic alterations were minimal and consisted primarily of buildings centrally located in several small complexes. There also were unimproved roads and utility poles. A perimeter fence enclosed the site and allowed strict control of human access.

Suburban Site

The suburban site approximated a collection of remnant habitat fragments that were small and scattered within a human-altered landscape. The extent of anthropogenic change in the suburban site spanned a continuum from minimal alteration of grasslands into rangeland, through outright destruction or complete removal of habitats for urban development.

METHODS

Estimates of Relative Abundance

We estimated relative abundance (Fuller and Mosher 1987) of ferruginous hawks at RMANWR and suburban study sites. We conducted 5 surveys each winter from December through February, 1993–94 and 1994–95. We replicated surveys every 2 weeks, and we randomized survey sequence and starting points a priori. We established a 38.6-km road transect in each site and surveyed between sunrise and 1100 at an average rate of 33 km/hr. At each ferruginous hawk sighting, we recorded the hawk's location and activity and estimated perpendicular distance from the transect route via a parallax rangefinder. We made an index of prey availability for each site by estimating the linear amount of occupied prairie dog town bisected by the survey route. We compared sighting probabilities between study sites (Andersen et al. 1985) via detection frequency distributions.

Data Collection

We trapped hawks using the Lockhart method (Harmata 1984, Bloom 1987). We also used weakened and padded leg-hold traps baited with live mice (Plumpton et al. 1995) or cottontail rabbit (*Sylvilagus* spp.) carcasses wrapped with noose carpets and dropped from a vehicle in view of perched hawks. We attached radiotelemetry transmitters to the rachis of the central rectrix or to 2 center rectrices of captured hawks. We clipped a small notch into 2 secondary feathers (Young and Kochert 1987) to aid in identifying radiotagged hawks in flight. Research followed approved University of Minnesota animal care and use protocols.

We randomly selected hawks for observation from the radiotagged cohort. Selection was again randomized after successfully tracking all radiotagged hawks for a complete day and with each additional capture. We radiolocated hawks before daylight and continuously recorded behaviors (Martin and Bateson 1986) throughout the daylight interval (specifically, at the start of each perch event, we recorded time to the nearest minute, noted perch substrate, and estimated location). To allow calculation of duration on the perch, we again recorded the time at the termination of that perch. We observed hawks from the farthest distance that allowed continuous visual contact (typically 0.5–1.5 km). We computed daily MCP home range areas with program MCPAAL (Stuwe and Blohowiak 1985).

We reconstructed diurnal time budgets for each hawk at each site. Time budgets included perched locations only because flight time was a negligible portion of the daily time budget during winter. Additionally, location estimates of flying hawks are imprecise, and flight could not be attributed to a particular behavior with certainty. Time budgets considered (1) activity level (total number of perch events per day); (2) number of perch events by substrate (e.g., poles, buildings, and other human-made structures, deciduous trees, and open ground); (3) mean duration of perch by substrate; (4) total daily duration allocated by substrate; (5) proportion of the total daily time budget allocated by substrate; and (6) the duration spent roosting during daylight. We defined diurnal roosting as the interval between daylight and the hawk's first change in location, and the interval between the final location and darkness.

We monitored feeding behavior concurrently with continuous observations. Whenever possible, we recorded prey species, the method of prey acquisition (e.g., killed by the hawk under observation, kleptoparasitized, scavenged as carrion), and other inter- and intraspecific interactions and their outcomes.

Experimental Design

We monitored radiotagged hawks in 2 treatment areas: RMANWR and the adjacent suburban site. This study was a mensurative experiment (Sinclair 1991), and treatments were inherently organismic because it was impossible to randomly assign captured hawks to each treatment. We assumed that we captured hawks randomly from our treatments, and we used radiotagged hawks as replicates within treatments.

We used general linear models (PROC GLM; SAS Institute 1988) to test for year effect and used the Shapiro-Wilk statistic to test continuous data to determine normality (Shapiro and Wilk 1965, SAS Institute 1988). We evaluated homogeneity of error variances between treatments via the folded-form F'-statistic (PROC TTEST; SAS Institute 1988).

We used t-tests when data satisfied parametric statistical assumptions, and nonparametric equivalents when data failed to satisfy these assumptions. We tested non-normally distributed percentage (proportion) data from time budgets with Kruskal-Wallis (H) tests (SAS Institute 1988).

We used Z-tests to contrast the proportions of predatory and competitive encounters in both treatment areas. We used 2-way frequency tables to test for differences between treatment areas in count data such as relative abundances and perch use (SAS Institute 1988). We averaged repeated observations of individual hawks (i.e., days observed; Martin and Bateson 1986: 29); thus, sample sizes (n) represent the number of hawks from which we collected data. We considered all differences significant when $P < 0.05$.

RESULTS

From 1 October 1992 to 19 February 1995, we monitored 38 radiotagged ferruginous hawks (RMANWR: n = 25 [1992–93 n = 10, 1993–94 n = 12, 1994–95 n = 8]; suburban site: n = 13 [1992–93 n = 2, 1993–94 n = 6, 1994–95 n = 6]). We recaptured 5 hawks in multiple winters at RMANWR, and 1 at the suburban site. We captured predominantly adult hawks (after-second-year age class; n = 31) and a few hatch-year–second-year hawks (n = 7). We collected data over 148 days (RMANWR: 104 days; suburban site: 44 days). There were no differences (Type III sums of squares) based on year ($P > 0.05$) for any variable except mean duration of ground perches ($P = 0.03$). However, the mean duration of ground perches showed no difference between treatment areas ($P = 0.143$), so we pooled data among years.

Relative Abundance

Relative abundance of ferruginous hawks differed by treatment area and year ($\chi^2_1 = 16.4$, $P < 0.001$). Detection distances for hawks in the

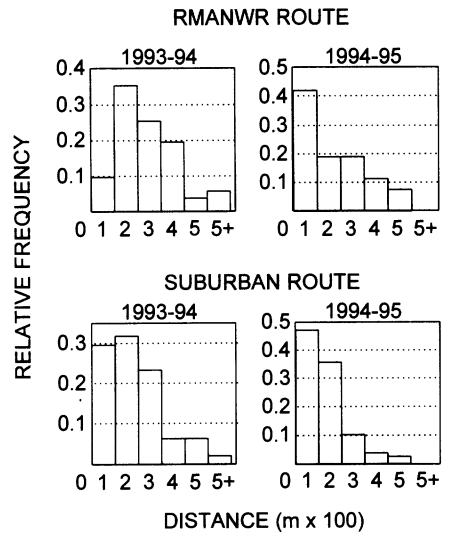

Fig. 2. Detection frequency distributions from roadside surveys of wintering ferruginous hawks in Colorado. Surveys were conducted in 2 treatment areas: the Rocky Mountain Arsenal National Wildlife Refuge (low anthropogenic influence) and a suburban study site (high anthropogenic influence) during 1993–94 and 1994–95.

treatment areas were similar, with most observations falling in the distance categories nearest the transect route (Fig. 2). During 1993–94, we observed equal hawk numbers at RMANWR ($\bar{x}$ = 10 hawks/survey) and in the suburban site ($\bar{x}$ = 9 hawks). However, in 1994–95, we recorded half the number of hawks per survey at RMANWR ($\bar{x}$ = 5), while the number at the suburban site nearly doubled ($\bar{x}$ = 16).

Prey availability also varied by year. During 1993–94, RMANWR had 12.2 km of active, roadside prairie dog colonies, and the suburban site had 15.8 km. In 1994–95, sylvatic plague (*Yersinia pestis*) eliminated prairie dogs over 92% of the area inhabited by prairie dogs at RMANWR in the previous year. After the plague epizootic, the RMANWR route bisected only 3.5 km of extant town, while the suburban route bisected 14 km.

Space Use and Time Budgets

The sizes of daily MCP home ranges did not differ (H_1 = 1.159, P = 0.281) between RMANWR ($\bar{x}$ = 4.71 km^2, SE = 1.33, n = 25) and the suburban site ($\bar{x}$ = 2.30 km^2, SE = 0.50, n = 13). Activity level, indexed by the number of perch positions occupied per day, was not different (t_{36} = −1.485, P = 0.146) in the 2 treatment areas (RMANWR: $\bar{x}$ = 18, SE = 1.39, n = 25; suburban: $\bar{x}$ = 14, SE = 1.66, n = 13). RMANWR hawks (n = 13) used ground and pole perches more frequently, and suburban hawks (n = 13) used deciduous tree perches more frequently (χ^2_2 = 67.7, P < 0.001). Pooled t-tests and nonparametric 1-way analyses of rank scores also indicated differences in the number, duration, and proportion of total time budget for use of perch substrates by treatment area (Table 1).

Ferruginous hawks in the treatment areas exhibited similar temporal patterns in activity level (Fig. 3). Although suburban hawks were slightly less active than hawks at RMANWR,

Table 1. Perch use by ferruginous hawks wintering in 2 adjacent sites with different levels of habitat alteration and human disturbance: the Rocky Mountain Arsenal National Wildlife Refuge, Colorado (low anthropogenic influence, n = 25) and an adjacent suburban area (high anthropogenic influence, n = 13), 1992–95.

		RMANWR		Suburban		
Perch	Variable[a]	$\bar{x}$	SE	$\bar{x}$	SE	P
Pole or building	Number/day	8	1.22	4	1.45	0.005[b]
	Sum (min)	192	27.58	96	36.35	0.012[b]
	Mean (min)	31	4.26	21	5.86	0.074[b]
	Percentage/day	36	4.87	18	6.08	0.013[b]
Ground	Number/day	6	0.76	3	0.71	0.004[c]
	Sum (min)	173	24.50	75	27.16	0.006[b]
	Mean (min)	26	2.99	18	4.08	0.143[c]
	Percentage/day	34	4.89	15	5.10	0.006[b]
Tree	Number/day	4	0.33	8	1.22	<0.001[c]
	Sum (min)	160	24.38	366	48.01	0.001[b]
	Mean (min)	45	5.93	62	14.47	0.288[b]
	Percentage/day	31	4.58	68	8.27	<0.001[b]

[a] Mean per hawk per treatment area.
[b] Kruskal-Wallis and Wilcoxon 2-sample test.
[c] t-test.

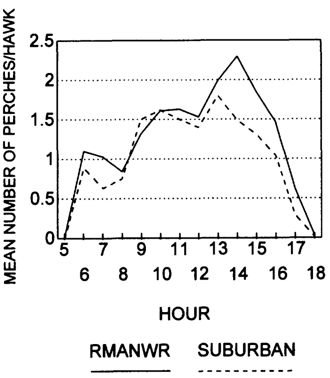

Fig. 3. Diurnal activity levels of ferruginous hawks wintering in 2 adjacent sites with different levels of habitat alteration and human activity: the Rocky Mountain Arsenal National Wildlife Refuge, Colorado (low anthropogenic influence, n = 25) and an adjacent suburban area (high anthropogenic influence, n = 13), 1992–95.

both groups exhibited similar peaks in activity throughout the day.

Hawks using RMANWR spent less time in the roost after daylight than did suburban hawks (P = 0.004), and hawks spent less time in the roost during daylight in the morning and evening combined (P = 0.009; Table 2). The daylight interval spent in the evening roosts did not differ (P = 0.416) between hawks in RMANWR and suburban sites. The duration spent in the roost after sunrise was longer than that spent roosting before sunset for hawks in both sites (RMANWR: morning $\bar{x}$ = 61 min, afternoon $\bar{x}$ = 39 min; H_1 = 5.384, P = 0.020, n = 25; suburban site: morning $\bar{x}$ = 138 min, afternoon $\bar{x}$ = 51 min; H_1 = 9.157, P = 0.002, n = 13).

Foraging

We saw hawks feeding 44 times during 1,325 hr of observation spanning 148 winter days (RMANWR: 104 days, 927 hr, n = 25; suburban site: 44 days, 398 hr, n = 13). Successfully scavenging prey represented 25 (57%) of the observations, whereas we observed direct predation 8 (18%) times. Although we detected no differences in the proportion of any type of prey contact between RMANWR and suburban hawks (Table 3), sample sizes were too low for the normal approximation of the sampling distribution to be accurate in 2 of the 5 comparisons.

Table 3. Summary of observations of foraging ferruginous hawks at Rocky Mountain Arsenal National Wildlife Refuge, Colorado (RMANWR; n = 104 days) and an adjacent suburban study site (n = 44 days), 1992–95.

Proportions	RMANWR	Suburb	$P > Z$
Days with any prey contact	0.278	0.341	0.441[a]
Days with a kill	0.038	0.091	0.192[a]
Days with prey scavenge	0.163	0.181	0.794[a]
Kills with competition	0.75	0.75[b]	
Scavenges with competition	0.29	0.37[b]	

[a] $1 - b < 0.1$.

[b] Sample size was insufficient for use of normal approximation.

DISCUSSION

The size of the home range, the activity level within the home range, and the mean perch duration did not differ between the 2 treatment areas. This result suggests that anthropogenic influences do not strongly affect spatial requirements nor activity level, and that home range size may be independent of the size of the available foraging patch. In urbanized environments, Cringan and Horak (1989) indicated that raptor species with small spatial requirements typically fare better than species with large spatial requirements.

Hawks differed consistently in their use of perch types. Ferruginous hawks at RMANWR

Table 2. Roost use by ferruginous hawks wintering in 2 adjacent sites with different levels of habitat alteration and human disturbance: the Rocky Mountain Arsenal National Wildlife Refuge, Colorado (RMANWR; low anthropogenic influence, n = 25) and an adjacent suburban area (high anthropogenic influence, n = 13), 1992–95.

		RMANWR		Suburban		
Roost	Variable[a]	$\bar{x}$	SE	$\bar{x}$	SE	$P > \chi^{2}$[b]
Morning	Duration (min)	61	8.51	138	22.71	0.004
	Proportion[c]	0.10	0.01	0.22	0.04	0.003
Evening	Duration (min)	39	8.20	51	15.91	0.416
	Proportion	0.06	0.01	0.08	0.02	0.395
Combined	Duration (min)	100	11.93	189	34.61	0.009
	Proportion	0.15	0.02	0.30	0.05	0.007

[a] Mean per hawk per treatment area.

[b] Kruskal-Wallis chi-square approximation.

[c] Duration-daylight interval.

used more exposed perches such as utility poles and open ground, and they used deciduous trees as roosts. In contrast, suburban hawks used more deciduous trees for daytime perches and used fewer pole and ground perches. This difference may be in response to human presence, because the probability of a vehicle passing a roadside pole or prairie dog town was higher at the suburban site than at RMANWR. Additionally, small fragments found in the suburban site had higher perimeter:area ratios, with the perimeter abutting some human-altered environments. Thus, even in the interior of some suburban fragments, perched hawks were close to human-altered areas, direct human disturbance, or both. These same edge effects may explain the prolonged use of morning roosts in the suburban site.

Presence of the primary forage species for ferruginous hawks wintering on our study area, the black-tailed prairie dog, does not alone confer availability to foraging hawks. To be suitable for wintering hawks, foraging habitats also must be free from anthropogenic influences that would preclude use by hawks. Variables that could influence use of foraging habitats by wintering ferruginous hawks include size, shape, isolation within human-altered landscapes or proximity to human structures, and presence of human activity. The minimum size habitat patch required to insulate a hawk from anthropogenic effects that would otherwise render it unsuitable would likely depend on the edge effects in question. Also, the relative size, connectivity or isolation, perimeter:area ratio, shape (and thus "edge" width) varied at each patch, so "boundary effects" (Janzen 1986, Wiens 1994) also varied.

Unlike breeding birds whose habitat use can be driven by availability of nest sites, wintering birds often use particular habitats because of food requirements (Newton 1979, Hutto 1985). Clearly, habitat suitability for wintering ferruginous hawks on our study area is contingent upon the availability of extant black-tailed prairie dog towns. The reasons that ferruginous hawks use some human-altered habitat patches are prey availability and the juxtaposition of roosting and elevated perch structures. Anthropogenic influences thus can either enhance or degrade ferruginous hawk habitats. Clumps of mature deciduous trees, encouraged by humans, have enhanced habitats by providing roost sites and diurnal perches in urban settings. Likewise, hawks used fences and utility poles as elevated perches. The primary anthropogenic influence that impoverishes habitats is extirpation of prairie dogs or reduction of towns to a size or level of isolation within human-altered landscapes that makes habitat unsuitable to ferruginous hawks.

MANAGEMENT IMPLICATIONS

Many urban raptors persist, or even thrive, because they are tolerant of human-altered habitats and derive benefit from human-enhanced prey sources. In contrast, ferruginous hawks in this study and other *Buteo* spp., bald eagles (*Haliaeetus leucocephalus*), and golden eagles (*Aquila chrysaetos*) overwinter in a human-affected environment but rely on nonanthropogenic prey sources.

The habitat fragments in the suburban study site are at risk by virtue of an expanding human population and attendant habitat alteration. As humans further subdivide and isolate grassland fragments, these areas become increasingly unsuitable to wintering raptors. The principal prey resource in this area for ferruginous hawks and a variety of other wildlife is the black-tailed prairie dog. As an ecological specialist, the ferruginous hawk will suffer local extirpation without preservation of adequate prey habitats. Conservation of the black-tailed prairie dog in this community clearly would benefit representatives from the entire ecosystem. Conversely, loss of the black-tailed prairie dog in this area via human conversion of grasslands will result in secondary extinctions throughout the grassland community.

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CHAPTER 16

Focal Areas for Conservation of Prairie Dogs and the Grassland Ecosystem

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Biologists disagree about the magnitude of the area inhabited by the prairie dog in the 1800s, and also about the magnitude of the area inhabited today (Wuerthner 1997; Vermeire et al. 2004; Chapter 6). But we all agree on one point: prairie dog populations have plummeted over the last 200 years because of poisoning, recreational shooting, plague, and loss of suitable habitat (Chapters 8, 10, and 11). This decline has precipitated similar declines for black-footed ferrets, mountain plovers, burrowing owls, and other species that depend on prairie dogs for survival (Chapters 4 and 17). Further, today's colonies are so small and isolated that their impact is trivial for the ecosystem processes that are pronounced in larger colonies (e.g., mixing of top- and subsoil, enhanced nitrogen uptake by plants, and changes in floral species composition; see Chapter 4).

In the 1800s, the geographic range of prairie dogs encompassed more than 160 million hectares (395 million acres), and extended from southern Canada to northern Mexico and from eastern Nebraska to the foothills of the Rocky Mountains (Hollister 1916; Hall 1981). Prairie dogs did not live everywhere in this huge range, and here we distinguish between geographic range and area actually inhabited within that range. About 200 years ago, prairie dogs inhabited about 30 million hectares (74 million acres) of the 160 million hectares in their geographic range—that is, prairie dogs inhabited about 19% of their geographic range (Table 16.1; Knowles et al. 2002; Vermeire et al. 2004). Today's prairie dogs, however, inhabit somewhere between 0.5–0.8 million hectares (1.2–2 million acres)—that is, they inhabit less than 0.5% of their former geographic range, and about 2% of the area that they inhabited 200 years ago (Table 16.1; Luce 2002; Chapters 12 and 14).

Despite this population crash (i.e., a reduction by about 98% of the area formerly inhabited), the plight of the prairie dog is not hopeless. Large areas of the former geographic range still contain grasslands suitable for colonization (The Nature Conservancy 2000). Further, relocation of prairie dogs into unoccupied suitable habitat is feasible (Dullum 2001; USFWS 2002b; Chapter 13), and prairie dog colonies will expand if we can protect them from poisoning, recreational shooting, plague, and conversion of colony-sites to farmland (Chapters 8, 10, and 11). For these reasons, we argue in this chapter that

Table 16.1. Past and current estimates of area inhabited by prairie dogs, and estimate of potential suitable habitat currently available, by state or province. References: Lance 1903; Burnett 1918; Anderson et al. 1986; Flath and Clark 1986; Oakes 2000; USFWS 2004; P. Fargey, personal communication, 2002; R. List, personal communication, 2002. Details are available from authors.

State or province	*Area within former geographic range (hectares)*	*Area within former geographic range inhabited by prairie dogs about 200 years ago (hectares)*	*Current area inhabited by prairie dogs (hectares)*		*Estimate of potentially suitable habitat currently available (hectares)*
			2002	*2004*	
Arizona	1,796,400	278,000	0	0	1,379,800
Colorado	11,513,300	2,800,000	87,000	256,000	8,016,100
Kansas	14,740,800	800,000	53,000	53,000	7,156,900
Montana	24,540,000	595,000	36,000	36,000	13,958,100
Nebraska	16,787,300	No reliable data	32,000	55,000	4,655,000
New Mexico	20,036,400	3,480,000	20,000	24,000	16,040,600
North Dakota	5,266,700	No reliable data	13,000	8,000	2,651,500
Oklahoma	9,239,100	No reliable data	9,000	26,000	4,293,700
South Dakota	13,460,900	711,000	65,000	165,000	8,140,200
Texas	33,813,200	23,300,000	35,000	96,000	22,857,200
Wyoming	8,501,300	No reliable data	133,000	51,000	7,006,700
Saskatchewan	854,800	No reliable data	1,000	1,000	557,200
Sonora	775,600	No reliable data	<1,000	<1,000	0
Chihuahua	3,020,500	No reliable data	20,000	20,000	399,300
TOTAL	164,356,300	>32,000,000	504,000	791,000	

restoration of prairie dogs to an ecologically functional role is feasible at numerous sites.

But wait: why should we bother to worry about today's prairie dogs when they inhabit more than 500,000 hectares (1.2 million acres) and, as detailed below, number between 25 and 40 million in late spring of each year? Three reasons come to mind. First, as noted above, these numbers, though large, are less than 2% of the numbers of about 200 years ago. Second, most of today's prairie dogs live in small, isolated colonies, and therefore are susceptible to local extinctions (Chapters 2 and 17). Third, and perhaps most important, a healthy grassland ecosystem requires more prairie dogs (Chapters 4, 12, 17, and 18). Black-footed ferrets need *large* prairie dog colonies and complexes (groups of nearby colonies) (see Chapter 2) for survival, for example (Clark 1989; Miller et al. 1996). Similarly, mountain plovers and burrowing owls are especially attracted to large prairie dog colonies (Knowles et al. 1982; Knowles and Knowles 1984; Olson 1985; Griebel 2000).

In this chapter we examine where prairie dogs lived prior to settlement of the Great Plains, and where they live now. We define a focal area and list the criteria for identification of good focal areas. We identify focal areas for western North America in general, and for Montana in particular. We emphasize the importance of establishing and maintaining large prairie dog colonies and complexes—i.e., colonies and complexes that span at least 4,000 hectares (9,884 acres)—because, as in other chapters (e.g., see Chapters 4, 12, 17, and 18), our concern is the persistence of not only the prairie dog, but also its grassland ecosystem.

Where Did Prairie Dogs Live Prior to European/American Settlement of the Great Plains?

Figure 16.1 shows the estimated geographic range of prairie dogs in the 1880s, and Table 16.1 shows occupancy by state or province in the early 1900s.

Not all land within the former geographic range is suitable for prairie dogs. Steep slopes, sandy soil, and tall vegetation, for example, render habitat unsuitable. Flat areas or gentle (less than 10%) slopes, by contrast, are more amenable to colonization and occupancy by prairie dogs (Dalsted et al. 1981; Knowles 1982). Prairie dogs live in most types and textures of soil, but highly sandy and poorly drained soils are unsuitable (Osborn 1942; Reid 1954; Sheets 1970; Knowles 1982). Prairie dog colonies vary in size and location over time in response to drought, fire, grazing, colony age, and plague, and also in response to human disturbances such as recreational shooting, poisoning, and conversion of colony-sites to farmland.

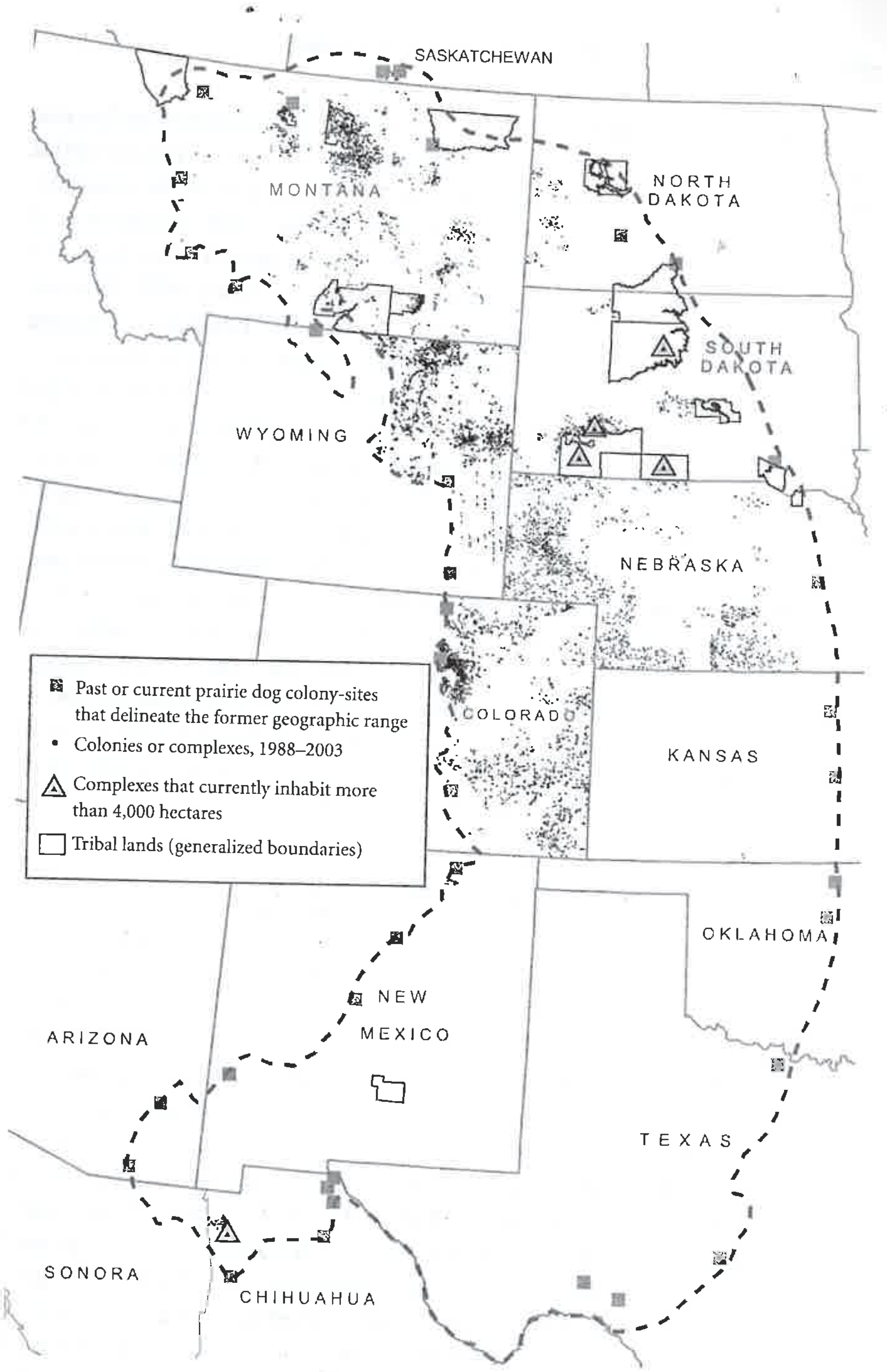

Figure 16.1. Maximal geographic range of prairie dogs about 1880, and distribution of mapped prairie dog colonies and complexes from 1988 to 2003. The dotted line indicates the prairie dog's geographic range of about 200 years ago. References and details are available from authors

Unfortunately, nobody undertook a systematic inventory of the distribution of prairie dogs prior to the many changes in land use in the late 1800s. Rough estimates from the late 1890s and early 1900s made by the Bureau of Biological Survey (Merriam 1902a) and others (Burnett 1918; Anderson et al. 1986; Oakes 2000; Knowles et al. 2002) yield only an approximate picture of the distribution of prairie dogs by state and province in about 1900. These estimates include information from all five species of prairie dogs and indicate that the five species inhabited roughly 41 million hectares (101 million acres) in the early 1900s. Because the former geographic range of the black-tailed prairie dog is 71% of the former cumulative geographic range for all five species, black-tailed prairie dogs probably inhabited roughly 30 million hectares (74 million acres) in about 1900 (41 million hectares × 0.71 = roughly 30 million hectares) (Nelson 1919; Anderson et al. 1986; Hoffmeister 1986; Vermeire et al. 2004). Good regional maps of areas inhabited by prairie dogs sometimes resulted from surveys, and other times, ironically, from efforts to poison prairie dogs (e.g., Flath and Clark 1986; Oakes 2000; Knowles et al. 2002). These data of varying reliability indicate that prairie dogs occupied 2%–15% of the Great Plains before the late 1800s. Large colonies inhabiting more than 20,000 hectares (49,000 acres) were numerous, and many colonies were exceptionally large. Some colonies, for example, occupied more than 2 million hectares (4.9 million acres) (Knowles et al. 2002).

Where Do Prairie Dogs Live Now?

Table 16.1 shows the area currently inhabited by prairie dogs by state or province, and Figure 16.1 shows the distribution of colonies that have been mapped over the last 20 years or so. Accuracy of mapping varies among states. Certain states (e.g., Texas and North Dakota) and certain Native American tribes (e.g., in North and South Dakota) do not publish information about the size and location of prairie dog colonies. Other states (Oklahoma, New Mexico, and Kansas) are still conducting surveys.

The large colony-sites of yesteryear (more than 20,000 hectares [49,000 acres]) are now gone. Remaining are smaller, scattered colonies, with only a few occupying more than 2,000 hectares (4,900 acres) (Figure 16.1). The cumulative area occupied by today's prairie dogs is between 0.5 and 0.8 million hectares (1.2–2.0 million acres) (Table 16.1). Today's cumulative population of adult and yearling prairie dogs, before the emergences of juveniles from their natal burrows in late spring, is therefore between 12.5 and 20 million. Following the first emergences of juveniles, today's cumulative population is between 25 and 40 million prairie dogs. These estimates assume densities of 25 adults and yearlings per hectare and 25 juveniles per hectare (Hoogland 1995; Chapter 2).

Patterns of land use, land ownership, and disease primarily determine how prairie dogs are distributed today. We estimate, for example, that conversion of grassland habitat to cropland has eliminated 37.6 million hectares (92.9 million acres, or 33%) of grassland within the former geographic range—almost entirely on private lands and primarily in the eastern one-third of the range (see also Choate et al. 1982; Bragg and Steuter 1996; Samson et al. 1998). In Montana—the only state with a rigorous statewide inventory of colonies, including the distinction of colony-sites with live prairie dogs versus colony-sites with no prairie dogs because of plague or poisoning—Native American lands have the highest percentage of occupancy by prairie dogs (1.5%), followed by federal and state lands (0.33%), and then private lands (0.08%). Plague, most prevalent in the western two-thirds of the former geographic range, often prevents prairie dogs from inhabiting or recolonizing certain large areas (Chapter 11). Only about 10% of the former geographic range is both uncultivated and plague-free (USFWS 2002a).

Fragmentation of colonies following population crashes from poisoning, plague, or some other catastrophe also affects the distribution and persistence of prairie dogs (Chapter 8). Small, isolated colonies are more likely than larger colonies to be ignored in poisoning campaigns, for example, but these same colonies are more prone to extinction from other causes such as genetic drift, inability to avoid extreme inbreeding, and predation (Chapter 2). In Oklahoma, the persistence of prairie dog colonies is highest for large, isolated colonies (Lomolino and Smith 2001).

What Are Focal Areas?

Because resources for conservation are always scarce, we need to target operations that are most likely to be successful (Groves 2003). A "focal area" for the restoration and conservation of prairie dogs is a site of sufficient size so that a colony or complex can be large enough to provide suitable habitat for black-footed ferrets, burrowing owls, mountain plovers, and other species that depend on prairie dogs for survival (Chapter 4). But what do we mean by "sufficient size"? Bigger is always better, but an area of 4,000 hectares (9,884 acres) for a colony or complex is probably the minimum necessary for a fully functional grassland ecosystem (Conservation Breeding Specialist Group 2004). Density varies among colonies (Chapters 2 and 6), but a colony that inhabits 4,000 hectares (9,884 acres) usually contains roughly 100,000 adult and yearling prairie dogs and, in late spring, roughly 100,000 juveniles as well; these estimates assume densities of 25 adults and yearlings per hectare and 25 juveniles per hectare (Hoogland 1995; Chapter 2).

Restoring prairie dogs to their former abundance over the entire former geographic range is unrealistic, but finding representative focal areas where prairie dogs can be restored, with complexes of at least 4,000 hectares (9,884 acres), is eminently feasible (see also Miller et al. 1994; Licht 1997; Wuerthner 1997; Gilpin 1999; EDAW 2000; Lomolino et al. 2003; Samson et al. 2004).

Factors That Affect the Suitability of Focal Areas

As described below, at least four factors affect the suitability of focal areas.

Quality of Habitat

Before restoring prairie dogs to a focal area (via translocation, for example; see Chapter 13), we must identify habitat likely to be suitable. For such identification, we used a model designed for Montana that combines information regarding slope, vegetation, and soil-type with a Geographic Information System (GIS) (Proctor 1998). Indications of suitability include slopes of less than 4% and short vegetation classified as grassland, salt-desert shrub, dry salt flats, or mixed barren sites. Two lines of evidence indicate the accuracy of our classification of habitat. First, 95% of known colonies in Montana are in areas classified by our model as suitable. Second, records of poisoning in 1924 show that numerous prairie dog colonies inhabited a large area on the Crow Reservation, Montana (Bureau of Biological Survey, 1924). Our model identified this same area as one of the largest areas of suitable habitat in the state, even though few prairie dogs live there today.

We modified Proctor's (1998) methodology for Montana to accommodate data from throughout the former geographic range of prairie dogs. Because only general information about vegetation was available for most areas, we used categories of preferred vegetation that were somewhat broader, though still consistent, with the Montana categories. Recent research indicates the presence of prairie dog colonies at slopes up to 10% (USGS 1999), so we changed our cutoff for slopes from 4% to 10%. We categorized the Sandhills region of Nebraska as unsuitable because we have found no evidence that large complexes of prairie dogs ever have lived there. We also classified farmland as unsuitable, but recognize that much farmland could become suitable for prairie dogs if agriculture ceases. Our model indicates that about 97 million hectares (240 million acres) of habitat—that is, about 61% of the former geographic range of 160 million hectares (395 million acres)—is currently suitable for prairie dogs (Table 16.1, Figure 16.2).

Opportunities for Management

Opportunities for management improve the suitability of focal areas for restoration and conservation. Public lands, especially those belonging to the Bureau of Land Management (BLM) and United States Forest Service (USFS), offer tremendous potential because: they often occur in large, contiguous blocks and are not cultivated for crops; conservation of biodiversity is a priority there; and large colonies of prairie dogs already live there in many cases. Consequently, when possible, a logical place to restore and conserve large prairie dog colonies and complexes is on public lands (see also Chapter 15).

Many Native American lands also offer excellent opportunities for conservation. Several reservations (e.g., Fort Belknap, Northern Cheyenne, Cheyenne River, and Rosebud) currently have programs for the conservation of prairie dogs and black-footed ferrets. Reservations in South Dakota (Cheyenne River, Pine Ridge, and Rosebud) contain three of today's five largest prairie dog complexes. The Northern Cheyenne Fish and Wildlife Enhancement Department has initiated a program with a goal of restoring complexes of prairie dogs that span 4,000 hectares (9,884 acres).

We use the term "key private land" for terrain that belongs to a landowner who actively promotes the conservation of prairie dogs. Key private lands can foster the restoration of large colonies and complexes, especially in states with only limited public lands (e.g., Kansas, Oklahoma, Texas, and Nebraska). Groups with key private lands include Turner Enterprises (with lands in South Dakota, Kansas, and New Mexico), The Nature Conservancy (Montana, Wyoming and Colorado), the Southern Plains Land Trust (Colorado), and the Gray Ranch (New Mexico).

The Current Existence of Colonies

The presence of prairie dogs in an area eliminates all doubt regarding suitability of habitat. Consequently, the most promising regions for conservation are those areas that already contain numerous colonies and complexes. Unfortunately, as noted above, good information on the existence and location of today's prairie dog colonies is lacking for certain states. Huge complexes that would meet our criteria for focal areas are so conspicuous that they cannot easily escape detection, however, and thus are more likely than smaller complexes to be discovered in states with incomplete inventories.

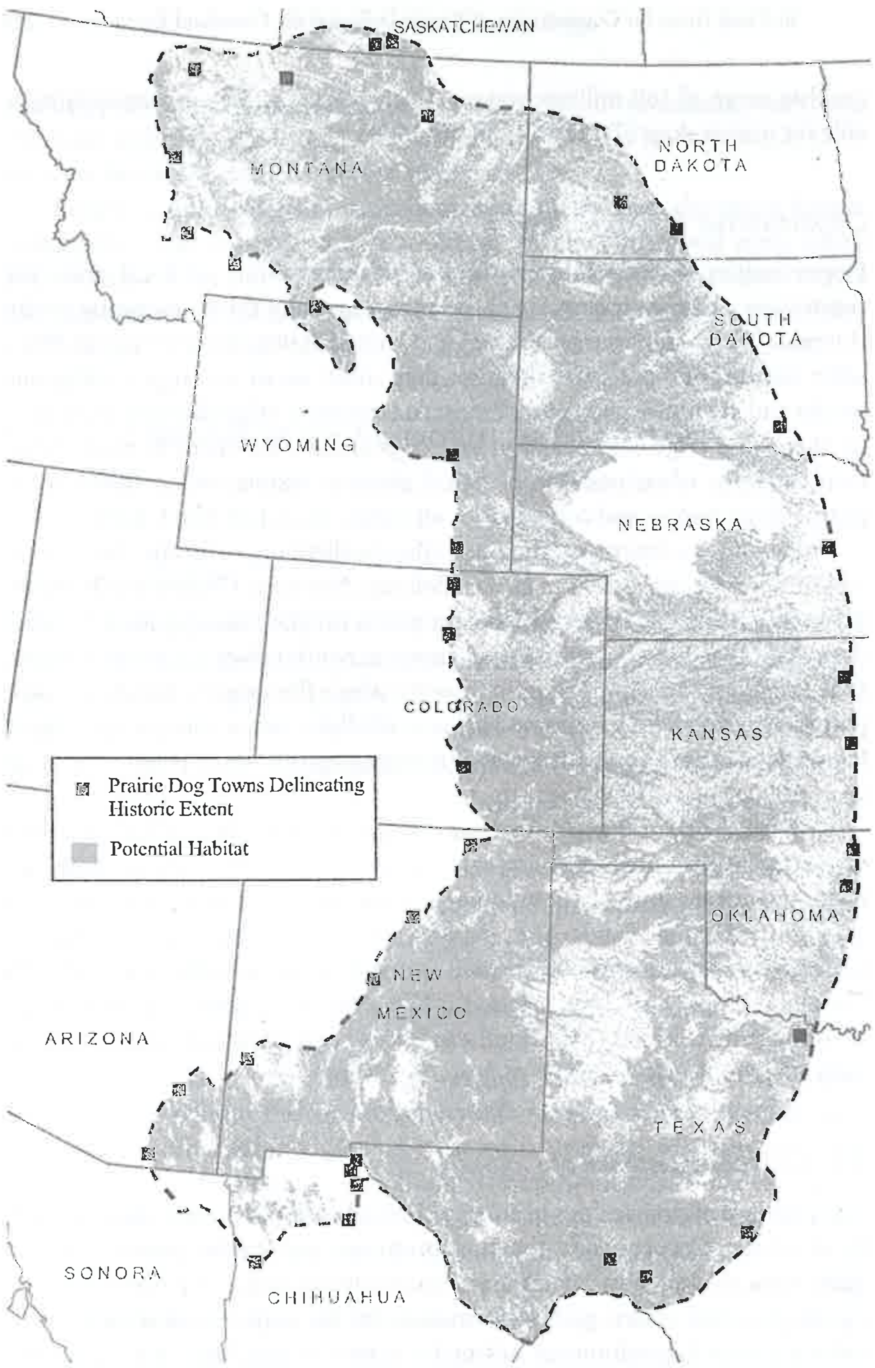

Figure 16.2. Suitable habitat, as determined from slope and vegetative cover, for today's prairie dogs. The dotted line indicates the prairie dog's geographic range of about 200 years ago.

Geography

In order to preserve possible genetic differences associated with geography, plans for conservation of prairie dogs should include focal areas distributed throughout the former geographic range, including the periphery (Lomolino and Smith 2001). Focal areas also should be sufficiently numerous and widespread to maximize the probability of long-term survival against plague. Focal areas in the eastern one-third of the prairie dog's current geographic range are especially promising, because plague is currently absent there (Chapter 11).

Best Opportunities for Restoring and Conserving Prairie Dogs Throughout North America's Great Plains

Using the criteria described above, we have identified 84 focal areas (all more than 4,000 hectares [9,884 acres]) for the restoration and conservation of prairie dogs (Figure 16.3), as follows:

- For 60 focal areas: when possible, we identified the five largest focal areas of suitable habitat on public lands in the eleven states and three provinces that currently have prairie dogs (or had them in the past [Arizona]). Oklahoma has only three focal areas of more than 4,000 hectares (9,884 acres), Kansas has only two, and no information is available for the Sonoran province of Mexico. The other nine states and two provinces all have five focal areas (N = 3 [Oklahoma] + 2 [Kansas] + 45 [9 states × 5] + 10 [2 provinces × 5] = 60 focal areas).
- For 21 focal areas: we also identified the largest focal area on Native American lands in each reservation (N = 13) and all focal areas within key private lands (N = 8).
- For the last three focal areas: because Kansas has only two focal areas (counted above) with at least 4,000 hectares (9,884 acres), we added the largest three blocks of suitable habitat in Kansas (regardless of landownership) as additional focal areas (N = 3).

The 84 focal areas range in size from 4,300 hectares to 2.4 million hectares (11,000 acres to 5.9 million acres) (Figure 16.3), and most focal areas are largely or entirely within federal or state, rather than private, lands. The cumulative area of these 84 focal areas is 10.5 million hectares (26 million acres): 9 million hectares (22.2 million acres) on federal and state lands, 1.3 million hectares (3.2 million acres) on Native American lands, 180,000

Table 16.2. Land ownership characteristics for some selected focal areas. All areas are in hectares; 1 hectare = 2.471 acres. Sources of data are available from authors.

Location	*Total potential habitat*	*Key private potential habitat*	*Native American potential habitat*	*BLM potential habitat*	*USFS potential habitat*	*NPS potential habitat*	*USFWS potential habitat*	*State potential habitat*	*Other*	*Maximum area occupied in past 20 years*
Glaciated Plains, Montana	230,939	11,791	0	154,440	0	0	40,839	23,869	0	9,629
Fort Belknap, Montana	169,481	0	163,316	0	0	0	0	6,165	0	6,612
Grasslands National Park, Saskatchewan/Bitter Creek, Montana	217,827	0	357	193,319	0	0	28	24,123	0	281
Little Missouri, North Dakota	125,490	0	0	399	111,310	4,225	0	9,556	0	477
Bad River-Fort Pierre, South Dakota	84,318	47,840	0	0	36,352	0	0	0	126	584
Buffalo Gap, South Dakota	114,058	0	0	0	82,252	26,234	0	5,549	23	7,125
Thunder Basin, Wyoming	139,996	0	0	6,094	117,660	0	0	16,242	0	15,947
Oglala, Nebraska and South Dakota	19,010	0	0	0	18,778	0	0	232	0	216
Comanche-Fort Carson, Colorado	155,198	0	0	83	53,565	0	0	16,991	84,559	383
Cimarron, Kansas, Oklahoma, and Colorado	42,220	0	0	0	42,220	0	0	0	0	unknown
Wichita Mountains, Oklahoma	35,933	0	0	0	0	0	11,158	0	24,775	unknown
Rita Blanca, Texas, Oklahoma, and New Mexico	127,920	0	0	10	121,566	0	0	6,354	0	unknown
Antelope Ridge, New Mexico	742,380	0	0	405,336	0	0	0	328,072	8,972	unknown
San Simon, Arizona	283,527	0	0	174,235	5,951	75	0	103,266	0	unknown
Pancho Villa, Mexico and New Mexico	100,708	0	0	0	0	0	0	0	100,708	20,417

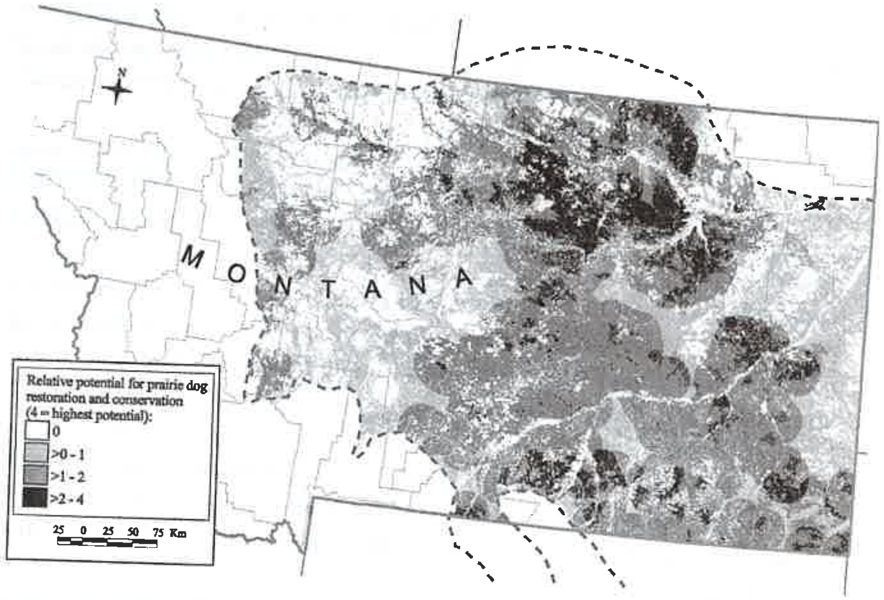

Figure 16.4. Ranking of habitat in Montana regarding suitability for occupancy by prairie dogs.

How Can Focal Areas Promote Restoration and Conservation of the Prairie Dog?

If prairie dogs are restored and conserved within only 15% of the suitable habitat within the 84 focal areas that we have identified (Figure 16.3), the cumulative area occupied will be about 1.6 million hectares (4 million acres)—two to three times the area currently occupied by prairie dogs, but still only about 1% of the 160 million hectares (395 million acres) within their former geographic range, and only about 5% of the 30 million hectares (74 million acres) inhabited by prairie dogs about 200 years ago.

Grazing by livestock often occurs on federal and state lands, but the vast majority of grazing occurs on private ranches. Because most focal areas are largely or entirely within federal or state lands, interference with agricultural and ranching operations should be minimal. We believe that focal areas can provide the habitat necessary for the restoration and long-term survival of both the prairie dog and its grassland ecosystem.

Summary

- In the 1800s, the geographic range of prairie dogs encompassed more than 160 million hectares (395

Canada to northern Mexico and from eastern Nebraska to the foothills of the Rocky Mountains. Prairie dogs did not live everywhere in this huge range, but rather inhabited about 30 million hectares (74 million acres), about 19% of their geographic range.

- Today's prairie dogs inhabit somewhere between 0.5–0.8 million hectares (1.2–2.0 million acres)—that is, they inhabit less than 0.5% of their former geographic range, and about 2% of the area that they inhabited 200 years ago.
- Large colonies encompassing more than 20,000 hectares (49,000 acres) were common 200 years ago, and many colonies were exceptionally large; some occupied more than 2 million hectares (4.9 million acres). Today's colonies are smaller and more isolated, and only a few occupy more than 2,000 hectares (4,900 acres).
- Today's cumulative population of adult and yearling prairie dogs is between 12.5 and 20 million. Following the weaning of juveniles each spring, today's cumulative population of adults, yearlings, and juveniles is between 25 and 40 million.
- A "focal area" for the restoration and conservation of prairie dogs is an area of sufficient size so that a colony or complex can provide suitable habitat for black-footed ferrets, burrowing owls, mountain plovers, and other species that depend on prairie dogs for survival. Bigger is always better, but an area of 4,000 hectares (9,884 acres) for a colony or complex is probably the minimum necessary for a fully functional grassland ecosystem.
- Four factors that affect the suitability of focal areas for the restoration and conservation of prairie dogs are quality of habitat, opportunities for management, the current existence of colonies, and geography.
- We have identified 84 focal areas for the restoration and conservation of prairie dogs. These focal areas range in size from 4,300 hectares to 2.4 million hectares (11,000 acres to 5.9 million acres), and their cumulative area is 10.5 million hectares (26 million acres).
- Grazing by livestock often occurs on federal and state lands, but the vast majority of grazing occurs on private ranches. Because most focal areas are largely or entirely within federal or state lands, interference with agricultural and ranching operations should be minimal.
- If prairie dogs are restored and conserved within only 15% of the suitable habitat within the 84 focal areas that we have identified, the cumulative area occupied would be about 1.6 million hectares (4 million acres)—two to three times the area currently occupied by prairie dogs, but still only about 1% of the 160 million hectares (395 million acres) within their former geographic range, and only about 5% of the 30 million hectares (74 million acres) inhabited by prairie dogs about 200 years ago. Focal areas evidently can provide the habitat necessary for the restoration and long-term survival of not only the prairie dog, but also its grassland ecosystem.

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REVIEW ARTICLE

Aluminium and zinc phosphide poisoning

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Introduction. Aluminium and zinc phosphides are highly effective insecticides and rodenticides and are used widely to protect grain in stores and during its transportation. Acute poisoning with these compounds may be direct due to ingestion of the salts or indirect from accidental inhalation of phosphine generated during their approved use. *Mechanisms of toxicity.* Both forms of poisoning are mediated by phosphine which has been thought to be toxic because it inhibits cytochrome c oxidase. While phosphine does inhibit cytochrome C oxidase *in vitro*, the inhibition is much less *in vivo.* It has been shown recently in nematodes that phosphine rapidly perturbs mitochondrial morphology, inhibits oxidative respiration by 70%, and causes a severe drop in mitochondrial membrane potential. This failure of cellular respiration is likely to be due to a mechanism other than inhibition of cytochrome C oxidase. In addition, phosphine and hydrogen peroxide can interact to form the highly reactive hydroxyl radical and phosphine also inhibits catalase and peroxidase; both mechanisms result in hydroxyl radical associated damage such as lipid peroxidation. The major lethal consequence of phosphide ingestion, profound circulatory collapse, is secondary to factors including direct effects on cardiac myocytes, fluid loss, and adrenal gland damage. In addition, phosphine and phosphides have corrosive actions. *Clinical features.* There is usually only a short interval between ingestion of phosphides and the appearance of systemic toxicity. Phosphine-induced impairment of myocardial contractility and fluid loss leads to circulatory failure, and critically, pulmonary edema supervenes, though whether this is a cardiogenic or non-cardiogenic is not always clear. Metabolic acidosis, or mixed metabolic acidosis and respiratory alkalosis, and acute renal failure are frequent. Other features include disseminated intravascular coagulation, hepatic necrosis and renal failure. There is conflicting evidence on the occurrence of magnesium disturbances. *Management.* There is no antidote to phosphine or metal phosphide poisoning and many patients die despite intensive care. Supportive measures are all that can be offered and should be implemented as required.

Keywords Aluminium (Aluminum) phosphide; Zinc phosphide

Introduction and uses

For many years aluminium and zinc phosphides have been highly effective insecticides and rodenticides with the major merits of being inexpensive and not leaving toxic residues. They are formulated as compressed discs, tablets or pellets that commonly weigh 3 g and contain variable amounts of a single phosphide in combination with other substances such as ammonium carbonate. The purity of the technical salt used varies, being of the order of 87% for aluminium phosphide and 80–95% for zinc phosphide. Phosphides are used widely to protect grain held in stores, the holds of ships and in wagons transporting it by rail and are admixed with the grain at a predetermined rate as it is put into storage. The phosphide then interacts with moisture in the air between the grains to liberate phosphine (hydrogen phosphide, phosphorus trihydride, PH_3) (Fig. 1) which is the active pesticide. The release of phosphine is even more vigorous after contact with an acid (Fig. 1). Acute poisoning with these compounds, therefore, presents two forms: direct ingestion of the salts themselves or indirect inhalation of the phosphine generated during their approved use.

Pure phosphine is colorless and odorless up to toxic concentrations (200 ppm), a view accepted by the International Programme on Chemical Safety and others (1–4), though Merck asserts that it has an odor of decaying fish (5). If the former view is accepted the smell emanating from phosphide-poisoned patients is probably due to contaminants in the pesticide formulations and not phosphine itself. It has been suggested that these volatile contaminants may be alkylphosphines (6). For "phosphine" liberated from one pesticidal formulation of aluminium phosphide, the odor threshold was 0.01–0.02 ppm, ten times lower than that derived from the technical salt alone (6).

The usefulness of phosphide pesticides is now threatened by the development of resistance to them.

Methods

In order to complete this review, the terms aluminium and aluminum phosphide, zinc phosphide, and phosphine were

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$$AlP + 3H_2O \qquad Al(OH)_3 + PH_3$$
$$AlP + 3H^+ \qquad Al^{3+} + PH_3$$

$$Zn_3P_2 + 6H_2O \qquad 3Zn(OH)_2 + 2PH_3$$
$$Zn_3P_2 + 6H^+ \qquad 3Zn^{2+} + 2PH_3$$

Fig. 1. Formation of phosphine from aluminium and zinc phosphides after interaction with water or acid.

searched using the Medline, Embase, Toxnet, and Google Scholar databases. All relevant articles in English were obtained. In addition, the *Current Awareness in Clinical Toxicology* database and the extensive files held by the UK National Poisons Information Service were searched. Older papers were used to identify original research prior to 1966. Not all articles obtained are referenced in this review. Many isolated case reports and small case series do not appear in the citation list. The only criterion for inclusion is the ability to highlight important aspects.

Epidemiology

In a recent series of 188 "phosphine" poisonings from Germany that occurred between 1983 and 2003, 28% were intentional and mainly by ingestion (presumably of metal phosphides though it is not stated) while most of the 65% unintentional exposures were by inhalation (7). A similar pattern has also been reported from the United Kingdom where the majority of 93 aluminium phosphide exposures over a period of 6.5 years (1997–2003) were accidental and involved inhalation of phosphine liberated from phosphides in agricultural settings (8); there was no evidence that the number of incidents was increasing.

Ingestion of phosphides

Phosphide ingestion is a particular problem in rural India, the origin of most of the data on this topic (9–13). The aluminium salt is most commonly involved. Indeed, in a prospective study of 559 acute poisonings admitted over 14 months to a single hospital in Harayana-Rohtak, India, no fewer than 379 (68%) involved aluminium phosphide (14). Similarly, reports to the National Poisons Centre in Delhi indicate that aluminium phosphide is the pesticide most commonly ingested by children (15). Occasionally parents attempting suicide with phosphides have given some to their children with fatal consequences (16) and aluminium phosphide was second only to burns as the cause of dowry deaths in the Allahabad region (17).

Much smaller numbers or only sporadic cases of phosphide poisoning have been reported from around the world, including Australia (18), Denmark (19), France (20), Germany (21), Greece (22), Iran (23), Jordan (24), Morocco (25–27), Nepal (28), Sri Lanka (29), Turkey (30), the United Kingdom (31,32), Canada, the United States (33,34), the former USSR (35), and Yugoslavia (36). A single death from ingestion of a falsely labeled rodenticide bait has been reported (37). Phosphide rodenticides were responsible for nine out of 349 deaths in 35,580 poisoning admissions to one hospital in Tehran (23).

Zinc phosphide ingestion is very much less common (12,22,28,29,33,36–41).

Occupational and environmental phosphine exposure

Occupational exposures to phosphine are uncommon and rarely severe (42,43) but accidental inhalation is a particular risk to those in close proximity to grain that has had a metal phosphide mixed in with it. Recurring locations include ships' holds (44–49), rail wagons (47–49), grain elevators (24), grain stores (50,51), and even stores in homes (24). Potentially lethal concentrations of the gas may develop in the head-spaces of unventilated or poorly ventilated storage containers and domestic premises (52).

Phosphine may be released during the illicit manufacture of methamphetamine (53,54); deaths have resulted (54). In another incident, a packet of aluminium phosphide in a container from abroad was burst and the sweepings placed in water causing immediate fizzing and liberation of phosphine (55).

Close proximity to a source of phosphine is not required to be at risk of toxicity as phosphine gas can travel some distance as it is heavier than air (vapor density 1.2:1). Many years ago 12 individuals in a house adjacent to a warehouse used to store aluminium phosphide developed vomiting and one died. The illnesses were attributed to phosphine (56). More recently exposures have been alleged after use of metal phosphides to control pests in adjacent buildings (57).

Mechanisms of toxicity

It is generally accepted that the toxicity of metal phosphides is due to phosphine liberated when ingested phosphides come into contact with gut fluids, the gas being absorbed through the alimentary mucosa and distributed to tissues. This view is supported by two facts which suggest, but do not prove absolutely, that the assumption is correct. First, blood phosphine concentrations were higher on admission to hospital and at 12 h after ingestion in those who were severely poisoned compared with those with mild or no toxicity. Second, concentrations were higher in patients who died than in those that survived (58). Furthermore, blood phosphine concentrations were higher in shocked patients poisoned with fresh tablets compared with those who consumed old ones or only powder from tablets (58) presumably because the salt in the latter had been hydrolysed, partially or totally, by moisture in the atmosphere.

There is evidence *in vitro* that phosphine inhibits cytochrome C oxidase (Complex IV) (59,60). However, it is unlikely that this interaction is the primary cause of toxicity as phosphine inhibits cytochrome C oxidase activity less dramatically *in vivo* than *in vitro* (61). Phosphine only partially inhibits cytochrome C oxidase activity in insects (625), rats (60), and humans (63). Thus, phosphine is different from other cytochrome C oxidase inhibitors such as cyanide, which strongly inhibit cytochrome C oxidase activity *in vivo* (64). Moreover, in humans, the features of phosphine and metal phosphide poisoning are not in keeping with those of cyanide and hydrogen sulfide.

It is therefore pertinent to consider what other mechanism(s) might be relevant.

1. Recent studies in nematodes have shown that phosphine perturbs mitochondrial morphology, inhibits oxidative respiration by 70%, and causes a severe drop in mitochondrial membrane potential within 5 h of exposure (65). This failure of cellular respiration is likely to be due to a mechanism other than inhibition of cytochrome C oxidase as phosphine inhibits cytochrome C oxidase activity less dramatically *in vivo* than *in vitro* (61,66) and only partially inhibits cytochrome C oxidase activity in humans (63).
2. Phosphine and hydrogen peroxide can interact to form the highly reactive hydroxyl radical. This is consistent with an observed increase in hydroxyl radical associated damage, such as lipid peroxidation, *in vitro* (67,68) and *in vivo* in mammalian cell lines (68–70).
3. Since phosphine also inhibits catalase and peroxidase (71,72), at least in insects, scavenging of peroxide radicals is reduced and the resulting lipid peroxidation damages cells. Data from humans poisoned with aluminium phosphide appear to support this mechanism (63,73–75), as do studies in rats (69).
4. Both aluminium (76) and phosphine (77,78) inhibit cholinesterases (79). Rastogi et al. (9) measured serum cholinesterase activity on admission to hospital and 12 and 72 h later in 25 patients with aluminium phosphide poisoning. Only one had a result comparable to the mean control value; the others were 75% or less including seven in whom it was below 20%. However, no reduction in brain (pre-frontal cortex) acetylcholinesterase activity was found in 10 patients who died. It seems unlikely that any of these reductions, except, perhaps, the most severe, is of clinical relevance. It is also possible that aluminium contributes to them (80,81).
5. Human serum cholinesterase activity was reduced after exposure to phosphine *in vitro*, the extent of the inhibition being related to the concentration and duration of exposure (78). However, limited data suggest that there is no *in vivo* reduction of erythrocyte cholinesterase activity in humans after accidental inhalation of phosphine (44,81). Whether this is due to lower blood phosphine concentrations after inhalation of the gas compared with those attained after ingestion of phosphides cannot currently be determined.
6. "Phosphine" liberated by hydrolysis of phosphide pesticides contains contaminants, the nature and toxicity of which are unclear (see Introduction and uses).
7. There is also evidence that phosphides are corrosive. Hematemesis has complicated phosphide ingestion (82) and on occasions it has been massive (10). Gastroduodenitis (83) and esophageal stricture (84–89) have been found at endoscopy as early as 2 weeks after consumption. Similarly, definitive diagnoses of esophagitis and gastritis have been made at autopsy (21) while others have commented on the frequent finding of deep congestion of the linings of the esophagus, stomach, and duodenum (11). The fact that it decreases in the ileum might also support a corrosive action. However, in these cases there is congestion of many organs. It is not clear if the salts or the gas generated from them are responsible for the corrosive features. On balance, the corrosive action of the phosphides is not an important component of their toxicity.
8. The metal moiety of the ingested molecule could also contribute to toxicity indirectly. Concentrations of metals in the tissues of those dying from phosphide ingestion have been measured relatively rarely but when they have been, very high concentrations have been found. For example, in one case the concentration of aluminium in blood was 1,537 μg/L with 36, 4.6 and 75 μg/g in brain, heart, and liver respectively (20). In other fatal cases an elevated, but much lower, aluminium concentration (713 μg/L) was found in one (90) and zinc in a concentration of 1,160 μg/L in another (33). The relevance of these to toxicity remains to be determined but there is clear evidence that aluminium (as well as phosphine (77)), can inhibit acetylcholinesterase (76,80,93).

Toxicokinetics

There are very few data on the toxicokinetics of aluminium phosphide, zinc phosphide, and phosphine. The short interval between ingestion of metal phosphides and the appearance of features of systemic toxicity indicates that phosphine must be rapidly and readily absorbed. Remarkably, there is also evidence that phosphides may be absorbed as microscopic particles of unhydrolysed salt (39,91).

Phosphine was detected in the blood of ten fatalities but not quantified (24). In one of two more deaths it was present in blood in a concentration of 0.5 μg/L (91) but undetectable in the other (20). Chugh and his colleagues (58) claimed to show higher blood phosphine concentrations in shocked patients poisoned with fresh aluminium phosphide tablets compared with those who consumed old ones or only powder from tablets. They also demonstrated higher concentrations in shocked patients who died than in shocked survivors. However, how their analytical method could have measured phosphine has been questioned (92).

There are no data on the distribution of phosphine to tissues but one would expect such a small molecule to reach all organs readily.

Similarly, the fate of phosphine in the body is obscure. It is known to interact irreversibly *in vitro* with free hemoglobin and hemoglobin in intact erythrocytes (rat and human) to produce a hemichrome (a methemoglobin derivative resulting from altered protein conformation) (93,94). Heinz bodies (denatured hemoglobin aggregates) are also formed *in vitro* at concentrations of 1.25 ppm (94). These reactions require oxygen and it has been suggested that phosphine must be degraded before they occur. Some 16% of phosphine interacted with rat hemoglobin was recovered as phosphite and phosphate but the remainder could not be accounted for (93). Rare cases of phosphide poisoning complicated by intravascular hemolysis and methemoglobinaemia (see clinical features) support the involvement of erythrocytes in the biotransformation of phosphine *in vivo* in humans.

Some unaltered phosphine may be cleared in expired air provided there is an appropriate concentration gradient between plasma and alveolar spaces. Phosphate and phosphite will be excreted in urine. The major degradation product in the urine of rats and guinea pigs was hypophosphite (39).

Clinical features

Whatever the prime cause of toxicity, the train of events that phosphides initiate rapidly compounds it. Foremost amongst these is circulatory failure resulting in congestion and edema of most organs (95,96) including, critically, the lungs. Others include disseminated intravascular coagulation and renal failure. Severe poisoning, therefore, has the potential to induce multi-organ failure and though it sometimes does, it would probably do so much more frequently if victims did not die so soon after ingestion.

Fatalities from phosphide ingestion have ranged from 40–77% (10,97–101), and in one series 55% occurred within 12 h of ingestion and 91% within 24 h (102).

Early features

Early symptoms include nausea, vomiting, retrosternal and epigastric pain, and dyspnea. Diarrhea is less common. Commonly, patients are anxious and agitated while mentally clear. There is often a smell of garlic (57,103,104) on the breath. Shock and peripheral circulatory failure are particularly important early signs of toxicity.

Cardiac toxicity

Circulatory failure is a common and frequent cause of death after ingestion of metal phosphides (21). Hypotension, often profound (30,34,82), can develop rapidly and may persist due to continuing absorption of phosphine (105). In 115 aluminium phosphide-poisoned individuals the severity of hypotension in life was considered to correlate with the degree of congestion of the abdominal organs at autopsy (11). At autopsy congestion of the heart, separation of myocardial fibres by edema, fragmentation of fibres, non-specifc vacuolation of myocytes, focal necrosis, and neutrophil and eosinophil infiltration are recurring findings (95,98, 100,106,107). However, they are not invariable; myocardial histology was normal in three patients who died within 12 h of consuming phosphide (106).

In life these pathological changes manifest as impaired myocardial contractility which is reversible if patients survive. Using echocardiography Gupta et al. (27,108) found significantly increased left ventricular dimensions on the first hospital day compared to those in patients who survived until the fifth day. Similarly, Bhasin et al. (109) studied 30 patients with a mean age of 23 years by the same technique. Hypokinesia of the left ventricle and septum was present in 80% and akinesia in 3% and ejection fractions were reduced to a mean of 36 ± 9%. Echocardiographic evidence of global, or less severe, hypokinesia has been found by others (8,27,110). Bajaj et al. (106) carried out radionuclide ventriculography in three patients. All had global dyskinesia and two had ejection fractions of 42 and 62% at 36 h. The third had values of 22, 30, and 62% at 24, 72, and 120 h respectively. Kalra et al. (111) made hemodynamic measurements in 25 patients poisoned with aluminium phosphide and considered that they presented a distinct profile characterized by severe hypotension, reduced cardiac output, raised systemic venous pressure, normal pulmonary artery wedge pressure and inadequate systemic vasoconstriction. Myocardial necrosis may be responsible for increased CK-MB activity in all of five patients tested in another study. The elevation was greatest in the earliest samples and returned to normal by the fourth day (106).

ECG abnormalities were present in 38% of 418 aluminium phosphide ingestions (10) and most commonly comprised ST and T-wave changes that have also been reported by others (27,112,113). Their occurrence in a population predominantly under the age of 50 years (10) suggests they may be due to the poison. There was no relationship between ECG changes and cardiac histology in one large series (98).

Both tachycardia and bradycardia are also common and the inappropriateness of the latter for the degree of shock has been observed (106,114). Virtually every other type of arrhythmia and conduction abnormality has been recorded in association with phosphide ingestion and they are very common (8,10,21,27,33,97,99,107,108,113,115,116). In one series all 30 patients had atrial and ventricular ectopic activity and almost half went on to sustained ventricular tachycardia (SVT) and ventricular tachycardia (VT) (99).

There is clear evidence that inhaled phosphine is cardiotoxic also. One child had electrocardiographic ST depression and short-lived dilatation and poor function of her left ventricle while another who was dead on discovery had biventricular failure and focal myocarditis at autopsy (81). Similarly, a 53-year-old man had hypokinesia of the inferior heart wall and a pericardial effusion without tamponade but recovered (117). A left ventricular ejection fraction of only 10% was estimated in a 20-year-old man who inhaled phosphine from treated grain in a railcar and died within 12 h of admission to hospital (49). Another of comparable age and exposed in the same incident had global dyskinesia and an ejection fraction of 15% on the first day in hospital. By the fourth day it had risen to 40% (49). Ventricular premature beats (>600/h) and bigeminy were present in one young man (118).

Respiratory toxicity

Tachypnea, dyspnea, crepitations, and rhonchi were present on examination in 192 out of 418 cases (46%) of phosphide poisoning (10) and have been found by others (82). Pulmonary edema is common but it is not always clear whether it is cardiogenic or non-cardiogenic in etiology. It tends to develop 4–48 h after ingestion and the finding of a reduced PaO_2 without an increase in pulmonary artery wedge pressure, suggested it was non-cardiogenic (111). Others have confidently diagnosed adult respiratory distress syndrome (102,106,108,119) and non-specifed pulmonary edema (11,12). The edema fluid may be protein-rich and hemorrhagic (11).

Gastrointestinal toxicity

Hematemesis occurred in one case (82) and in four others it was described as massive (10). Corrosive lesions of the esophagus and stomach may be the source (21,95,100). Chhina et al. (83) endoscoped four patients with vomiting and epigastric pain following ingestion of aluminium phosphide. All had severe gastric erosions and three had duodenal erosions. Repeat examination of two survivors 2 weeks later was normal.

Several patients have gone on to develop esophageal strictures (84,85–89,120), two of which (89,120) were associated with tracheo-oesophageal fistulae. In the latter cases coughing after swallowing (Ono's sign) should alert the physician to the diagnosis (120). Dysphagia may be apparent as soon as 3 or 4 days after ingestion of aluminium phosphide (88,120) but is more usual about 2 weeks later.

Hepatic toxicity

Transient elevations of alanine aminotransferase and aspartate aminotransferase activities are not infrequent after ingestion of metal phosphides (22,27,30,52) but jaundice secondary to liver damage (12) is much less common. It was present in 12 out of 92 cases (102) and was said to be common in another series of 15 patients (121) but confirmatory laboratory data were not provided. Jaundice was alleged to be present in 16 (52%) members of the crew of a grain freighter who inhaled phosphine after an accidental release (81) but, in the six tested, serum bilirubin concentrations were normal and transaminase activities only minimally disturbed, casting doubt on the clinical observation. Acute hepatic failure and encephalopathy was considered to be the cause of death in one man (122), while a 12-year-old girl died from a combination of acute hepatic failure and encephalopathy with renal failure (30). Portal edema, congestion of the portal tract and central veins, and vacuolization of hepatocytes are the most frequent findings at autopsy (123).

Hematological toxicity

Although phosphine causes Heinz body formulation and hemoglobin oxidation *in vitro* (93,94), intravascular hemolysis and methemoglobinaemia are unusual complications of phosphide poisoning in humans. Nine individuals with intravascular hemolysis after ingestion of aluminium phosphide have been identified from the literature. Three were glucose-6-phosphate dehydrogenase deficient (124), including one young man who had previously developed haemolysis when given primaquine (104). Two others had no history to suggest this possible predisposing disorder (103,110) and in the remaining four the issue was not addressed (10). Intravascular hemolysis was associated with renal failure and severe metabolic acidosis to which 3 days of vomiting and diarrhea may have partly contributed (52).

In addition to hemolysis one man was found to have methemoglobinaemia of 17% 32 h post-ingestion (110) while another developed Heinz bodies (124), a further indicator of damage to hemoglobin. Rats given aluminium phosphide had methemoglobin concentrations measured at 10 and 30 min intervals. They increased simultaneously with those of malonyldialdehyde suggesting that methemo-glo-binaemia was secondary to increased oxygen free radical generation (125).

Disseminated intravascular coagulation was present in six out of 418 patients poisoned with aluminium phosphide (10).

Electrolyte and metabolic abnormalities

Hypokalemia is common soon after ingestion of metal phosphides and is probably secondary to vomiting, though catecholamine release could also contribute. Metabolic acidosis, or mixed metabolic acidosis and respiratory alkalosis, and acute renal failure are also frequent. Hypoglycemia has been reported (41,113) and may be persistent and severe (22). It is thought to be the result of impaired gluconeogenesis and glycogenolysis (22) possibly secondary to adrenal gland damage and low circulating cortisol concentrations (113). Hyperglycemia (107,126) appears to be rare.

The main controversy relates to the existence or otherwise of disturbances of magnesium homeostasis. In 1989, prompted by reports of the empirical use of magnesium sulphate to treat phosphide toxicity, Singh and his co-workers (101,127) demonstrated that serum magnesium concentrations were increased, possibly secondary to release from damaged cardiac myocytes and hepatocytes, and confirmed the findings in subsequent studies (102,128).

Unfortunately, other studies have found the converse, that is serum and erythrocyte concentrations were reduced rather than increased. Chugh et al. (129) compared serial serum and erythrocyte magnesium concentrations in four groups of people. One comprised patients poisoned with aluminium phosphide who had resulting shock (not defined) and cardiotoxicity (not defined) while the second included those poisoned but without shock or cardiac features. The remaining two groups acted as controls, the first being patients in shock secondary to trauma or hemorrhage but without other features of cardiac toxicity and the second, normal volunteers. The only significant finding in admission samples was that cell and serum concentrations were lower in shocked, cardiotoxic patients (mean serum and RBC concentrations 0.9 and 3.7 mEq/L respectively compared with 1.8 and 5.2 mEq/L in volunteers). Since, first, hypomagnesemia was found in toxic shocked patients but not in those with non-toxic shock and, secondly, 75% of those in the toxic/shock group had ECG changes, it was concluded that the evidence supported a causal relationship between hypomagnesemia and phosphide-induced shock. Without intervention both serum and cell values returned to normal by about 24 h. The authors confirmed their findings in a later study (130) and thought the hypomagnesemia secondary to consumption in combating free radical stress (131). Hypomagnesemia has also been found in a recent single case of phosphine inhalation from aluminium phosphide (118).

The situation became even more complicated when, in 1994, Siwach and his colleagues (132,133) found themselves unable to agree with either the Singh (101,102,127,128) or Chugh (129) groups. They found pre-treatment mean serum and red cell magnesium concentrations to be normal. Concentrations were increased in the brains, lungs, hearts, livers, kidneys, and stomachs of fatalities but later studies showed this to be the result of magnesium administration and not phosphide toxicity (134).

Clearly, these studies cannot all be correct and the analytical method used to generate the results may be an important factor. The results of Siwach and his colleagues (132,133) carry particular weight because they used atomic absorption spectroscopy, a technique that is superior to the colorimetric method published in 1977 and used by Singh and his co-workers (102) and the titan yellow method employed by Chugh et al. (129) despite it being claimed that results obtained using the former method correlated extremely well with those from atomic absorption spectroscopy (135). If the studies of Siwach et al. (132,133) are considered the most reliable, there is no choice but to accept that neither hypomagnesemia nor hypermagnesemia is a feature of aluminium phosphide poisoning, though confirmation by another independent study would be welcome.

Uncommon features

Unusual complications of phosphide ingestion include atrial infarction (136), pleural effusion (30,112), ascites (30), skeletal muscle damage (137), rhabdomyolysis (107), a bleeding diathesis (138), adrenocortical congestion, hemorrhage and necrosis (95), pancreatitis (139), and renal failure (10,11,30,82). Acute pericarditis has also been reported infrequently (140,141) though pericardial fluid was detected by echocardiography in a third of patients in one study (109). Subendocardial infarction complicated the recovery of a 16-year-old male (142) and a 26-year-old woman who had recovered from aluminium phosphide ingestion suffered an intracranial hemorrhage 5 days after the event. No explanation other than the poison was found (143).

Management

Decontamination

Gastric lavage is probably best avoided after ingestion of phosphides as it might increase the rate of disintegration of the pesticide and increase toxicity. There is limited evidence from an experimental study in rats that activated charcoal may reduce the toxicity of zinc phosphide (144). However, vomiting may make the administration of charcoal difficult.

In vitro studies suggested that vegetable oil and liquid paraffin inhibit phosphine release from phosphides (145) but these oils have not been tested in clinical practice. However, coconut oil was given as one component of a therapeutic approach involving early gastric emptying and a combination of sodium bicarbonate and activated charcoal by mouth (23,126). Both patients had ingested potentially lethal amounts of aluminium phosphide (16.8 and 11.76 g, respectively) but survived. Formal investigation on a larger scale is required before a recommendation can be reached.

Although the administration of sodium bicarbonate via a gastric tube to decrease gastric hydrochloric acid has been proposed in the belief that hydrochloric acid assists the conversion of phosphide to phosphine, there is no experimental support for its use. Moreover, based on an understanding of the mechanisms of toxicity of metal phosphides, this strategy is unlikely to reduce morbidity and mortality. Similarly, the use of dilute potassium permanganate in lavage solution has been advocated without experimental support (23,126).

Removal of victims of phosphine inhalation from the contaminated atmosphere will have been carried out by the emergency service first on scene. Supplemental oxygen may be given if necessary but further measures for airway control are unlikely to be required.

Supportive care

Many patients will die from metal phosphide poisoning despite intensive care. Supportive measures are all that can be offered and should be implemented as required by clinical developments.

The blood glucose concentration should be measured in every case and hypoglycemia corrected if found. Similarly, hypokalemia should be sought and, if clinically indicated, at least partially corrected; cardiac features have resolved in occasional patients on correction of potassium concentrations (146). It must be remembered, however, that the onset of acidosis, renal failure and cell damage may produce life-threatening hyperkalemia. Metabolic acidosis should be managed conventionally.

Magnesium supplementation

The problematic decision is whether or not supplemental magnesium should be given. If magnesium depletion does not occur such a course would appear illogical but single cases have been reported where magnesium administration appeared to terminate atrial fibrillation (147) and SVT and VT (148). On the other hand, magnesium sulphate 3 g given intravenously over 30 min did not abolish very frequent ventricular ectopic beats and bigeminy though it restored a normal magnesium concentration (118).

Only a few studies have attempted to assess the value of magnesium sulphate in large groups of patients and their results are conflicting. Fifty consecutive patients selected on the basis of a systolic blood pressure of less than 70 mm Hg after aluminium phosphide ingestion were given high doses (4 g intravenously as a loading dose, 2 g 1 h later and 1 g 3-hourly until recovery or death) and the outcome compared with the same number of consecutive controls of comparable severity dating from immediately before the study group. Twenty-one of those given supplemental magnesium (42%) survived compared with 20 (40%) not so treated. Moreover, treatment did not significantly improve survival at any dose (number of tablets) consumed. In this study, therefore, magnesium supplementation was of no value (132).

Unfortunately, Chugh et al. (130) came to the opposite conclusion. They randomized 105 shocked aluminium phosphide-poisoned patients to two groups. Fifty were not given magnesium while 55 received 1 g intravenously then, 1 h later, 1 g by constant infusion hourly for 3 h followed by 1 g 6-hourly till death or recovery or a maximum of 5 days. Overall, 69% of treated patients survived compared with only 48% not given magnesium. Survival was significantly improved at each dose (number of tablets) ingested. The Chugh group then extended their study to compare the above regimen with a simpler one entailing administration of magnesium sulphate 1 g intravenously every 6 h. Survival in the 50 patients receiving the latter was not significantly better than in those not given it (149).

Further studies are required to clarify the potential benefit of magnesium supplementation.

N-acetylcysteine

Reduced concentrations of glutathione have been found in the tissues of rats (69,150) and blood of humans (131) poisoned with aluminium phosphide and provide a rationale for investigating N-acetylcysteine as a therapeutic agent. A dose of 6.25 mg/kg/min intravenously significantly prolonged survival time in rats (151) but only one report of its use in human phosphide poisoning has been identified (8). In this case it was only one component of a multi-therapy approach that also included administration of magnesium sulphate. It did not appear to alter the course of poisoning and the patient died.

Pralidoxime

There is experimental and clinical evidence that phosphine (77) and aluminium (76,80) inhibit acetylcholinesterase. Mittra et al. (152) investigated the benefit of administering atropine 1 mg/kg and pralidoxime 5 mg/kg parenterally to rats dosed with aluminium phosphide 10 mg/kg (5.55 × LD_{50}) 5 min previously. Treatment increased the survival time by 2.5-fold in nine out of 15 animals and resulted in the survival of the six remaining animals. There were no survivors in the two control groups. Further studies are required to confirm the benefit of oximes.

Hyperinsulinemia-euglycemia and hyperventilation oxygenation

Preliminary observations suggest that a combination of hyperinsulinemia-euglycemia and hyperventilation oxygenation is worthy of more extensive assessment as a therapy for aluminium phosphide intoxication (153) on the basis that insulin promotes energy production from carbohydrates rather than fats and, in so doing, restores calcium fluxes and improves myocardial contractility. Of five patients managed in this way, four survived despite all having ingested large amounts resulting in peripheral circulatory failure with metabolic acidosis or cardiac disorders.

Trimetazidine

Trimetazidine 20 mg orally twice daily appeared to abolish numerous ventricular ectopic beats and bigeminy in a young man poisoned with aluminium phosphide (118). Since trimetazidine acts to preserve oxidative metabolism, its use is rational but further experience is required before its wider use in phosphide-induced cardiotoxicity can be endorsed.

Protection of staff

Clinical staff

Of particular current concern and controversy is whether carers of patients poisoned with phosphides are at risk from inhalation of the odors emanating from those receiving their attention. In one case the smell was such that emergency department staff were advised to follow fire service evacuation instructions, clear the department and restrict ambulance arrivals to those transporting patients with life-threatening illnesses only (18). An almost identical incident in the United Kingdom resulted in a major incident being declared, closure of the emergency department for about 15 h, diversion of seven patients to nearby hospitals and referral of 13 fire personnel and three police officers to another hospital for assessment after possible exposure (31,154). Other responses have been more measured (32).

The contrast of the more extreme of these responses to aluminium phosphide-poisoned patients with the apparent lack of concern in less developed countries to the same and considerably more common problem could not be starker. Christophers et al. (155) pointed out that in India hospital staff take no specific precautions and do not perceive any threat. The features developed by carers exposed to phosphide-poisoned patients are invariably vague, referring merely to "mild symptoms," "no lasting symptoms," anxiety, nausea, dizziness, and headache without giving frequencies of occurrence or durations. One physician developed an unexpected headache lasting an hour after caring for a woman giving of a strong smell after drinking a solution of zinc phosphide (156) and in the UK incident that resulted in declaration of a major disaster many of the department's staff of 30 were anxious though only five had possible exposure and two had mild, unspecified, symptoms. Notably, the two paramedics, three nurses and two doctors who dealt with the patient suffered no lasting symptoms though what they did experience is not stated (31,154).

The first task is to try to determine whether the risk is real; an odor, however unpleasant, no more indicates toxicity than absence of one does the contrary. Since pure phosphine is odorless up to toxic concentrations (see Introduction and uses), the smell emanating from phosphide-poisoned patients is probably not phosphine but arises from some contaminant or contaminants in the pesticide formulation. For this reason, it cannot be assumed that the stronger the smell the greater is the exposure to pure phosphine.

Pathologists

In contrast to clinicians and medical administrators, the response of pathologists to chemically poisoned bodies has been very low-key. In studies from India reporting the findings in 115 (11), 30 (95,96), and 53 (96) autopsies, performed on individuals dying from phosphide ingestion there is no mention of adverse consequences to those carrying them out or concern about the possibility. However, one pathologist hit by a jet of phosphine from an excised stomach required first aid for unspecified symptoms (157). In general, therefore, the risk, if any, appears low but the available data are inadequate to assess its magnitude (158). General recommendations on the management of chemically contaminated bodies (159) appear as relevant to the victims of phosphide poisoning as to those dead from other toxins. The autopsy should be carried out in an area with effective down-draught ventilation and since the stomach can be expected to contain the highest concentrations of the gas, pathologists should consider carefully whether it is necessary that it be opened. If so, the organ should be removed intact and further dissection performed in a fume chamber.

Conclusions

Acute poisoning with metal phosphides, particularly aluminium phosphide, is a worldwide problem most commonly encountered in the Indian Sub-Continent. The clinical features have been well described though it is only recently that the mechanisms of toxicity have been more clearly understood. Poisoning from phosphides is mediated by phosphine which has been shown to rapidly perturb mitochondrial morphology, inhibit oxidative respiration, and cause a severe drop in mitochondrial membrane potential. This failure of cellular respiration is likely to be due to a mechanism other than inhibition of cytochrome C oxidase as phosphine inhibits cytochrome C oxidase activity less dramatically *in vivo* than *in vitro* and only partially inhibits cytochrome C oxidase activity in humans. Phosphine can also form the highly reactive hydroxyl radical and inhibit both catalase and peroxidase leading to lipid peroxidation.

The gas or gases given of in addition to phosphine when phosphide formulations come into contact with water or acid need to be identified and their toxicity determined. The observation that both aluminium and phosphine may inhibit acetylcholinesterase activity needs to be investigated further as does the report that the administration of atropine and pralidoxime reduces morbidity and mortality in aluminium phosphide poisoning. There is conflicting evidence also on the occurrence and clinical importance of magnesium disturbances which some have described. The benefit of magnesium supplementation has still to be determined.

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Factors Influencing Burrowing Owl Abundance in Prairie Dog Colonies on the Southern High Plains of Texas

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FACTORS INFLUENCING BURROWING OWL ABUNDANCE IN PRAIRIE DOG COLONIES ON THE SOUTHERN HIGH PLAINS OF TEXAS

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Abstract.—Large numbers of Western Burrowing Owls (*Athene cunicularia hypugaea*) nest in black-tailed prairie dog (*Cynomys ludovicianus*) colonies in the southern high plains of Texas. Because the Western Burrowing Owl is a species of concern with an uncertain future due to widespread extirpation of prairie dogs, we examined the roles of prairie dog colony size, burrow density, proxies of prey availability, and vegetative composition and structure on owl abundance and reproductive rate. The number of nesting Burrowing Owl pairs was positively correlated to colony area ($r^2 = 0.550$, $P = 0.006$) and to number of prairie dog burrows in a colony ($r^2 = 0.733$, $P = 0.0230$). Burrowing Owl numbers and reproductive rate (maximum number of young seen per successful pair) were not related to our measures of vegetative composition and structure in prairie dog colonies, nor to indices of prey availability.

Key Words: *Western Burrowing Owl*; Athene cunicularia hypugaea; *prairie dog*; Cynomys ludovicianus; *population size*; *reproductive rate.*

FACTORES QUE INFLUYEN LA ABUNDANCIA DE *ATHENE CUNICULARIA HYPUGAEA* EN COLONIAS DE *CYNOMYS LUDOVICIANUS* EN LAS ALTIPLANICIES DEL SUR DE TEJAS

Resumen.—Grandes cantidades de individuos de *Athene cunicularia hypugaea* anidan en las colonias de *Cynomys ludovicianus* en las altiplanicies del sur de Tejas. Dado que *A. c. hypugaea* es una especie de interés conservacionista con un futuro incierto debido a la extendida eliminación de *C. ludovicianus*, examinamos el papel del tamaño de la colonia de *C. ludovicianus*, de la densidad de madrigueras, de los indicadores de disponibilidad de presa y de la composición y estructura de la vegetación sobre la abundancia y la tasa reproductiva de *A. c. hypugaea*. El número de individuos de *A. c. hypugaea* estuvo positivamente correlacionado con el área de la colonia ($r^2 = 0.550$, $P = 0.006$) y con el número de individuos de *C. ludovicianus* en una colonia ($r^2 = 0.733$, $P = 0.0230$). Las cantidades y las tasas reproductivas (número máximo de pollos vistos por pareja exitosa) de *A. c. hypugaea* no estuvieron relacionadas con nuestras medidas de composición y estructura de la vegetación en las colonias de *C. ludovicianus*, ni con los índices de disponibilidad de presa.

[Traducción del equipo editorial]

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Western Burrowing Owls (*Athene cunicularia hypugaea*) are widely distributed across the western portion of North America from deserts to grasslands to agricultural areas (Haug et al. 1993). Declines in the range and numbers of Burrowing Owls across the species' North American distribution have been attributed primarily to habitat destruction and land conversion (Desmond et al. 2000, Korfanta et al. 2001, Martell et al. 2001, Murphy et al. 2001, Sheffield and Howery 2001). Burrowing Owls are thus considered a U.S. Fish and Wildlife Service (U.S.F.W.S.) regional conservation priority (U.S.F.W.S. 2001).

Burrowing Owls are migratory over much of their range. One region that has both summer (breeding) and winter populations is the southern high plains of Texas, although relatively little research has been done on Burrowing Owls in this region. McIntyre (2004) found a long-term decline since the 1940s in the number of wintering owls recorded in Christmas Bird Counts for this area, whereas Breeding Bird Survey data suggested that summer Burrowing Owl populations may have remained stable since the 1960s. These factors, as well as a dearth of information on nearly all aspects of Burrowing Owl ecology for this region, make this an important area in which to examine owl abundance and reproductive rate.

In this region, Burrowing Owls nest almost exclusively in burrows excavated by black-tailed prairie dogs (*Cynomys ludovicianus*). Published reports differ on whether Burrowing Owl numbers are related to prairie dog colony size. Orth and Kennedy (2001) in Colorado and Restani et al. (2001) in Montana found no relationship between colony size and number of Burrowing Owls, whereas Desmond and Savidge (1996) found a positive correlation between colony size and number of Burrowing Owls in Nebraska. In the southern high plains of Texas, the number of Burrowing Owls observed while surveying prairie dogs in a 12-county area was positively, but weakly, correlated to prairie dog colony size, with a >20-fold range in the number of owls seen in smaller (2 to 20 ha) prairie dog colonies (Pruett 2004). Given this preliminary information and the variation in the relationship between colony size and owl abundance in other locations, we hypothesized that: (1) prairie dog colony size (area) would be positively correlated to numbers of Burrowing Owls; moreover, since such a relationship may be driven more by the number of vacant prairie dog burrows (representing potential nest burrows for owls) than by current prairie dog population size or colony extent, we hypothesize that (2) both owl numbers and reproductive rate would be positively correlated to burrow density. We also hypothesized that (3) Burrowing Owl abundance would be negatively associated with the amount of vegetative cover, and (4) owl abundance and reproductive rates would be positively associated with prey abundance, based on published literature (vegetation: Bonham and Lerwick 1976, Whicker and Detling 1988, Schmutz 1997, Trulio 1997, Clayton and Schmutz 1999; and prey: Gleason and Johnson 1985, Orth and Kennedy 2001). Finally, we also expected that (5) there would be fewer owls (and lower reproductive rates) in nest burrows located farther from wetlands because the latter are well-known regional foci for biodiversity (Bolen et al. 1989).

Linkages among prairie dog colony traits, vegetation, and owl prey have not been investigated in west Texas: it is currently unknown to what extent prairie dog colony size (and other factors such as vegetation changes elicited by prairie dogs, and owl prey abundance) influences owl breeding population size, nest-site (nest burrow) selection, and reproductive success of Burrowing Owls. Here, we provide information about Western Burrowing Owls from the southern high plains of Texas, a region that supports a relatively stable population of this species. Studies of Burrowing Owls in association with prairie dogs are scarce in this region, however, which is especially important in light of declining prairie dog populations and subsequent conservation concern.

METHODS

Study Sites. We selected three sites on the U.S. Department of Energy/National Nuclear Security Administration Pantex Plant in Carson County, TX, and three in the Lubbock area, Lubbock County, TX (Table 1). Study sites were chosen to have regionally representative patterns of surrounding land use (namely, agriculture and urbanization in the form of industrial use and residential development) and histories of on-site control of prairie dog numbers. The Pantex Plant is a controlled-access facility; it included two pastoral (grazed) agricultural sites and one urbanized/industrial site; two of the three Pantex sites had a known history of prairie dog control activities but primarily limited to where perimeters extended into operational areas. The Lubbock sites included three urbanized sites, one of which was on industrial property; the other two were located near housing developments. We knew from previous surveys (McCaffrey 2001, Pruett 2004) that these areas provided nesting sites for

Table 1. Data on Burrowing Owls, prairie dogs, and burrows from six intensively monitored sites from Lubbock and Carson counties, Texas, and data known prior to the start of the 2003–2004 field seasons.

SITE	COUNTY	HISTORIC TREATMENT[a]	SURROUNDING LAND USE	COLONY AREA (ha)	OWLS[b]	PRAIRIE DOGS[c]	NUMBER OF BURROWS	BURROW DENSITY[d]	INDEX OF BURROW VACANCY[e]
L103	Lubbock	None	Residential/ urban	14.37	27	80	938	80.10	11.73
School	Lubbock	None	Residential/ urban	12.78	18	142	595	78.77	4.19
X-Fab	Lubbock	None/PT	Industrial/ urban	37.15	14	22	649	58.36	29.50
12-36	Carson	PT	Industrial/ urban	11.61	15	84	1179	99.39	14.04
Pantex Lake	Carson	None	Agricultural	22.63	10	145	810	107.93	5.59
Zone 4	Carson	PT	Agricultural	5.20	2	28	266	86.44	9.50

[a] PT denotes known (2003–2004) prairie dog control efforts using Phostoxin.
[b] Numbers of Burrowing Owls counted during prairie dog surveys in 2002 (Pruett 2004).
[c] Number of prairie dogs estimated using model based on three independent surveys (Pruett 2004).
[d] Number of prairie dog burrows per hectare.
[e] Index of the abundance of vacant burrows, based on number of prairie dog burrows per prairie dog.

Burrowing Owls on prairie dog colonies ranging from 3.1 to 37.1 ha.

Capture and Marking of Owls. We used bal-chatri traps, noose carpets, walk-in traps, and bow nets (Bloom 1987, Bloom et al. 2007) to capture Burrowing Owls from 2002–2004; details may be found in Teaschner (2005). We banded captured owls with one aluminum band issued by the U.S. Geological Survey Bird Banding Laboratory, and one red alphanumerically coded anodized band. We recorded captured individuals as adult or juvenile based on plumage (Haug et al. 1993). All research was conducted following methods approved by the Texas Tech University animal care and use committee (protocol # 03014-02). All owls were captured/ marked under U.S.G.S. banding permit #22801 (C.W. Boal) and Texas Scientific Permit SPR-0201-137.

Owl Abundance and Reproductive Rate. We endeavored to resight banded owls in both summer (breeding season) and winter to determine site and burrow fidelity, as well as inter-seasonal and inter-annual movements. We monitored Burrowing Owls with spotting scopes and binoculars from parked vehicles, which we used as viewing blinds (Coulombe 1971). Identification of individual Burrowing Owls was used to determine individual nest sites, between-year area and pair fidelity as well as timing of seasonal migrations. We considered pairs of adult owls occupying a nest burrow and engaging in typical pair behaviors (e.g., allopreening, prey deliveries) as a nesting pair. However, determination of nesting success by Burrowing Owls is challenging because nests are not directly observable inside nest burrows; quantifying productivity in Burrowing Owls is thus not straightforward, and various methods have been used, potentially confounding comparisons among studies (Garcia and Conway 2009). We assessed nesting success on the basis of "apparent productivity" determined by documenting the number of nestling or fledgling owls at a given owl pair's known nest burrow. To do so, we monitored nest burrows for three separate 10-min periods within a 2-wk period as nestlings began to emerge from nest burrows (Gleason and Johnson 1985). We defined a nesting pair of owls as successful if at least one nestling was observed outside of the pair's nest burrow, and we defined estimated productivity for each nesting pair as the maximum number of young birds seen during any one observation period for each nest burrow. Once a nestling was observed aboveground it was considered "fledged," although this term is here used in a broad sense because the owlets were not flighted and would retreat down the nest burrow. We recorded the number of Burrowing Owls, marked Burrowing Owls, nest burrows, and maximum number of young seen per nest burrow (Martin 1973, Green and Anthony 1989, Desmond and Savidge 1996). We attempted to search all six main sites ≥1 time/wk to minimize underestimations of owl abundance due to imperfect detections of this burrowing species that alters its activity according to ambient conditions (Conway et al. 2008, Manning 2011).

Prairie Dog Abundance and Burrow Density. We examined correlations between number of Burrowing Owl pairs and productivity to (1) prairie dog colony size (spatial area), (2) number of prairie dogs, and (3) number of vacant prairie dog burrows in 2003–2004. We conducted an average of 3.5 (±1.8) searches per mo at each of our six focal colonies between September 2003 and April 2005 to count the number of marked Burrowing Owls observed. We determined perimeters of the study colonies by walking around the exterior burrows with a handheld global positioning satellite (GPS) unit (Garmin model 12, Garmin International Inc., Olathe, KS), and uploaded the GPS track to a computer to determine colony area. We estimated the number of prairie dogs during three counts, following Pruett (2004).

During 2004, we made a complete count of all burrows on each of our sites. We recorded locations of each prairie dog burrow at the six sites, including burrows used as nest burrows by Burrowing Owls, with a GPS unit. To obtain overall burrow density per prairie dog colony, we created 50-m buffers from prairie dog colony centers using ArcView GIS and counted the number of owl nest burrows per unit area. Given the size of prairie dog colonies on our sites, all nest burrows were within three of these 50-m buffers from the colony center. We also derived an index of burrow vacancy as a function of prairie dog population per colony by dividing the number of burrows counted at each site by the estimated number of prairie dogs present (Pruett et al. 2009; Table 1). Although this index may be an overestimate (if prairie dogs used more than one burrow), we reasoned that sites with a higher index (more burrows per prairie dog; e.g., a portion of the colony with higher burrow availability) should have more vacant burrows available for Burrowing Owls to use. If true, then there may also be a positive relationship between number of owl nest burrows and prairie dog burrow spacing (i.e., the average distance among prairie dog burrows). To estimate burrow spacing, we randomly selected an equal number of prairie dog burrows as there were Burrowing Owl nests on each site, and compared distance from each nest burrow to its five closest prairie dog burrows to the distance from the random burrows to their five closest prairie dog burrows.

Indices to Prey Abundance. Distance to playas (ephemeral freshwater wetlands) containing water was used as one index of food availability, because many amphibians and insects in this area use playas to complete their life cycle (Anderson 1997). Playas are regional foci of biodiversity (Bolen et al. 1989). The locations of playas were identified from digital layers based on hydric soils (Fish et al. 1998, Pruett 2004). We checked for the presence of water while Burrowing Owls were nesting and recorded distances to nearest playas containing water to correlate distance to playas containing water to number of Burrowing Owl nests and nest success using Pearson's product moment correlation.

We also assessed relative abundance of small mammals, a potential food source for Burrowing Owls, on the six prairie dog colonies in June–August 2003 and 2004. Trapping grids consisted of 100 Sherman live traps, 10 m apart, set for three consecutive nights during summer (Burrowing Owl nesting season). All captured mammals were identified to species and sexed, weighed, measured, and marked for identification upon recapture as part of a concurrent project (Pruett et al. 2010). We compared numbers of initial captures between sites for all species that we considered possible prey for Burrowing Owls to assess relative abundance of foods in relation to Burrowing Owl nest-burrow density and nesting success.

Vegetation Structure and Composition. We also examined vegetative data to assess characteristics of Burrowing Owl nesting sites and vegetative structure and composition. Two 25-m line intercept transects were randomly placed in each prairie dog colony. During summer in 2003 and 2004, we record the percent cover (intercept distance) of vegetation along each transect by mutually exclusive category: grass, forb, shrub, litter, bare ground, or other (Bullock 1996). Visual obstruction was estimated using Robel pole measures (n = 6/transect; Vermeire et al. 2002) taken at 5-m intervals along each 25-m transect. We modified the lowest 2 decimeters of our pole, marking off 2-cm intervals to record <1 decimeter vegetation heights. Raw data on visual obstruction scores and percent cover by site may be found in Teaschner (2005).

Statistical Analyses. We used SAS 9.4 (SAS Institute Inc., Cary, NC) to perform all statistical tests at an $\alpha = 0.05$ level of significance, and we report means and standard errors for variables of interest. We used a generalized linear model analysis of variance (ANOVA) to examine differences in owl abundance and productivity by site type (agricultural vs. residential urban vs. industrial urban) and year. Pearson correlation analysis was used to explore possible relationships between owl abundance and prairie dog colony size, number of burrows, prairie dog

Table 2. Summary of Burrowing Owl captures and resightings by season for Burrowing Owls captured at six study sites in Lubbock and Carson counties, Texas, between January 2003 and May 2005, including three additional winter owls captured on adjacent Carson County sites in February 2004. More winter-marked owls were residents than summer-marked ones ($\chi^2_1 = 10.20$, $P = 0.004$).

SEASON	NUMBER BANDED	NUMBER COLOR-BANDED	NUMBER NEVER OBSERVED AGAIN	NUMBER OBSERVED IN THE SEASON BANDED[a]	NUMBER OBSERVED IN ≥1 OTHER SEASON	NUMBER OBSERVED IN THE SAME SEASON THE NEXT YEAR[b]	NUMBER OF KNOWN RESIDENTS[c]
Winter	16	9	3	4	1	0	4
Summer	123	108	51	57	2	10	4

[a] Burrowing Owls seen in season they were banded (includes late-migrating owls that were no longer observed within 2 wk of the end of the season of capture).

[b] Burrowing Owls seen, in this case, the summer after the summer that they were banded. These birds may have remained in the area but wintered at sites where we did not observe them.

[c] Burrowing Owls seen in ≥3 consecutive seasons.

abundance, vegetation parameters, and prey availability. A Pearson chi-square analysis was used to examine whether the distribution of prairie dog burrows (our density index) behaved according to chance (with the expected distribution of burrows equal across all portions of a prairie dog colony). We analyzed data separately for each year to determine whether pooling data across years was possible, and then subsequently pooled and re-ran our analyses on productivity.

RESULTS

We captured Burrowing Owls ($n = 153$; 137 adults, 16 juveniles) between January 2002 and July 2004. Most owls (89%; 137 of 153) were captured during the summer breeding periods. Only 12% ($n = 16$; three on the added sites) of all owls were captured during the winter periods. Our sites had 3–7 times more Burrowing Owls during the summer breeding period (between March and September) than they did during the winter (October through February).

There were more known resident winter-marked owls (44.4%; four of nine) than summer-marked (3.7%; four of 108) owls (Table 2). Some additional owls may have been resident, including owls that were observed the summer following the year in which they were marked (9.3%; 10 of 108). These owls may have overwintered in the region undetected at sites that we did not survey, or they may have migrated south and returned to the same sites to breed the following summer. Additionally, 2.6% of our marked owls (3 of 117) were seen in only two consecutive seasons (one seen winter and the following summer, and two seen summer and the following winter). We therefore determined that most Burrowing Owls in this area were summer residents only, with only a small proportion (6.8–18.0%, or 8–21 of 117 total marked owls) likely remaining overwinter between consecutive breeding seasons. Furthermore, in over 406 d of searching at the six intensively monitored sites and 43 d of searching adjacent sites within 8 km of the focal colonies, no marked owl was ever observed at any site other than the one at which it was captured.

We identified 98 nesting pairs on our six sites during 2003 ($n = 57$) and 2004 ($n = 41$). The earliest date we recorded seeing young was May 19, and the last observed emergence of new young was June 25. Numbers of nesting pairs/ha ($F_{3,8} = 1.80$, $P = 0.2251$) and productivity (number of chicks per nesting pair; $F_{3,8} = 0.87$, $P = 0.4940$) did not differ between years. Therefore, we pooled these data across years for analyses of owl productivity. There was an average of 1.02 (±0.40) nesting pairs/ha on our sites, and productivity averaged 2.80 (±0.13) young per nesting pair (Table 3). There was no significant difference in overall owl abundance ($F_{2,3} = 5.60$, $P = 0.0972$), number of nesting pairs ($F_{2,3} = 1.576$, $P = 0.3418$), or number of young per nesting pair ($F_{2,3} = 0.78$, $P = 0.5321$) by site type.

The number of Burrowing Owl pairs was positively correlated ($r^2 = 0.5498$, $P = 0.0060$) to prairie dog colony size. The number of prairie dog burrows increased with colony size ($r^2 = 0.7006$, $P = 0.0377$). The number of Burrowing Owl pairs was positively correlated ($r^2 = 0.7327$, $P = 0.0296$) to the number of prairie dog burrows on our six sites in 2004, and mean distance between burrows of nesting pairs was 66.3 m (±4.22). However, number of Burrowing Owl pairs was not related to either the density of prairie dogs (estimated prairie dogs per ha; $r^2 < 0.3$, $P > 0.1$) or the index of vacant burrows

Table 3. Burrowing Owl nesting data for the six intensively monitored sites in Lubbock and Carson counties, Texas, for 2003 and 2004.

YEAR	SITE	NO. PAIRS	NO. YOUNG/SUCCESSFUL PAIR[a]	AREA (ha)	SPACING[b]
2003	L103	13	3.3	11.71	49.03 ± 7.86
	School	8	2.0	7.55	55.91 ± 21.75
	X-Fab	13	2.5	14.48	67.22 ± 12.94
	12-36	9	3.4	11.86	62.80 ± 16.06
	Pantex Lake	11	2.9	7.50	64.75 ± 10.67
	Zone 4	3	3.7	1.57	71.85 ± 7.96
2004	L103	8	2.5	11.71	81.62 ± 21.01
	School	6	3.0	7.55	91.56 ± 26.43
	X-Fab	5	3.0	11.12	77.78 ± 25.32
	12-36	13	3.2	11.86	59.85 ± 8.28
	Pantex Lake	5	1.8	7.50	85.00 ± 3.03
	Zone 4	4	1.5	3.08	44.59 ± 7.38

[a] Mean maximum number of nestlings seen aboveground for successful nesting Burrowing Owl nesting pairs.
[b] Mean and standard error for distances between Burrowing Owl nest burrows in meters.

(number of burrows/estimated prairie dogs; $r^2 < 0.3$, $P > 0.1$) for our six intensively monitored sites. Burrowing Owls did not use more or less dense areas of burrows within the prairie dog colonies. There was no difference ($P > 0.10$) between distances from Burrowing Owl nests and total burrow distances, or between the five closest burrows to Burrowing Owl nests and the five closest to randomly selected burrows. There were more nest burrows in zones farther from the colony center but because buffers farther from the center also incorporated much larger areas, the number of nest burrows was not greater than expected if owls nested at equal densities in each zone from the center to the outer edges of prairie dog colonies ($\chi^2 = 2.40$, $P = 0.3009$).

Measures of visual obstruction and vegetative composition were not correlated to Burrowing Owl numbers or productivity ($r^2 < 0.4$, $P > 0.1$). Our measures of relative food abundance (distance to playas containing water and relative abundances of small mammals) did not show significant relationships to Burrowing Owl nesting pairs or productivity ($r^2 < 0.1$, $P > 0.1$).

DISCUSSION

As hypothesized, we found a positive relationship between prairie dog colony size and numbers of Burrowing Owl nesting pairs. We believe this is due to an increased number of burrows and, hence, nesting opportunities on larger prairie dog colonies (although Powell et al. [1994] point out that numbers of burrows may not be directly related to number of prairie dogs). Although we do not know how many burrows were actually vacant, it did not appear that the number of vacant burrows in prairie dog colonies limited Burrowing Owls, as there were more burrows with little or no evidence of prairie dog activity than there were pairs of owls. Sidle et al. (2001) found that Burrowing Owls appear to prefer prairie dog colonies that are occupied by prairie dogs to those that are abandoned: they cited lack of burrow maintenance by prairie dogs and possible increases in predation as potential reasons. (With other prey [prairie dogs] absent, predators may focus more on Burrowing Owls.) In 2004, we found Burrowing Owl numbers particularly high on the 12–36 site, even following prairie dog control with Phostoxin just prior to the spring arrival of owls. However, this site was rapidly recolonized by prairie dogs from nearby untreated areas, so burrows were seldom vacant for very long.

Contrary to our hypothesis that Burrowing Owls should be associated with vegetative cover and obstruction, vegetative differences over all sites and years were not related to either Burrowing Owl nest density or productivity. This was unexpected, as vegetation height may negatively affect Burrowing Owls by obscuring prey or potential predators (Green and Anthony 1989). The lack of response we saw could be due to the fact that all six of our study sites were located on prairie dog colonies with low vegetation, mostly on grazed shortgrass prairie or neglected sites in an agricultural-suburban interface where there was minimal visual obstruction (2.7 ± 0.16 cm). Similarly, although we hypothesized that there would be positive relationships among owl abundance, owl nesting success and productivity, and prey abundance, we found no such significant relationships. It is possible that there were abundant resources for both of our study years, or at least comparable prey availability across sites.

Most owls on our sites were resident in summer only (noted as a relatively stable long-term population by McIntyre 2004). Only 6.8%–18.0% of the owls we marked were observed overwintering or breeding on our sites in a second season. This was much lower than reported returns of owls in Florida (68%; Millsap and Bear 1997) or in California (20–25%; Coulombe 1971). A higher proportion of wintering owls than summering owls were sighted again in another season in our study. Our returns were similar, although somewhat higher, than those previously reported for other studies in the southern Great Plains. Butts (1976) reported <1% of the summer owl population present in late July returned to his study site in the Oklahoma Panhandle to breed in the following year, whereas in Dallam County, Texas, 2.7% of the owl population from late July returned the following year. However, all banded owls known to have overwintered at both the Oklahoma and Texas sites remained to breed the following breeding season. Our higher numbers relative to those reported by Butts (1976) may reflect a change since the 1970s, with fewer owls using the northern parts of their continental range (Clayton and Schmutz 1999) and more remaining or breeding in Texas. To date, we have had only two band recoveries from the 153 owls that we banded. One was killed by a car adjacent to its Lubbock banding site shortly after banding, and the other was recovered in Apatzingan, Michoacán, México, in January 2004, 7 mo after it was banded in Lubbock County during June 2003. This band recovery rate was similar to that of Butts (1976), who reported one banded female from the breeding season in the Oklahoma Panhandle, which was shot 17 mo later during early winter in Zapotlanejo, Jalisco, México. Another similar record was from an owl captured and banded in this region by Ross and Smith (1970) in March 1968 in Swisher County, Texas, and recaptured the following year in El Paso, Texas.

The productivity observed in our study area was comparable to reports from an urban site (grassland portion of an airport) in California (Thomsen 1971), residential-urban (Millsap and Bear 2000) sites in Florida, prairie dog colonies in Montana (Restani et al. 2001), and prairie dog colonies in New Mexico (Arrowood et al. 2001). However, productivity on our sites was less than that reported in agricultural areas of central Argentina (Bellocq 1997), mixed grasslands-agricultural areas in Saskatchewan (Haug and Oliphant 1990, James et al. 1997, Wellicome 1997), prairie dog colonies on shortgrass prairie in South Dakota (Griebel and Savidge 2007), and prairie dog colonies on shortgrass prairie in North Dakota (Konrad and Gilmer 1984). These differences may be due in part to differences in habitat type among these studies compared to ours, with associated potential differences in predation risk and prey availability, but may also result from differing measurements of productivity.

Each prairie dog colony exists at a unique location in space, meaning that its inhabitants (prairie dogs and burrowing owls) are subject to unique forms of disturbance. All our study sites were subject to some form of anthropogenic disturbance. However, the number of nesting pairs of owls and the number of young per pair did not differ among the different forms of disturbance (agriculture vs. industrial urbanization vs. residential urbanization), possibly because all of the owls in our study were nesting in a similar sort of immediate environment (a prairie dog colony).

Prairie dogs are clearly important to Burrowing Owls in our area; however, the characteristics that make one prairie dog colony more suitable than others are largely unknown. It does seem that the lack of visual obstruction from tall vegetation and the large number of potentially vacant burrows are key elements in making good Burrowing Owl habitat. Lethal control of prairie dogs may initially reduce burrow occupancy by prairie dogs, leaving more burrows available for owls, although the quality of available burrows may be lacking, as well as the supply of future Burrowing Owl nest sites. Additionally, the lack of prairie dogs in a colony can lead to an increase in visual obstruction and potential loss of valuable nesting habitat.

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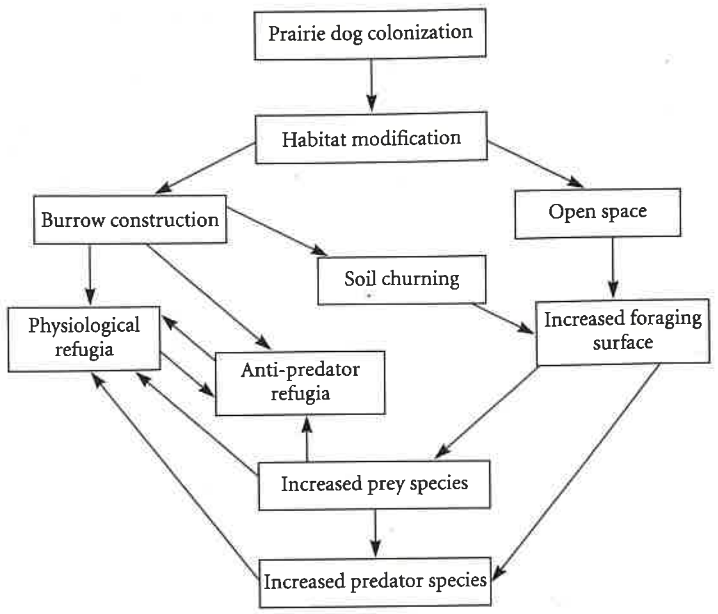

Figure 6.3. Ecological interactions that result from prairie dog colonization.

keystone species can have an inordinate effect on community structure through ecosystem engineering (Mills et al. 1993).

Prairie Dogs and the Grassland Ecosystem

There is little doubt that prairie dogs have a strong effect on their grassland ecosystem (Figure 6.2). Initially, research on species associations with prairie dog towns was anecdotal and observational. However, recent experimental studies are more profoundly uncovering the role of prairie dogs in the grassland system. While some scientists still remain cautious of the keystone term, it is clear that prairie dogs play a strong, influential role in the functioning of North American grasslands and their influence is mainly through bottom-up forces. Prairie dogs affect the species diversity and species composition of plants on colonies, influence nutrient cycling, improve water percolation and soil mixing, and provide a habitat for numerous other species of animals, both vertebrates and invertebrates (Figure 6.3). Their existence contributes to a number of processes that keep the grassland ecosystem both healthy and diverse.

Interlude:
Vertebrate Species Associated with Prairie Dogs

By Richard Reading

Updated from Kotliar et al. (1999).

Species	Benefit[a]	Citation[b]
Obligate associate (N = 1)		
Black-footed ferret, *Mustela nigripes*	PD, BU	1, 8, 38
Strong, well documented benefits of association (N = 16)		
Tiger Salamander, *Ambstoma tigrinum*	BU, TP	2, 3, 13, 14, 25, 27, 28
Lesser earless lizard, *Holbrookia maculata*	BU, PV	2, 4, 13, 30
Prairie rattlesnake, *Crotalus viridus*	BU, PD, OP	13, 14, 27, 28, 32, 33
Mountain plover, *Charadrius montanus*	OV	2, 3, 7, 11, 26, 34
Killdeer, *Charadrius vociferous*	OV	2, 3, 6, 7, 8, 10, 28, 33, 34
Golden eagle, *Aquila chrysaetos*	PD, OP	1, 2, 3, 7, 8, 33
Ferruginus hawk, *Buteo regalis*	PD, OP	2, 3, 4, 6, 7, 8, 11, 21, 28, 29, 31, 33, 36
Burrowing owl, *Athene cunicularia*	BU, OV	2, 3, 4, 6, 7, 8, 11, 17, 18, 19, 20, 22, 28, 33, 34, 35, 36
Horned lark, *Eremophila alpestris*	OV	2, 3, 4, 6, 7, 8, 10, 11, 28, 33, 34, 36
Eastern cottontail, *Sylvilagus floridanus*	BU, PV	8, 27, 28, 33
Desert cottontail, *Sylvilagus audubonii*	BU, PV	1, 2, 3, 4, 8, 9, 12, 14, 33, 37
N. grasshopper mouse, *Onychomys leucogaster*	PV	1, 3, 6, 8, 27, 28, 33
Coyote, *Canis latrans*	BU, PD, OP	1, 2, 3, 4, 7, 8, 12, 27, 28, 33
Badger, *Taxidea taxus*	BU, PD, OP	1, 2, 3, 4, 7, 8, 12, 27, 28, 33
Swift fox, *Vulpes velox*	PD, OP	2, 8, 27, 28, 33
Pronghorn, *Antilocapra americana*	PV	1, 3, 4, 7, 8, 27, 28, 33
Some documented benefits of association (N = 38)		
Plains spadefoot toad, *Spea bombifrons*	BU, TP	2, 13, 14, 27, 28
Woodhouse's toad, *Bufo woodhousii*	BU, TP	2, 13, 27, 28

Species	Benefit[a]	Citation[b]
Great plains toad, *Bufo cognatus*	BU, TP	8, 27, 28
Ornate box turtle, *Terrapene ornate*	BU, PV	2, 4, 13, 27, 28
Texas horned lizard, *Phrynosoma cornutum*	BU, PV	2, 4, 13, 27, 28
Little striped whiptail, *Cnemidophorus inornatus*	BU, PV	4, 30
*Plateau striped whiptail, *Cnemidophorus velox*	BU, PV	30
Plains garter snake, *Thamnophis radix*	BU, OP	8, 14, 27, 28
Long-billed curlew, *Numenius americanus*	PV, TP, OV	2, 6, 7, 8, 10, 11, 33
*Aplomado falcon, *Falco femoralis*	PD, OP, OV	16
American kestrel, *Falco sparverius*	OP	2, 3, 4, 6, 7, 8, 9, 10, 33
Swainson's hawk, *Buteo swainsoni*	PD, OP	2, 3, 4, 6, 7, 8, 9, 10, 11
Red-tailed hawk, *Buteo jamaicensis*	PD, OP	1, 2, 3, 6, 8, 9, 33
Scaled quail, *Callipepla squamata*	PV	2, 10, 33
Scissor-tailed flycatcher, *Tyrannus forficatus*	PV	2, 28, 33
Loggerhead shrike, *Lanius ludovicianus*	PV, OP	2, 3, 6, 7, 8, 10, 28, 33
Barn swallow, *Hirundo rustica*	PV	2, 3, 6, 7, 8, 10
Lark sparrow, *Chondestes grammacus*	PV	2, 4, 7, 8, 10, 11, 28, 33
Eastern meadowlark, *Sturnella magna*	PV	2, 28, 33
Brown-headed cowbird, *Molothrus ater*	PV	2, 3, 7, 8, 28, 33
Chestnut-collared longspur, *Calcarius ornatus*	OV	2, 3, 6, 7, 8, 28, 33, 36
*Banner-tailed kangaroo rat, *Dipodomys spectabilis*	BU, OV	12, 23
*Merriam's kangaroo rat, *Dipodomys merriami*	BU, OV	12
Deer mouse, *Peromyscus maniculatus*	PV	1, 2, 3, 6, 8
W. harvest mouse, *Reithrodontomys megalotis*	BU, PV	6, 8, 12
Silky pocket mouse, *Perognathus flavus*	BU, PV	3, 8, 9, 12
Hispid pocket mouse, *Chaetodipous hispidus*	PV	6, 8, 12
*Tawny-bellied cotton rat, *Sigmodon fulviventer*	PV	12
*White-throated woodrat, *Neotoma albigula*	BU, OV	12
*S. grasshopper mouse, *Onychomys torridus*	BU, OV	12
Mearn's grasshop. mouse, *Onychomys arenicola*	PV	9
Spotted ground squirrel, *Spermophilus spilosoma*	BU, PV	2, 12
Thirteen-lined ground squirrel, *Spermophilus tridecemlineatus*	BU, PV	1, 2, 3, 4, 6, 8, 27, 28, 33
Long-tailed weasel, *Mustela frenata*	BU, PD, OP	3, 4, 8, 12
*Kit fox, *Vulpes macrotis*	BU, PD, OP	12, 15
Spotted skunk, *Spilogale putorius*	OP	8, 12
*Hog-nosed skunk, *Conepatus mesoleucus*	BU, OP	12
White-tailed deer, *Odocoileus virginianus*	PV	8, 27, 28
Mixed or inconclusive evidence of a beneficial association (N = 13)		
Chorus frog, *Pseudacris triseriata*	BU, TP	3, 8, 14
Gopher snake, *Pituophis melanoleucus catenifer*	BU, PV	2, 3, 13
*Great Plains skink, *Eumeces obsoletus*	BU, PV	13
*Wandering garter snake, *Thamnophis elegans*	BU, OP	14
Northern harrier, *Circus cyaneus*	OP	1, 2, 3, 6, 7, 8, 11, 33
Mourning dove, *Zenaida macroura*	OV	2, 3, 4, 6, 7, 8, 33, 34
Lark bunting, *Calamospiza melanocorys*	PV	2, 3, 6, 7, 10, 11, 34, 36
McCown's longspur, *Calcarius lapponicus*	OV	2, 3, 7, 8, 28, 33
Western meadowlark, *Sturnella neglecta*	PV	2, 3, 4, 6, 7, 8, 10, 28, 33, 34
Common grackle, *Quiscalus quiscula*	PV	6, 10
White-footed mouse, *Peromyscus leucopus*	PV	5, 23
Black-tailed jackrabbit, *Lepus californicus*	PV	1, 2, 4, 8, 9, 27, 28
Striped skunk, *Mephitis mephitis*	BU, OP	2, 3, 8, 12, 27, 28
No, or insufficient, evidence of a beneficial association (N = 105)		
Couch's spadefoot toad, *Scaphiopus couchi*	TP	2
Green toad, *Bufo debilis*	TP	2
Texas toad, *Bufo speciosus*	TP	2
Gr. plains narrow-mouthed frog, *Gastrophryne olivacia*	BU, TP	2
Yellow mud turtle, *Kinosternon flavescens*	BU, TP	2, 12
Bullsnake, *Pituophis melanoleucus sayi*	BU, OP	14
Western diamondback rattler, *Crotalus atrox*	PD, OP, BU	1, 2
Mohave rattlesnake, *Crotalus scutulatus*	PD, OP, BU	9
*Black-tailed rattlesnake, *Crotalus molossus*	BU, PD, OP	12
*Lined snake, *Tropidoclonion lineatum*	BU, OP	14
*Mexican garter snake, *Thamnophis eques*	BU	12
*Milk snake, *Lampropeltis triangulum*	BU, OP	13
Eastern fence lizard, *Sceloporus undulates*	BU	2
Short horned lizard, *Phrynosoma douglassi*	BU, PV	3, 14
6-lined racerunner, *Cnemidophorus sexlineatus*	BU, OP	2, 13
Texas spotted whiptail, *Cnemidophorus qularis*	BU, PV	2
*Desert grassland whiptail, *Cnemidophorus uniparens*	BU	12
Chihuahua spotted whiptail, *Cnemidophorus exsanguis*	BU	12
*Desert grassland whiptail, *Cnemidophorus uniparens*	BU	12
*Many-lined skink, *Eumeces multivirgatus*	BU, PV	14
American avocet, *Recurvirostra americana*	TP	7

Species	Benefit[a]	Citation[b]
Lesser golden plover, *Pluvialis dominica*	OV, TP	2
Marbled godwit, *Limosa fedoa*	TP	7
Willet, *Catoptrophorus semipalmatus*	TP	7
Greater yellowlegs, *Tringa melanoleuca*	TP	7
Lesser yellowlegs, *Tringa flavipes*	TP	7
Wilson's phalarope, *Phalaropus tricolor*	TP	7, 8
Long-billed dowitcher, *Limnodromus scolopaceus*	TP	8
Bairds's sandpiper, *Calidris bairdii*	OV, TP	2
Buff-breasted sandpiper, *Tryngites subruficollis*	OV, TP	2
*Whimbrel, *Numenius phaeopus*	OV, PV	11
*Greater roadrunner, *Geococcyx californianus*	OP	11
Turkey vulture, *Cathartes aura*	PD, OP	2, 6, 8, 10
Prairie falcon, *Falco mexicanus*	OP	1, 2, 3, 6, 7, 8, 11
Bald eagle, *Haliaeetus leucocephalus*	PD, OP	2, 8
Mississippi kite, *Ictinia mississippiensis*	OP	2, 10
Sharp-shinned hawk, *Accipiter striatus*	OP	7
*Zone-tailed hawk, *Buteo albonotatus*	OP	11
Rough-legged hawk, *Buteo lagopus*	PD, OP	1, 2, 8, 33
Crested caracara, *Polyborus plancus*	PD, OP	9
Merlin, *Falco columbarius*	OP	7, 8, 10
Lesser prairie chicken, *Tympanuchus pallidicinctus*	OV	2
Sharp-tailed grouse, *Tympanuchus phasianellus*	OV	1, 6, 7, 8
Sage grouse, *Centrocerus urophasianus*	OV	3, 7
Great horned owl, *Bubo virginianus*	OP	3, 6
Snowy owl, *Nyctea scandiaca*	PD, OP	8
*Short-eared owl, *Asio flammeus*	PV	11
Northern flicker, *Colaptes auratus*	PV	2, 7, 8
Eastern kingbird, *Tyrannus tyrannus*	PV	2, 6, 7, 8, 10
Western kingbird, *Tyrannus verticalis*	PV	2, 3, 6, 7, 8, 10
Cassin's kingbird, *Tyrannus vociferans*	PV	10
*Ash-throated flycatcher, *Myiarchus cinerascens*	PV	11
Say's phoebe, *Sayornis saya*	PV	6, 8
Violet-green swallow, *Tachycineta thalassina*	PV	8
N. rough-winged swallow, *Stelgidopteryx serripennis*	PV	6, 8
Cliff swallow, *Hirundo pyrrhonota*	PV	2, 3, 7, 8, 10
*Tree swallow, *Tachycineta bicolor*	PV	11
*Bank swallow, *Riparia riparia*	PV	11
Black-billed magpie, *Pica pica*	PV	3, 7, 8
Chihuahuan raven, *Corvus cryptoleucus*	PV	2, 10
American crow, *Corvus brachyrhynchos*	OP	2, 6, 8, 10
Common raven, *Corvus corax*	OP	8
American robin, *Turdus migratorius*	PV	7, 8
Northern shrike, *Lanius excubitor*	OP	8
Sage thrasher, *Oreoscoptes montanus*	PV	7
Curved-billed thrasher, *Toxostoma curvirostre*	PV	4, 10
Water pipit, *Anthus spinoletta*	PV	8
Sprague's pipit, *Anthus spragueii*	PV	2
Rufous-sided towhee, *Pipilo erythrophthalmus*	PV	8
Vesper sparrow, *Pooecetes gramineus*	PV	2, 3, 7, 8, 10, 11
Savannah sparrow, *Passerculus sandwichensis*	PV	2, 3, 7
Chipping sparrow, *Spizella passerine*	PV	8
*Song sparrow, *Melospiza melodia*	PV	11
*Black-throated sparrow, *Amphispiza bilineata*	PV	11
Slate-colored junco, *Junco hyemalis*	PV	8
White-crowned sparrow, *Zonotrichia leucophrys*	PV	8
Lapland longspur, *Calcarius lapponicus*	PV	2
Snow buntings, *Plectrophenax nimalis*	PV	3
Dickcissel *Spiza americana*	PV	8
Bobolink, *dolichonyx oryzivorus*	PV	8
*Cactus wren, *Campylorhynchus brunneicapillus*	PV	11
*Rock wren, *Salpinctes obsoletus*	BU	24
*Lucy's warbler, *Vermivora luciae*	PV	11
*Yellow-rumped warbler, *Dendroica coronata*	PV	11
Brewer's blackbird, *Euphagus cyanocephalus*	PV	2, 7, 8
Yellow-headed blackbird, *Xanthocephalus xanthocephalus*	PV	6, 7, 8, 11
Boat-tailed grackle, *Quiscalus major*	PV	2
Pine siskin, *Carduelis pinus*	PV	8
American goldfinch, *Carduelis tristis*	PV	8
*House finch, *Carpodacus mexicanus*	PV	11
*Blue grosbeak, *Guiraca caerulea*	PV	11
Eastern mole, *Scalopus aquaticus*	PV	2
White-tailed jackrabbit, *Lepus townsendii*	PV	1, 3, 7, 8
Least chipmunk, *Eutamias minimus*	PV	3
Northern pocket gopher, *Thomomys talpoides*	PV	8
Plains pocket gopher, *Geomys bursarius*	PV	2, 4, 8
Southern plains woodrat, *Neotoma micropus*	PV	2, 4
Richardson's ground squirrel, *Spermophilus richardsonii*	BU, PV	7
Elk, *Cervus elaphus*	PV	7
Mule deer, *Odocoileus hemionus*	PV	3, 7, 8
Bison, *Bison bison*	PV	1, 2, 8
Red fox, *Vulpes fulva*	OP	3, 7, 8
Bobcat, *Lynx rufus*	PD, OP	1, 2, 8
*Ringtail, *Bassariscus astutus*	OP	12

Species	Benefit[a]	Citation[b]
At least some documented evidence of a negative association (N = 16)		
*Yellow-bellied racer, *Coluber constrictor*	BU, OP	13
Upland sandpiper, *Bartramia longicauda*	PV	2, 6, 7, 8, 33
Northern bobwhite, *Colinus virginianus*	PV	2, 33
Common nighthawk, *Chordeiles minor*	PV	2, 3, 7, 10, 33
Grasshopper sparrow, *Ammodramus savannarum*	PV	6, 7, 8, 11, 33, 34, 36
Cassin's sparrow, *Aimophila cassinii*	PV	10, 11, 33, 36
Brewer's sparrow, *Spizella breweri*	PV	7, 11, 36
Baird's sparrow, *Ammodramus bairdii*	PV	7, 36
Northern mockingbird, *Mimus polyglottos*	PV	2, 8, 10, 33
Bullock's oriole, *Icterus bullockii*	—	2, 33
Red-winged blackbird, *Agelaius phoeniceus*	PV	2, 6, 7, 8, 10, 33
Ord's kangaroo rat, *Dipodomys ordi*	PV	1, 2, 4, 8, 9
Plains harvest mouse, *Reithrodontomys montanus*	PV	8
Prairie vole, *Microtus ochrogaster*	PV	6, 8
Raccoon, *Procyon lotor*	—	2, 3, 8, 12
*Hooded skunk, *Mephitis macroura*	BU, OP	12
No data on association, but species life history suggests an accidental occurrence (N = 48)		
Northern leopard frog, *Rana pipiens*		3
Western toad, *Bufo boreas*		3
Bullfrog, *Rana catesbeiana*		8
Sagebrush lizard, *Sceloporus graciosus*		3, 4
Chihuahua spotted whiptail, *Cnemidophorus exsanguis*		4, 12
Smooth green snake, *Opheodrys vernalis*		8
Common garter snake, *Thamnophis sirtalis*		3
Eared grebe, *Podiceps nigricollis*		7
Pied-billed grebe, *Podilymbus podiceps*		7
White pelican, *Pelecanus erythrorhynchos*		7
Double-crested cormorant, *Phalacrocorax auritus*		7
Black-crowned night heron, *Nycticorax nycticorax*		7
Great blue heron, *Ardea herodias*		7, 8
*Osprey, *Pandion haliaetus*		11
Trumpeter swan, *Cyngus buccinator*		8
Snow goose, *Chen caerulescens*		2
Canada goose, *Branta canadensis*		7, 8
Mallard, *Anas platyrhynchos*		6, 7, 8
Gadwall, *Anas strepera*		7, 8
Ruddy duck, *Oxyura jamaicensis*		7
Green-winged teal, *Anas crecca*		3, 7
American wigeon, *Anas americana*		7
Northern pintail, *Anas acuta*		6, 7, 8
Northern shoveler, *Anas clypeata*		8
Blue-winged teal, *Anas discors*		6, 7, 8
Canvasback, *Aythya valisineria*		8
Redhead, *Aythya americana*		7
Lesser scaup, *Aythya affinis*		7
Sora, *Porzuna Carolina*		6, 8
American coot, *Fulicaa americana*		7
Ring-billed gull, *Larus delawarensis*		7, 8
Herring gull, *Larus argentatus*		7
California gull, *Larus californicus*		7
Belted kingfisher, *Ceryle alcyon*		8
Red-headed woodpecker, *Melanerpes erythrocephalus*		8
Downy woodpecker, *Picoides pubescens*		8
Ladder-backed woodpecker, *Picoides scalaris*		2
Blue jay, *Cyanocitta cristata*		8
Eastern bluebird, *Sialia sialis*		8
Mountain bluebird, *Sialia currocoides*		7, 8
Gray catbird, *Dumetella carolinensis*		8
Yellow warbler, *Dendroica petechia*		8
Common yellowthroat, *Geothlypis trichas*		8
Yellow-breasted chat, *Icteria virens*		8
Western tanager, *piranga ludoviciana*		8
Common redpoll, *Carduelis flammea*		8
Porcupine, *Erethizon dorsatum*		8
Mink, *Mustela vison*		3, 8
Domestic or introduced species (N = 10)		
Gray partridge, *Perdix perdix*		7
Ring-necked pheasant, *Phasianus colchicus*		8, 33
Rock dove, *Columbia livia*		2, 6, 8, 10
European starling, *Sturnus vulgaris*		2, 6, 7, 8
House sparrow, *Passer domesticus*		2, 6, 8
Norway rat, *Rattus norvegicus*		8
House mouse, *Mus musculus*		6, 8
Domestic horse, *Equus caballus*		3, 7
Domestic cattle, *Bos Taurus*		3, 7, 33
Domestic sheep, *Ovis aries*		3, 7

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* New species associated reported since Kotliar (1999).

a. From Kotliar et al. (1999): PD = prairie dogs as prey or carrion; OP = other vertebrate prey or carrion found on colonies; BU = burrows for nesting/shelter; OV = open vegetation or bare ground for nesting/foraging; PV = prairie vegetation for nesting/foraging; TP = temporary pools for breeding/forage.

b. Citations: 1 = Koford 1958; 2 = Tyler 1968; 3 = Campbell and Clark 1981; 4 = Clark et al. 1982; 5 = O'Meilia et al. 1982; 6 = Agnew et al. 1986; 7 = Reading et al. 1989; 8 = Sharps and Uresk 1990; 9 = Mellink and Madrigal 1993; 10 = Barko 1996; 11 = Manzano-Fischer 1996 and Manzano-Fischer et al. 1999; 12 = Ceballos et al. 1999; 13 = Kretzer and Cully 2001; 14 = Shipley and Reading In press; 15 = List and MacDonald 2003; 16 = Truett, J. C. 2002; 17 = Restani et al. 2001; 18 = Sidle et al. 2001; 19 = Sheffield and Howery 2001; 20 = Arrowood et al. 2001; 21 = Bak et al. 2001; 22 = Desmond et al. 2000; 23 = Davidson et al. 1999 (Gunnison's prairie dogs); 24 = Price 2002 (white-tailed prairie dogs); 25 = Kolbe et al. 2002; 26 = Ellison Manning and White 2001; 27 = Lomolino and Smith 2003; 28 = Lomolino and Smith 2004; 29 = Cook et al. 2003; 30 = Davis and Theimer 2003; 31 = Cartron et al. 2004; 32 = Holycross and Fawcett 2002; 33 = Smith and Lomolino 2004; 34 = Winter et al. 2003; 35 = VerCauteren et al. 2001; 36 = Desmond 2004; 37 = Dano 1952; 38 = Miller et al. 1996.

7

Economics: How Much Is a Prairie Dog Worth?

The natural world provides us with food, water, timber, stone, medicines, sunsets, mountains, open plains, plants, wildlife, and many other useable resources. We can manufacture none of these, with the exception of some medicines, yet all are intrinsically valuable to us and most are crucial to our existence. From our beginnings, humans have been dependent on the natural world for survival, but the way in which we view this connection is constantly changing.

From earlier days of barter and trade to our current market economy, natural resources have been exchanged by different means; however one thing has remained the same. At the moment when humankind conceived of owning and trading we entered into the dilemma of assigning value. Setting up a system that requires a clear economic value is very convenient for some commodities but not for others. In our modern economy, we assign values to privately-owned commodities and make purchases of those we deem valuable at what we see as a fair price. Most of the time, because we pay for the things we purchase, we have ownership of them and we take care of them. We clean and service our cars to keep them running, we wash our clothes, and repair our houses.

Economic value is relatively easy to assign when ownership is apparent, when someone manufactures something, or when something is rare. But what happens to those commodities and services that are not clearly owned, are never produced or provided by anyone, or are perceived as free or unlimited? How do you assign an economic value to the air when no one ever has to purchase it? What value is assigned to the feeling one gets looking at a

Attitudes toward a Proposed Reintroduction of Black-Footed Ferrets (*Mustela nigripes*)

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Abstract: *Sociological considerations are crucial to recovery efforts such as the proposed reintroduction of endangered black-footed ferrets (*Mustela nigripes*) into Phillips County, Montana. Many past reintroduction attempts have failed or been less successful because they neglected these concerns. This study examined knowledge, attitudes, and opinions of ranchers toward black-footed ferrets, prairie dogs (*Cynomys *spp.), and the proposed ferret reintroduction using informal, unstructured interviews and a mail sample survey. Ranchers within the proposed reintroduction site were antagonistic toward the program, the ferret, and especially the prairie dogs upon which black-footed ferrets depend for survival. Of six sample groups, local ranchers scored highest on negativistic, libertarian/dominionistic, and utilitarian attitude scales and lowest on moralistic, humanistic, and naturalistic/ecologistic attitude scales. Their attitudes were most similar to those of ranchers statewide, followed by residents of Phillips County, Montana, Billings, Montana, residents, and members of the Montana Wildlife Federation; they were least similar to attitudes of members of conservation organizations other than the Montana Wildlife Federation. Local ranchers perceived themselves as having little knowledge of black-footed ferrets, even though they received significantly higher scores on the black-footed ferret knowledge scales than did most other groups, and they perceived themselves as having great knowledge of prairie dogs, even though their scores on the prairie dog knowledge scales were no better than any other group. These results are useful for ranking*

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Actitudes hacia una propuesta para la reintroducción del hurón de patas negras (*Mustela nigripes*)

Resumen: *Las consideraciones sociológicas son cruciales para la recuperación de esfuerzos tales como la propuesta de reintrodución del hurón de patas negras (*Mustela nigripes*) en peligro de extinción en el distrito territorial de Phillips, en Montana. Varios intentos de reintroducción en el pasado fracasaron o han sido poco exitosos por haber descuidado dichas consideraciones. Este estudio examina el conocimiento, actitudes y opiniones de los rancheros hacia los hurones de patas negras, los perros de las praderas (*Cynomys sp.*) y la propuesta de reintroducción del hurón utilizando entrevistas informales, no estructuradas y un modelo de encuestas por correo. Los rancheros dentro del área de reintroducción fueron antagónicos hacia el programa, el hurón y especialmente hacia los perros de las praderas de los cuales los hurones de patas negras dependen para sobrevivir. De 6 grupos de muestras, los rancheros locales tuvieron el puntaje mas alto en escalas de actitud negativistas, libertarios/dominadores y utilitaristas y el resultado más bajo en cuanto a una actitud moralista, humanista y naturalista/ecologista dentro de la misma escala. Sus actitudes fueron más similares a la de los rancheros a lo largo del estado, seguidos por los residentes del distrito territorial de Phillips, Montana, los residentes de Billings, Montana, los miembros de la Federación de Vida Silvestre de Montana y fueron menos similares a los miembros de organizaciones conservacionistas diferentes de la Federación de Vida Silvestre de Montana. Los rancheros locales percibieron ellos mismos la falta de conocimiento sobre los hurones de patas negras, a* *the suitability of reintroduction sites, for formulating policies, and for developing more effective public relations campaigns. The results highlight the need for education and public relations programs that do more than simply provide facts and information. Well-conceived public relations programs should use pressure, purchase, and persuasion to try to change or neutralize opposition and to develop, conserve, and strengthen support. Endangered species reintroduction and recovery programs will rarely succeed if they do not actively consider and incorporate the values, attitudes, behaviors, and desires of the local public.*

pesar de que ellos recibieron un puntaje significativamante más alto en relación con otros grupos dentro de la escala de conocimiento sobre el hurón de patas negras. Ellos mismos también percibieron tener un gran conocimiento sobre los perros de las praderas a pesar de que su puntaje dentro de la escala de conocimiento de los perros de las praderas no fue mejor que el de cualquier otro grupo. Estos resultados son útiles para clasificar los sitios más convenientes para la reintroducción, para formular planes de acción y para desarrollar campañas de relaciones públicas más efectivas. Estos resultados ponen de relieve la necesidad de programas de educación y de relaciones públicas, los cuales proveen algo más que simples hechos e información. Los programas de relaciones públicas bien concebidos deben utilizar presión, movilizar y persuadir para tratar de cambiar o neutralizar oposiciones y para desarrollar, conservar y fortalecer el apoyo. La reintroducción de especies en peligro de extinción y los programas de recuperación dificilmente van a prosperar si no consideran e incorporan activamente los valores, actitudes, comportamientos y deseos de la comunidad local.

Introduction

As the number of endangered species grows, reintroduction as a conservation tool increases. Most reintroductions fail, however (Griffith et al. 1989). We propose that many of these failures occur because the socioeconomic and political aspects of reintroduction programs are not adequately addressed. Reintroductions of endangered species are especially problematic because of both real and perceived restrictions under the Endangered Species Act. Of particular concern is the impact on resource-dependent populations such as farmers, loggers, and miners by the presumption of restricted access to and use of natural resources on both private and multiple-use public lands.

In this paper we explore some of the social aspects of a proposed black-footed ferret (*Mustela nigripes*) reintroduction in Montana. The knowledge, attitudes, and opinions of ranchers within the proposed reintroduction site toward black-footed ferrets, prairie dogs (*Cynomys* spp.), and the proposed reintroduction are examined. Knowledge, attitudes, and opinions are discussed in relation to ranchers statewide, other residents of Phillips County, Montana, residents of Billings, Montana, and members of conservation organizations from Montana.

Sociology of Reintroductions

A generalized paradigm for the reintroduction of endangered species has been developed that includes socioeconomic variables (Reading et al. 1991). The paradigm also involves the integration of science/technical, organizational, and political or power/authority variables. Traditionally, reintroduction plans have concentrated almost exclusively on the scientific and technical aspects. We assert that a more holistic reintroduction paradigm could provide managers and conservationists with a readily accessible framework for future species reintroductions, both expediting and rendering more effective the policy process (Kellert & Clark 1991). As Kellert (1985*a*:528) states, "A compelling rationale and an effective strategy for protecting endangered species will require recognition that contemporary extinction problems are [largely] the result of socioeconomic and political forces."

An examination of the socioeconomic aspects of reintroduction programs requires investigating values, attitudes, and perceptions held by people involved with and potentially affected by endangered species reintroductions. These considerations are usually lacking or insufficiently considered in endangered species management efforts (Kellert 1985*a*). Here we concentrate on the knowledge, attitudes, and opinions of local ranchers—one of several important socioeconomic aspects—to a proposed black-footed ferret reintroduction into Montana.

Local support is crucial to conservation efforts. As Carlton (1986:266) states, "Only when citizens perceive the protection of species as a public good, deserving of a cooperative effort . . . will a long-range, effective preservation program be possible." Assessing public views and knowledge of wildlife often permits development of pertinent and effective public relations campaigns designed to develop support and to enable people to make more rational and intelligent decisions (Kellert & Berry 1980). If the local public is antagonistic, it is difficult to develop support, and disastrous consequences may result (for example, see Hook & Robinson 1982 and Belden et al. 1990).

For wildlife, important factors influencing attitudes toward reintroduction include many characteristics of the species (such as phylogeny, morphology, size, sentient capacity), the perceived worth of the animal, and its symbolic nature (Kellert 1980; Kellert & Berry 1980). It is far easier to garner support for species with high public appeal, the "charismatic megafauna," than for lesser-known, "lower" life forms (Eckholm 1978; Westman 1990). Attitudes toward predators are also often negative or hostile (Arthur et al. 1977; Kellert 1985*b*, 1986, 1990; Bath 1989). Several values influence the perceived worth of the animal, including aesthetic, ethical, ecological, biological, recreational, cultural, utilitarian, genetic, and unknown or undiscovered values of wildlife (Ehrlich et al. 1977; Pister 1979; Rolston 1981; Kellert 1983, 1986). The perceived worth of a species is often influenced by knowledge of the species, moral and ethical issues of animal rights, and traditional market values (pelt values). Local norms and customs can also play a strong role in shaping attitudes and values, especially in the absence of accurate knowledge (Rokeach 1972; Chaiken & Stangor 1987). Variations in norms and customs are often influenced by demographic and geographic factors.

Montana Black-Footed Ferret Reintroduction

Black-footed ferrets are medium-sized mustelids that formerly inhabited the American Great Plains from southern Canada to northern Mexico and are now thought to be extinct in the wild. Because black-footed ferrets are obligate associates of prairie dogs, upon which they prey and in the burrows of which they den and seek refuge, values and attitudes associated with prairie dogs are also important (Forrest et al. 1985; Clark 1989).

Attitudes toward endangered species, especially black-footed ferrets and their associated recovery efforts, are also critical considerations. Endangered species status under the Endangered Species Act often elicits negative attitudes associated with real and perceived restrictions and limitations to farming operations. This study thus focuses on achieving a better understanding of the attitudes, perceptions, and knowledge of affected people towards black-footed ferrets, prairie dogs, and reintroduction as a recovery strategy as an important step toward developing an effective species conservation program.

Methods

To analyze some of the social variables of the proposed black-footed ferret reintroduction, informal, unstructured meetings and interviews and a sample mail survey were utilized. The values, attitudes, opinions, and knowledge of local ranchers and Phillips County residents were examined and compared with those of ranchers state-wide, those of Billings residents, and those of members of wildlife and conservation organizations. Because they represent the group potentially most affected by a ferret reintroduction, particular attention was paid to local ranchers.

All ranch households within the proposed reintroduction site were given the opportunity to meet informally with a team of wildlife biologists from the Bureau of Land Management, the U.S. Fish & Wildlife Service, and the Montana Department of Fish, Wildlife, and Parks. Twenty-seven meetings were attended by 53 local ranchers during the summer of 1990. R. P. Reading attended the meetings as an observer and recorded all pertinent conversation. Agency personnel discussed the proposed black-footed ferret reintroduction and its implications, answered questions, and listened, recorded, and, where possible, responded to the concerns of the ranchers. Content analysis was performed on the data. Additional informal, unstructured interviews ($n = 25$) with local ranchers were performed during the summers of 1988–1990.

A structured mail survey investigated the knowledge, values, attitudes, and perceptions about prairie dogs, black-footed ferrets, the black-footed ferret recovery program, and involved government agencies. The sample included 935 randomly selected individuals, consisting of 300 residents of Phillips County (which contains the proposed reintroduction site), 300 residents of Billings (the largest city in Montana), 150 ranchers in Montana, 150 members of conservation organizations from Montana, and residents of 35 ranches located within the proposed reintroduction site. Samples from Phillips County and Billings were randomly selected from telephone directories. Montana ranchers were randomly selected from a list provided by the Montana Stockgrowers Association. Five conservation organizations provided membership lists from which random samples were taken from two groups, the Montana Wildlife Federation ($n = 75$) and Montana members of the National Audubon Society ($n = 34$), The Nature Conservancy ($n = 30$), Defenders of Wildlife ($n = 8$), and the American Wildlands Association ($n = 3$).

An advance letter informed selected individuals about the purpose of the study and that they would soon receive a survey, and it requested their assistance in the survey's completion and prompt reply. The 121-question survey, along with an explanatory cover letter, a question and answer sheet, a self-addressed, stamped return envelope, and a $2 incentive, were mailed one week following the advance letter. A reminder postcard was mailed after an additional two weeks. A second survey was mailed to nonrespondents one month after the initial mailing. The overall response rate to be survey was 76%. Fifty surveys were undeliverable, giving a 80% return rate for deliverable surveys. Within the sample groups, overall response rates were 74% of the local ranchers, 85% of Montana ranchers, 76% of Phillips County residents, 64% of Billings residents, and 84% of the members of both the Montana Wildlife Federation and the other conservation organizations.

A five-point Likert format of response options was used for attitude and opinion questions. Six attitude scales were constructed based on principal component and factor analyses of the individual attitude questions. Scales were comprised of five to nine questions addressing a similar basic attitude toward prairie dogs and ferrets. Specific questions and scale procedures are available upon request. The scales, though conceptually based on a typology of basic attitudes toward wildlife developed by Kellert (1980) and using the same labels, consisted of question items unique to this study. Scale reliability was tested with Cronbach's Coefficient Alpha, which examines internal consistency based on correlations of items on a single scale. One-sentence definitions of the six basic attitude scales are found in Table 1.

Table 1. Black-footed ferret/prairie dog attitude scale definitions.

Attitude Scale	*Definition*	*Cronbach's α**
Negativistic	Strong dislike or indifference towards black-footed ferrets and prairie dogs and their conservation	0.878
Libertarian/ Dominionistic	Strong interest in individual rights and freedoms and in the mastery, control, and domination of wildlife	0.878
Utilitarian	Strong support for the direct utilization of wildlife and subordination of wildlife habitat for human use	0.887
Moralistic	Strong concern for the possible infliction of cruelty, harm, and exploitation of black-footed ferrets and prairie dogs	0.882
Humanistic	Strong emotional attachment to, and support for the existence value of, black-footed ferrets and prairie dogs	0.876
Naturalistic/ Ecologistic	Strong interest in direct outdoor recreational contact with black-footed ferrets and prairie dogs and in their ecological value	0.882

** Cronbach's α is a measure of the scale's internal consistency. Interpretation is similar to that for a correlation coefficient ranging from 0 to 1.*

Three knowledge scales (black-footed ferret knowledge, prairie dog knowledge, and overall knowledge) were developed from 10 questions about black-tailed prairie dogs (*C. ludovicianus*) and 13 questions about black-footed ferrets. Two points were awarded for a correct answer, one point was awarded if the respondent realized he or she did not know the answer to a question, and no points were given for an incorrect response. All knowledge and attitude scales were standardized on a 100-point scale.

Pearson chi-squared values were used to test for significant differences among individual attitude questions. Demographic group variation in opposition to ferret reintroduction was assessed using step-wise and multiple regressions. Means of paired scale scores were computed and compared using analysis of variance for all groups and Tukey's studentized range (HSD) test between groups.

Results

Fifty-six percent of the local ranchers within the proposed reintroduction site opposed black-footed ferret reintroduction (Table 2). Ranchers disliked both ferrets and prairie dogs. No local rancher indicated that he or she cared strongly or even moderately about black-footed ferrets (Table 3). Very few agreed that it would be a thrill to see a black-footed ferret in the wild (6%) or thought they were likely to make a trip to see ferrets if they were reintroduced (3%). Alternatively, equal percentages of local ranchers (28%) agreed and disagreed that black-footed ferrets have a right to exist.

Ranchers were even more strongly antagonistic toward prairie dogs. Every respondent considered prairie dogs to be pests and few respondents cared about them. Ninety-one percent thought ranchers should not have to accept losses due to prairie dogs on public lands, and the vast majority (97%) favored controlling prairie dog numbers.

Informal meetings and interviews supported the survey data. Local ranchers were clearly concerned about prairie dogs, particularly prairie dog control, and especially in relation to proposed black-footed ferret reintroduction. Concerns over continued prairie dog control were voiced at 25 of 27 meetings held with local ranchers, and in 11 meetings ranchers expressed concern over the loss of forage to prairie dogs that might result from black-footed ferret reintroduction. Typical comments included:

> Personally I'm all for it [black-footed ferret reintroduction], but in 10 years if prairie dogs aren't controlled, I'll be against it because then you'll be hitting my pocketbook.
>
> I'm not against the ferret, it's the prairie dog. I want to kill every last one.

Table 2. Attitudes toward black-footed ferret reintroduction.

Question *Sample Group*	*Strong or Moderately Agree*	*Neither Agree Nor Disagree*	*Strongly or Moderately Disagree*	*n*
I oppose black-footed ferret reintroduction				
Local Ranchers	56%	16%	28%	25
Statewide Ranchers	42	23	35	124
Phillips County Residents	32	25	43	224
Billings Residents	8	29	63	190
Montana Wildlife Federation Members	11	19	70	61
Other NGO[a] Members	7	8	85	61
I would be willing to donate $5 to support the establishment of black-footed ferrets in Phillips County, Montana				
Local Ranchers	4%	4%	92%	26
Statewide Ranchers	9	10	81	127
Phillips County Residents	13	22	65	221
Billings Residents	33	29	38	188
Montana Wildlife Federation Members	40	34	26	62
Other NGO Members	67	14	19	63

[a] NGO = non-governmental organization.

The endangered status of the ferret elicited fears of restrictions to ranching operations, of loss of control over public and private lands, and of increased interference from people from outside the area (Table 4). Local ranchers strongly favored private control of ranching operations, especially on private lands, and were fearful of restrictions if black-footed ferrets were reintroduced. Ranchers were also afraid that black-footed ferret reintroduction would lead to restrictions on hunting (77%). Nearly all local ranchers (97%) believed that if black-footed ferrets were reintroduced, environmentalists would use them to try to restrict ranching, and 56% believed that federal agencies were reintroducing ferrets to increase their control over grazing.

Content analysis supported the findings from the survey. Fear of restrictions and strong libertarian attitudes were evident. In seven meetings, ranchers expressed concern that the reintroduction would lead to ranching restrictions, and in eight meetings they demonstrated a distrust of government agencies. In eight meetings, ranchers voiced concerns over outside interference and influence on ranching and lifestyles, especially from environmental groups. Typical comments included:

> I'm worried about increasing government control. Our lifestyle is in danger.
>
> Ferrets give the environmentalists a way to get in and try to take over.
>
> I don't mind the ferrets coming back, but it's all the restrictions that come with it.

These findings demonstrate the concern of local ranchers toward loss of control over public and especially private lands in Phillips County, and they demonstrate ranchers' distrust of people, agencies, and ideas from outside the region.

A step-wise regression of the variation in opposition to ferret reintroduction by all respondents led to the inclusion of six individual attitude questions in a multiple regression model (Table 5). This model was highly significant ($f = 57.72, p < 0.001$, adjusted $r^2 = 0.325$), and it suggests that lack of support for reintroduction

Table 3. Local ranchers' attitudes toward black-footed ferrets and prairie dogs.

Question	*Strongly or Moderately Agree/Care/Favor*	*Neither Agree/Disagree Care/Not Care Favor/Oppose*	*Strongly or Moderately Disagree/Not Care/Oppose*
How much do you care about black-footed ferrets?	0	24	76
It would be a real thrill to see a black-footed ferret in the wild.	6%	45%	49%
If black-footed ferrets were introduced into Phillips County, Montana, I would probably make trip to seem them.	3	25	72
Black-footed ferrets should be conserved because they have a right to exist.	28	44	28
Prairie dogs are pests.	100	0	0
How much do you care about prairie dogs?	9	3	88
Ranchers should accept losses due to prairie dogs as a part of the costs of raising cattle on public lands.	3	6	91
How much do you favor or oppose using poisons to control prairie dog numbers?	97	0	3

Table 4. Responses of local ranchers toward selected libertarian questions.

Question	*Strongly or Moderately Agree*	*Neither Agree Nor Disagree*	*Strong or Moderately Disagree*
I would be more supportive of endangered species if they did not restrict what you can do on private land.	79%	15%	6%
I am concerned that the reintroduction of black-footed ferrets would limit application of fertilizers.	52	25	13
I am concerned that the proposed reintroduction of black-footed ferrets would restrict hunting.	77	13	10
I believe that if black-footed ferrets are reintroduced, environmentalists will use them as an excuse to restrict ranching.	97	3	0
The rancher who leases grazing land should be allowed full control over its management.	50	22	28
The main reason the federal agencies want to reintroduce the black-footed ferret is to gain more control over grazing.	56	25	19
Ranchers exert too much influence on the management of public lands.	3	12	85

stems most of all from (1) low affinity for black-footed ferrets, (2) strong dislike for prairie dogs, and (3) presumptions about restrictions to hunting, mineral extraction, grazing, and access to public lands associated with black-footed ferret reintroduction.

The fears and concerns of local ranchers were also expressed in results derived from the attitudinal scales developed from the mail survey questions. Local ranchers were at the extremes of each of the six attitude scales. They had the highest mean scores on the negativistic, libertarian/dominionistic, and utilitarian scales and the lowest scores on the moralistic, humanistic, and naturalistic/ecologistic scales (Fig. 1). These results reveal a clear pattern of rancher hostility toward black-footed ferrets and prairie dogs, and an associated view of these animals as having little ecological or ethical value. Scale scores of all other sample groups differed significantly from local ranchers, except for Phillips County residents on the moralistic scale and ranchers statewide on all but the negativistic scale (Table 6).

Table 5. Questions incorporated in a regression model explaining the variation in opposition to black-footed ferret reintroduction.

Question	*Cumulative R^2*
How much do you care about Black-footed ferrets?	0.240
I am concerned that releasing black-footed ferrets would prevent oil, gas, and mineral exploration in the area.	0.294
I am concerned that the proposed reintroduction of black-footed ferrets would restrict hunting.	0.310
Prairie dogs significantly reduce the number of cattle that can be raised on a plot of land.	0.322
Ranchers exert too much influence on the management of public lands.	0.328
Prairie dogs are pests.	0.331

$F = 57.723$, $p < 0.001$, *adjusted* $R^2 = 0.325$.

Of the groups sampled, local ranchers displayed the greatest hostility toward black-footed ferrets and prairie dogs and the strongest interest in individual rights and freedoms and in the subordination and control of wildlife and wildlife habitat (Table 6; Fig. 1). The mean score for the negativistic attitude scale among local ranchers (64.2) was over 33% greater than ranchers statewide, the next closest scoring group, and over eight times higher than the negativistic scores of conservation organization members other than Montana Wildlife Federation members (7.9). Differences between local ranchers and other sample groups were almost as great as on the libertarian/dominionistic and utilitarian attitude scales.

Similar results were revealed on the moralistic, humanistic, and naturalistic/ecologistic attitude scales, with local ranchers scoring lowest of all the sample groups (Fig. 1; Table 6). Local ranchers had a score of 4.2 on the humanistic scale, over 12 times lower than the highest scoring group—members of conservation organizations not including the Montana Wildlife Federation. A similar pattern of results occurred on the moralistic and naturalistic/ecologistic attitude scales. Members of wildlife and conservation organizations, therefore, revealed the greatest concern for the protection, recreational value, and ecological and ethical worth of black-footed ferrets and prairie dogs. Attitudes of local ranchers were most similar to those of ranchers statewide, followed by those of residents of Phillips County, and were most dissimilar from those of residents of Billings and members of conservation organizations.

Attitudes toward the proposed black-footed ferret reintroduction among the different groups closely paralleled the attitude scale results (Table 3). Sample groups most hostile to black-footed ferrets and prairie dogs (those scoring highest on the negativistic, libertarian/dominionistic, and utilitarian attitude scales) were the most antagonistic towards the proposed reintroduction.

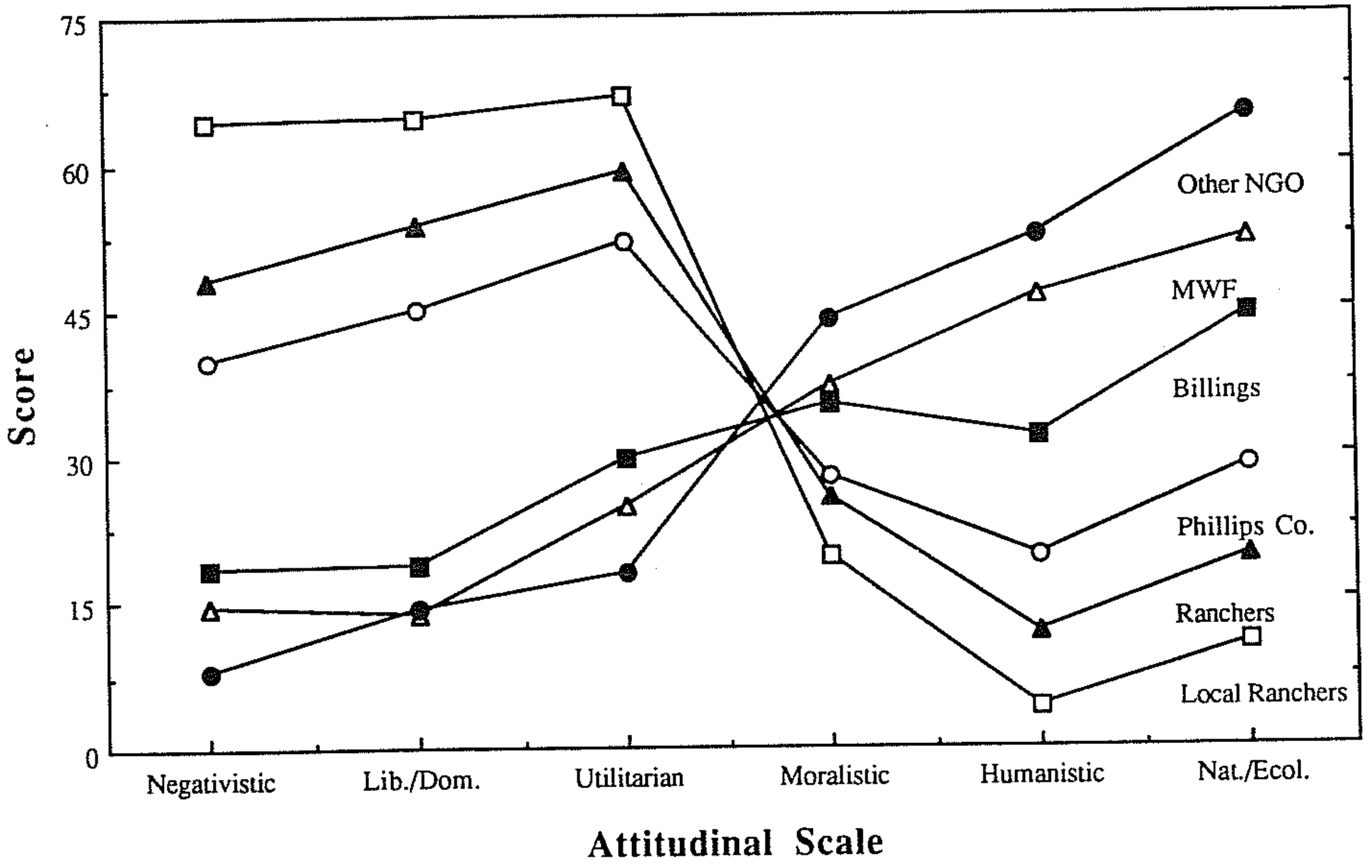

Figure 1. Mean attitude scale scores of the six sample groups.

In marked contrast, groups with sympathetic attitudes toward these animals (those scoring highest on the moralistic, humanistic, and naturalistic/ecologistic attitude scales) were the most supportive of ferret reintroduction. The group order of antagonism/support for reintroduction was identical to that displayed on most of the attitude scales (Table 3; Fig. 1).

These results also illustrate important differences between rural and urban attitudes. Attitude scale scores of Billings residents, the largest city in Montana, differed significantly from residents of Phillips County, a rural county with a population density of less than 0.4/km^2, on all but the humanistic scale (Table 6; Fig. 1).

Differences in scores on the knowledge scale were less striking and consistent (Fig. 2; Table 7). While significant differences occurred among sample groups with respect to knowledge of the black-footed ferret, prairie dog knowledge scores were surprisingly similar. Local ranchers obtained significantly higher scores on black-footed ferret knowledge than all other groups, with the exception of members of conservation organizations other than the Montana Wildlife Federation. No group had significantly higher scores on prairie dog knowledge, as less than five percentage points separated them all.

Perceived knowledge results are indicated in Table 8.

Table 6. Comparison of mean attitude scale scores among sample groups.

	Scale					
Group	*Negativistic*	*Libertarian/ Dominístic*	*Utilitarian*	*Moralistic*	*Humanistic*	*Naturalistic/ Ecologistic*
Local Ranchers	64.18	64.56†	66.83†	19.44†	4.23†	10.71†
Ranchers	47.95ς	53.52†	59.08†ς	25.61†	11.95†	19.64†
Phillips Co.	39.80ς	45.08	52.03ς	27.70†	19.61	28.79
Billings	18.46•	18.79•	29.72●	35.13●	31.82	44.53●
Montana Wildlife Federation	14.48•	13.83•	24.80•●	37.21•●	46.35•	52.15•●
Other NGOs	7.94•	14.40•	17.86•	43.92•	52.54•	64.85•

Scores in the same column with the same symbol are not significantly different (p < *0.05) using Tukey's Studentized Range (HSD) Test.*

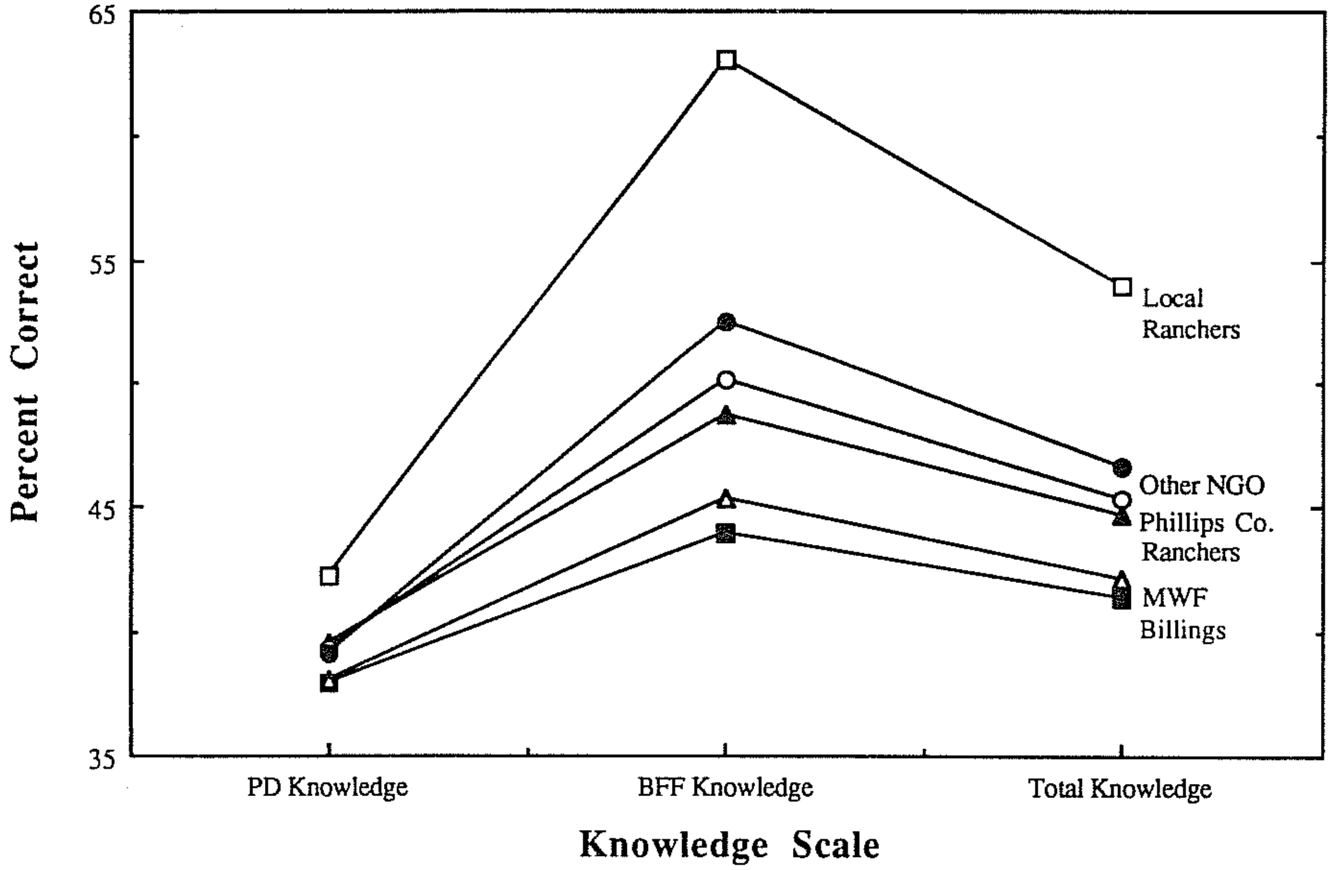

Figure 2. Mean knowledge scale scores of the six sample groups.

With the exception of Billings residents, the groups sampled had similar perceptions about their knowledge of black-footed ferrets. Local ranchers did not recognize their greater knowledge of ferrets. The situation was quite different with respect to knowledge of prairie dogs. Sixty-two percent of Phillips County residents, 61% of statewide ranchers, and 88% of local ranchers perceived themselves as knowing a great deal about prairie dogs, although none of these groups actually had significantly different scores on prairie dog knowledge (Table 8; Fig. 2).

Table 9 indicates where people believe they obtained information about black-footed ferrets and prairie dogs. A majority of all groups asserted that they had obtained information about prairie dogs from personal experience. This was particularly true for ranchers. Other important sources of information included books and articles, newspapers, and, to a lesser extent, friends, relatives, and television. In addition, a large percentage of Phillips county residents, including local ranchers, acknowledged receiving information from the Bureau of Land Management.

Table 7. Comparison mean knowledge scale scores among sample groups.

	Scale		
Group	*Prairie Dog*	*Ferret*	*Total*
Local Ranchers	42.23	63.02†	53.98†
Ranchers	39.52	48.70ς•	44.71ς•
Phillips Co.	39.27	50.06•	45.37•
Billings	37.86	43.98ς●	41.32ς●
Montana Wildlife Federation	37.97	45.35•●	42.14•●
Other NGOs	39.05	52.43†•	46.61†•

Scores in the same column with the same symbol are not significantly different ($p < 0.05$) *using Tukey's Studentized Range (HSD) Test.*

Personal experience was not an important source of information concerning black-footed ferrets for most people. Books and articles, newspapers, and, to a lesser extent, friends, relatives, and television were important (Table 9). Again, many Phillips County residents, especially local ranchers, reported receiving information from the Bureau of Land Management.

Data from informal meetings and interviews supported these findings. Typical quotes include:

> I'm not sure we ever had ferrets, I've been living here all my life and I've never seen one.
>
> I don't believe the results of those studies [prairie dog-cattle experiments] over in South Dakota. Sure my cows prefer to graze on [prairie dog] towns, but they have to leave them to fill up.
>
> You've been out on those [prairie dog] towns, you know

Table 8. Perceived knowledge about black-footed ferrets and prairie dogs.

Question *Sample Group*	*Know Little (1 & 2)*	*Medium Knowledge (3)*	*Know A Lot (4 & 5)*	*n*
On a scale of 1 to 5, how much do you know about black-footed ferrets?				
Local Ranchers	46%	35%	19%	26
Statewide Ranchers	57	26	16	124
Phillips County Residents	59	21	20	224
Billings Residents	69	20	11	191
Montana Wildlife Federation Members	65	17	18	63
Other NGO Members	52	25	23	60
On a scale of 1 to 5, how much do you know about prairie dogs?				
Local Ranchers	0%	12%	88%	26
Statewide Ranchers	21	18	61	124
Phillips County Residents	21	17	62	224
Billings Residents	38	35	27	190
Montana Wildlife Federation Members	44	25	30	63
Other NGO Members	28	43	28	60

Note: Some rows' percentages do not add to 100 due to rounding.

> how devastating they [prairie dogs] can be. I don't care what those studies say. It's just different here.

Discussion

Sociological factors must be considered as a means of increasing the likelihood of successful species reintroduction programs. Of particular importance are public attitudes, especially the attitudes of those most likely to be affected by the reintroduction programs. Attitudinal data is useful for ranking the suitability of reintroduction sites, for devising socially acceptable policies, and for developing more effective public relations campaigns (Cutlip & Center 1964; Arthur et al. 1977).

In this study, local residents, especially ranchers, were found to be especially antagonistic toward prairie dogs, black-footed ferrets, and the proposed reintroduction of black-footed ferrets into Phillips County, Montana. The attitudes present a significant challenge to the reintroduction program. Local ranchers are most antagonistic toward prairie dogs, which they perceive as competitors with livestock for forage, despite recent research that questions the extent of such competition and the economic justifications of prairie dog control (O'Meilia et al. 1982; Collins et al. 1984; Uresk & Paulson 1989). Because black-footed ferrets are known to survive only on prairie dog colonies (Clark 1989), the necessity of maintaining prairie dogs as black-footed ferret prey is a main issue preventing more favorable attitudes toward black-footed ferret reintroduction.

Local ranchers also fear that a black-footed ferret reintroduction would restrict ranching and farming oper-

Table 9. Sources of information about black-footed ferrets and prairie dogs.

Question *Sample Group*	*Personal Experience*	*T.V.*	*Books & Articles*	*Newspapers*	*Friends & Relatives*	*BLM*
From where do you get most of your information about prairie dogs?						
Local Ranchers	85%	15%	35%	27%	31%	31%
Statewide Ranchers	70	7	34	18	23	5
Phillips County	66	12	31	28	38	21
Billings	54	19	24	32	15	3
Montana Wildlife Federation Members	59	11	41	22	13	3
Other NGO Members	51	21	60	33	14	8
From where do you get most of your information about black-footed ferrets?						
Local Ranchers	4%	12%	27%	35%	15%	58%
Statewide Ranchers	13	13	8	38	14	9
Phillips County	12	20	32	44	25	22
Billings	9	34	25	55	9	1
Montana Wildlife Federation Members	11	19	49	38	8	3
Other NGO Members	11	24	67	48	6	5

Note: More than 1 answer was possible, so rows add to over 100%.

ations, result in a loss of control over grazing lands, and affect their rural, western lifestyle. These concerns certainly have some justification. In recent years, western livestock producers have witnessed a gradual erosion of power over public grazing lands that they traditionally controlled and increasing regulation of farming and ranching practices (Culhane 1981; Clark & McCool 1985). Reintroduction of an endangered species represents an additional threat to the ranchers' traditional power and prerogatives, and fear and resistance to change are common among individuals living in rural, western livestock areas (Carlson et al. 1981).

Other studies of rural residents dependent upon natural resource extraction—such as farmers, ranchers, fishers, miners, and loggers—have revealed similar results (Bath 1989; Kellert 1990, 1992). People employed in such natural resource extraction industries are typically very conservative and libertarian in their views toward government control, and inclined to assert a strong attitude toward the mastery and utilitarian exploitation of wildlife. They are also often the most affected by wildlife conservation, especially endangered species restoration programs. Not surprisingly, these views often collectively result in antagonism toward endangered species programs among resource-dependent groups. Addressing local opposition, especially among such groups, is one of the greatest challenges facing the field of conservation biology.

Decreasing opposition and developing a supportive public are clearly desirable objectives. Traditional education programs, however, are often inadequate because of a tendency to stress simplistically the provision of additional information and knowledge about a species and recovery program as a presumed basis for altering traditional values and attitudes. Although public relations and education programs have been successful in developing support for some reintroduction programs (see Kleiman et al. 1990), they are rarely successful at changing attitudes and values, especially if they are strongly held (Rokeach 1979; Chaiken & Stangor 1987). As the data on prairie dogs suggest, personal experiences and the perceptions drawn from them may be the most important factors influencing attitudes (Cutlip & Center 1964; Tessler & Shaffer 1990). If people perceive themselves as possessing knowledge of an issue, it is typically difficult to change their attitudes or convince them of information with which they do not agree, especially if their knowledge is derived from personal experience (Chaiken & Stangor 1987; Tessler & Shaffer 1990). Indeed, the local ranchers in this study were contacted extensively and educated about ferrets and the ferret recovery program, and although they received the highest scores on ferret knowledge of all sample groups, they were the most antagonistic toward the proposed reintroduction. Similar results have been obtained in other studies of wildlife and endangered species (see Arthur et al. 1977; Kellert 1986, 1990).

These results highlight the difference between knowledge and attitudes. The implications for public relations programs are significant: simply providing more facts and information will not necessarily result in more supportive public attitudes because knowledge is only one of several factors influencing attitudes (Rokeach 1972; Sinden & Worrell 1979; Brown & Manfredo 1987; Kellert 1992). Education programs may be important for people with low knowledge and poorly developed attitudes and values, but for people with strongly held attitudes and values, effective public relation programs require more than simply education.

Public relations programs should seek (1) to change or neutralize opposition, (2) to develop support among uninformed or undecided individuals, and (3) to conserve and strengthen supporters (Cutlip & Center 1964; Anonymous 1991). Cutlip and Center (1964) suggest three basic methods for accomplishing these goals: pressure, purchase, and persuasion. Ideally, all three methods should be employed in a coordinated, carefully planned public relations program. First, power and authority, in the form of law enforcement, control over access to and use of resources, and penalties can be used to apply pressure. The prohibitive aspects of the Endangered Species Act represent a potentially powerful use of authority, but they should be very carefully and cautiously applied.

To be truly successful, public relations programs will require carrots as well as sticks. Programs should attempt to entice or purchase support using financial or other incentives. For example, Miller et al. (1990) suggest redirecting federal dollars from prairie dog control operations to black-footed ferret and prairie dog conservation efforts in the forms of incentives, compensation, or conservation easements.

Finally, public relations programs should seek to persuade people to support species reintroduction, or at least not actively oppose it. Receptivity to persuasion depends on several factors, including social setting, relevance, style of presentation, number of independent sources of information, direct experience, and the strength, salience, clarity and source of the message (Chaiken & Stangor 1987; Tessler & Shaffer 1990). Using people with similar cultural and socioeconomic characteristics to convey the message can often help. Phillips County ranchers may be more receptive to information presented by ranchers from other reintroduction sites. Public relations programs should also research the most effective methods of conveying information. For example, the results of this study suggest that newspapers, books, and articles, and, to a lesser extent, television and certain federal and state agencies may provide the best venues for a public relations program.

Persuasive messages should provide information, but they should also stress the possible benefits of reintroduction as well as the program's responsiveness to the needs, desires, and opinions of the local public. The latter requires an expanded public relations program that researches and addresses the values, attitudes, behaviors, and desires of the local community. Such programs are rare, although endangered species recovery programs will rarely succeed if they do not actively consider and incorporate those views that are the basis for local support.

Acknowledgments

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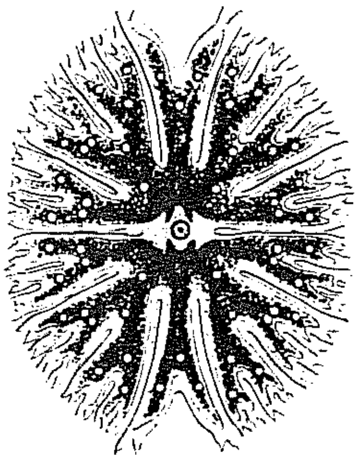

Black-footed ferret (*Mustela nigripes*): Conservation update

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Brian J. MILLER[5], Dean E. BIGGINS[6], and Paul E. MARINARI[3]

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INTRODUCTION

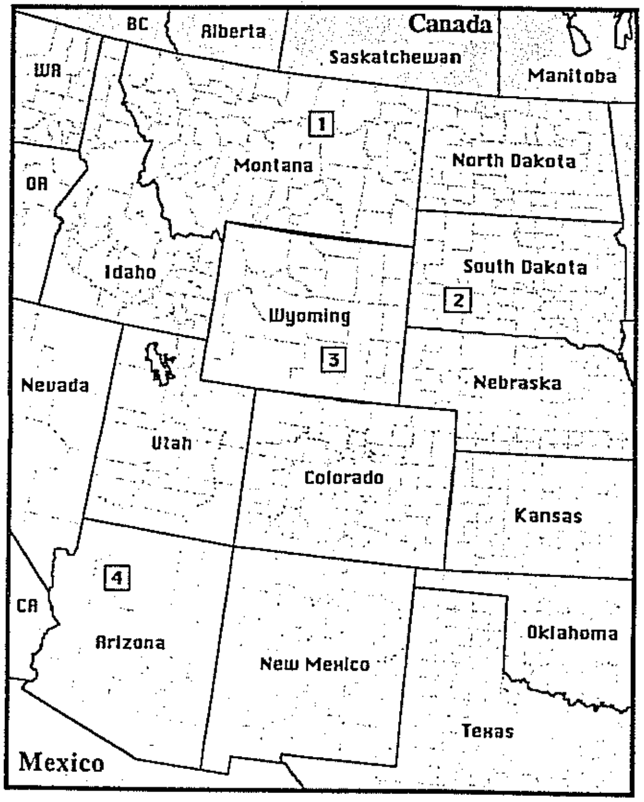
Black-footed ferrets (*Mustela nigripes*) remain one of the world's most endagered mammals despite recent advances and 15 years of conservation efforts. No wild population is known, although a captive propagation program initiated in 1987 has succeeded in greatly increasing the number of captive animals and ferrets have been reintroduced into four sites within their former range (Fig. 1). From October 1995 to March 1996, the black-footed ferret recovery program is being reorganized and the 1988 Recovery Plan (U.S. Fish & Wildlife Service, 1988) will be revised. We briefly review the history of ferret decline and early recovery efforts, discuss recent successes and failures, and conclude with discussion of future recovery challenges.

A BRIEF HISTORY OF FERRET DECLINE AND EARLY RECOVERY EFFORTS

Black-footed ferrets are obligate associates of prairie dogs (*Cynomys* spp.), upon which they depend for food and in whose burrows they find shelter (Forrest *et al.*, 1985). Ferret decline began as prairie dog numbers and distribution declined throughout the short and mid-grass prairies of North America due to large-scale conversion to agriculture, prairie dog eradication, and the effects of the exotic disease plague (*Yersinia pestis*)(Miller *et al.*, 1990). Prairie dogs are largely perceived as competitors with domestic livestock for forage by livestock interests despite several range studies which question the extent of competition (O'Meilia *et al.*, 1984; Uresk & Paulson, 1989; Archer *et al.*, 1987), economic analyses that indicate that eradication programs are not cost effective (Collins *et al.*, 1984), and ecological research that illustrates the importance of prairie dogs as ecosystem regulators (Krueger, 1988; Whicker & Detling, 1988; Reading *et al.*, 1989). Prairie dog poisoning programs, some government sponsored, and prairie conversion to cultivation continue today. These factors, combined with plague, have created a highly fragmented distribution of relatively small complexes of prairie dogs covering less than 2% of their former range (Miller *et al.*, 1994a, 1996; Roemer & Forrest, 1996). With the loss of their habitat, ferret populations became small and fragmented, and began disappearing from a variety of deterministic and stochastic factors (Thorne & Williams, 1988; Harris *et al.*, 1989).

After a small ferret population disappeared from South Dakota in the 1970s, the species was feared extinct until a population was discovered near Meeteetse, Wyoming in 1981. This population was studied until 1985, when both plague and canine distemper devastated the population to near extinction (Thorne & Williams, 1988; Clark, 1994). Biologists captured 18 ferrets, many closely related, just prior to extinction of the wild population, and a captive breeding program was initiated (Miller *et al.*, 1988). Captive propagation succeeded in increasing ferret numbers, and today over 350 individuals are distributed among seven facilities in the United States and Canada. The Black-footed Ferret Recovery Plan, drafted after the Meeteetse population crash, calls for establishing at least 10 separate populations of 30 or more over-wintering adults with a minimum of 1,500 total individuals (US Fish & Wildlife Service, 1988).

Figure 1. Black-Footed Ferret Reintroduction Sites. 1. South Phillips County, Montana; 2. Conala Basin, South Dakota; 3. Shirley Basin, Wyoming; and 4. Aubrey Valley, Arizona.



Reintroduction of ferrets bred in captivity began in 1991 with release of young of the year into Shirley Basin, Wyoming. Reintroduction has since expanded to other sites in Montana, South Dakota, and Arizona, and several animals have survived to reproduce. Despite progress, ferrets remain far from recovered and the program has been plagued by unproductive conflict (May, 1986; Weinberg, 1986; Clark & Harvey, 1988; Clark & Westrumn, 1987; Clark, in press; Alvarez, 1993; Reading & Miller, 1994; Miller *et al.*, 1996). Many biological and non-biological challenges remain (see Clark, 1989, in press; Seal *et al.*, 1989; Miller *et al.*, 1996; Reading & Clark, 1996).

RECENT DEVELOPMENTS IN FERRET RECOVERY

CAPTIVE BREEDING

After a relatively slow start in mid-1980s, the captive population began to increase in late 1980s and early 1990s before leveling of (Fig. 2). As the captive population grew, it was eventually split. About half the animals remain in the recently named National Black-footed Ferret Conservation Center at Sybille, Wyoming, but by 1992, ferrets were also being maintained and bred in the Omaha Zoo, Nebraska; the National Zoo's breeding facility at Front Royal, Virginia; the Toronto Zoo, Ontario; the Phoenix Zoo, Arizona; the Louisville Zoo, Kentucky; and the Cheyenne Mountain Zoo, in Colorado Springs, Colorado. Although the population has been stabilized, productivity has varied, especially in recent years (Figs. 2 & 3).

From the original wild caught animals, only 7 were represented in the breeding pool. Initial genetic analyses recommended maintaining 200 adults in the captive breeding program to maintain 80% of the genetic diversity of founders over 200 years (Ballou & Oakleaf, 1989), but this was later increased to 240. Ferrets produced in excess of those needed to replace loss of captive animals were available for reintroduction (Godbey & Biggins, 1994). Emphasis was placed on genetic management of the captive population because of the comparative ease of managing its genetics relative to wild populations (Russell *et al.*, 1994), and because mortality of reintroduced animals was expected to be high. Therefore, only genetically "surplus" animals (i.e. high inbreeding coefficients and high representation in the captive population) were chosen for release in the wild. Genetic studies to determine relatedness of "founders" were called for and funding was provided (Captive Breeding Specialist Group Meeting Minutes, 12 December 1985), but these studies have not been conducted and ferret lineages remain estimates based on the locations of animals captured from the wild. In addition, three ferrets of disputed paternity entered the breeding population in 1989. As a result, genetic management has been compromised.

Although the captive breeding program has produced many kits, the full effects of inbreeding may express themselves at anytime in the future. In 1993, low fertility, high loss of post-natal kits, and other factors prevented proposed reintroductions in Montana and South Dakota. Genetic relationships should be investigated as soon as possible.

Ferret reproduction was quite successful in 1996. From the 316 kits born and 234 which survived to weaning, approximately 125 were allocated for reintroduction into the three active release sites (Montana, South Dakota, and Arizona, see below). The captive breeding program retained 106 kits (the most genetically valuable) to maintain adequate numbers of ferrets. An increasing proportion of older animals in the captive population is creating problems of space within captive facilities. Several of these older animals are being provided to zoos as display animals, and by late 1996, 11 zoos maintained ferrets as display animals.

Figure 2. Black-Footed Ferret Captive Propagation.

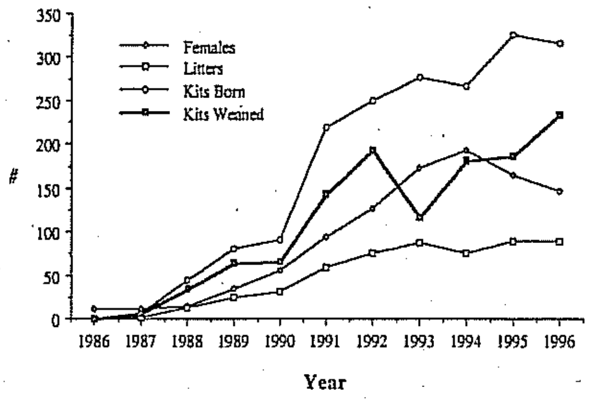
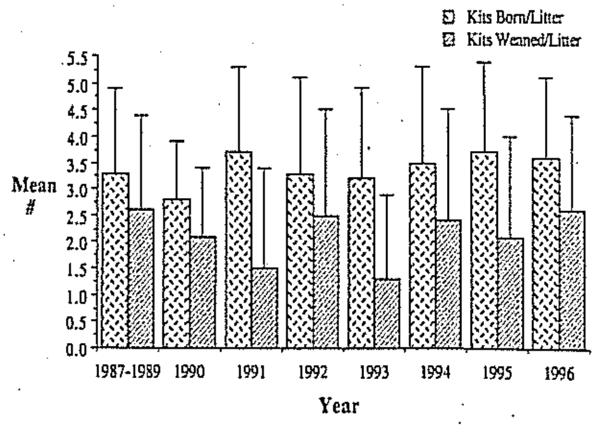


Figure 3. Mean (±S.D.) Black-Footed Ferret Kits Born and Weaned Per Litter.

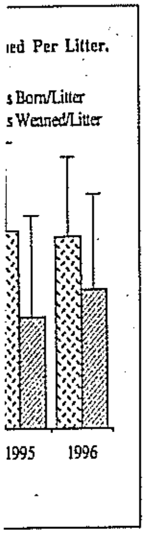


A variety of research on captive animals has contributed substantially to ferret recovery. Studies directed at increasing reproduction rates of captive ferrets examined reproductive physiology (Seal *et al.*, 1989; Carvalho *et al.*, 1991; Williams *et al.*, 1991,1992a), artificial insemination (Howard *et al.*, 1991, 1996), reproductive behavior (Miller, 1988; Miller *et al.*, 1996), development biology (Vargas, 1994; Miller *et al.*, 1996; Vargas & Anderson, 1996a, 1996b), captive management (Miller *et al.*, 1991), and disease prevention protocols, including the development of vaccinations (Williams *et al.*, 1992b; Williams *et al.*, in press). Additional studies on black-footed ferrets and closely related Siberian polecats (*M. eversmanni*) examined methods of increasing post-release survival. Studies included raising animals in enriched environments and in arenas with resident prairie dogs to stimulate a more natural environment (Miller *et al.*, 1990a, 1990b, 1992; Biggins *et al.*, 1991, 1993a; Vargas, 1994), providing young with opportunities to kill prey (Miller *et al.*, 1990a, 1992; Vargas, 1994; Vargas & Anderson, 1996a), providing aversive stimuli in the presence of potential predators (Miller *et al.*, 1990b), and exploring the possibility of food imprinting (Vargas & Anderson, 1996b). These latter studies were conducted in collaboration with test reintroductions of Siberian polecats and actual reintroductions of black-footed ferrets to examine effects on survivorship.

REINTRODUCTION

Prior to reintroducing black-footed ferrets, biologists experimented with trial releases of Siberian polecats. Siberian polecats which had experience killing prey, which had less contact with people, and which were raised in arenas as opposed to cages were better predators and exhibited more developed predator avoidance behaviors (Biggins *et al.*, 1990, 1991, 1993a; Miller *et al.*, 1990a, 1990b, 1992, 1993). Similarly, more recent releases of black-footed ferrets found that animals raised in enriched environments and those with previous experience killed prey more effectively (Vargas, 1994). Only recently have these techniques been incorporated into reintroduction protocols (Miller *et al.*, 1996).

Other research focused on reintroduction sites. Research on prairie dogs examined colony dynamics and habitat preferences (Conway, 1989; Reading *et al.*, 1989; Reading, 1993). Other



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studies developed standardized monitoring and evaluation methods for complexes of prairie dog colonies (Biggins *et al.*, 1993b). Trial releases of Siberian polecats found greater survival in areas with smaller predator populations (Biggins *et al.*, 1991), and therefore populations of potential ferret predators were assessed and monitored (Reading, 1993). Both canine distemper and plague epidemics are potentially disastrous for ferrets, necessitating disease studies (Thorne & Williams, 1988; Williams, 1990; Williams *et al.*, 1992b, 1994, in press). Because carnivores such as coyotes (*Canis latrans*) can survive such epidemics, studies focused on sampling carnivores for disease (Williams, 1990).

Local support is crucial for conservation efforts. An evaluation of local values, attitudes, and concerns found that people were often antagonistic towards ferrets (Reading, 1993). This antagonism stemmed from the dependence of ferrets on prairie dogs, which many people view as pests that compete with livestock for forage, and from ferrets' endangered status, which elicited fears of loss of control over public grazing lands and restrictions on land uses under the Endangered Species Act (Reading & Kellert, 1993). Results of these and other studies permitted site ranking on a number of biological and social science criteria and development of proactive strategies to improve a site's suitability for ferret reintroduction.

Reintroduction began in 1991 with the release of 49 ferret kits (32 males, 17 females) into Shirley Basin, Wyoming. These animals were deemed excess to the captive population and were selected as the most genetically redundant animals from captivity. All animals were young of the year, released during autumn, when young ferrets would normally disperse from their natal prairie dog colonies. They were all held on the release site in raised cages for a minimum of 10 days to permit acclimation, given access to cages for several days post release, and provided with supplementary food (Wyoming Game & Fish Department, 1991). None had pre-release acclimation to the local environment.

Of the 49 ferrets, 37 were monitored by radio-telemetry for several months post-release, and then via occasional spotlighting and snow tracking (U.S. Fish & Wildlife Service, 1992). Release cages were used after release and about half of the ferrets moved relatively large distances (4-17 km) from the release site. Some ferrets killed prairie dogs and four survived the winter, with two producing litters. This progress was tempered by a lack of experimental design and the use of only one release technique (Miller *et al.*, 1996). This limited the ability of the program to develop improved techniques and increase success rates.

During the second release in 1992, 90 black-footed ferret kits (55 males, 35 females) were released into the same site. Controversy over the use of telemetry resulted in a study designed to test the effects of telemetry on ferret survival. Unfortunately, confounding variables prevented reliable evaluation of the results. In addition, 17 animals raised in outdoor arenas were compared with 73 cage-reared ferrets. Pre-conditioned arena animals dispersed less and survived significantly longer than cage-reared animals, with seven individuals from each group surviving the first month (Biggins *et al.*, 1993a; Vargas, 1994). Dispersal from the release site was extensive and mortality was high, with 26% of the released animals killed by predators within 18 days (Godbey & Biggins, 1994). A minimum of eight animals survived the winter and at least four litters were born the following summer, but animals were not individually identified.

A second site in Montana was biologically ready to receive ferrets in 1992, but political pressure at the state governors level delayed the release (Reading & Miller, 1994; Miller *et al.*, 1996). In 1993, all field preparations for a third release site in South Dakota were completed. However, because of a large decline in captive production, not enough ferrets were produced for either Montana or South Dakota that year. So Shirley Basin, Wyoming, was the only site to reintroduce animals. Forty-eight kits (29 males, 19 females) were released that autumn. By late 1993, Wyoming estimated 24 surviving ferrets, including 4 from the 1993 release, 9 born to animals released in 1992, 2 from the 1992 release, and 9 that were not captured (Luce *et al.*, 1994). By the summer of 1994, that number observed had dropped to 6 animals of unknown origin (none were captured). By October, about 10 individuals (including both adults and kits) were observed.

Black-footed ferrets were reintroduced into three sites in 1994. Forty-one (24.17 total; 24.13 kits and 0.4 adults) were released into Wyoming, an additional 36 (22.14 total; 20.12 kits and 2.2 adults) were released into the Conata Basin of South Dakota, and 40 (16.24 total; 13.22 kits and 3.2 adults) were released in south Phillips County, Montana. The fate of ferrets released in Wyoming is unknown. By early December, at least 8 ferrets (3.4.1 unknown) were still alive in South Dakota, of which 5 were pre-conditioned animals raised in outdoor arenas and 2 were cage-reared without pre-conditioning. By July 1995, at least 4 adults (0.3.1) had produced 5 kits in 2 litters. In Montana, at least 9 animals (3.6) survived the winter, producing a minimum of 5 kits in 3 litters. At least 5 of the 6 surviving females were pre-conditioned. The Montana reintroduction included the most rigorous study to date of release techniques. It found significantly higher short-term survival for pre-conditioned ferrets than for cage-reared animals ($P<0.001$: D. Biggings, unpubl. data). However, at least half of the ferrets (20) were killed by coyotes, and 11 of these were killed within 3 days after release. Telemetric data revealed that all ferrets were highly active the first few days following release, increasing their susceptibility to predators. An overall assessment of data from Montana and South dakota (1994) and Wyoming (1992,1993) showed a significant effect of pre-conditioning on short-term and long-term survival (Biggins *et al.*, in review).

A dramatically different reintroduction protocol was attempted in the spring of 1995 when South Dakota experimented with 2 releases of older 4- and 5-year-old animals. This experiment tested the potential contribution of adult reintroductions to the overall recovery effort. If successful, reintroduced animals would breed in the wild, while simultaneously freeing cage space in the captive breeding program for prime aged breeders (i.e. 1-3 year old). The first release consisted of 12 females reintroduced in April and the second release included 14 animals (12.2) reintroduced in June. Only the second group was monitored with telemetry and of those, 12 were found dead soon after release and the other 2 signals lost. Primary cause of death was predation by coyotes. Due to the high losses, further planned releases were canceled.

During 1994-95, plague decimated the complex of white-tailed prairie dog (*C. leucurus*) colonies in Shirley Basin, Wyoming. With a greatly depleted prey base, Wyoming Game & Fish Department decided not to release additional animals into the site that autumn. As a result, ferrets were only reintroduced into Montana and South Dakota in 1995. Thirty-three (18.15) ferrets were released in South Dakota that autumn. An additional 7 (6.1) animals were released in February to reduce over-winter mortality prior to breeding. Montana released 37 (23.14 total; 20.11 kits and 2.3 adults) animals. By late November/early December, at least 16 ferrets (4.7.5) survived in South Dakota, including 9 animals (3.6) reintroduced in 1995, 2 released (1.1) in 1994, 3 kits born in 1995, and 2 unidentified animals. Survivorship of animals known to be alive through December increased from 22% in 1994 to 30% in 1995. In Montana, both lethal control of coyotes and temporary electric fences were used to reduce ferret mortality during the first couple weeks after release. All ferrets were intensively monitored using radio telemetry for several weeks and then monitored periodically using spotlights. Thirty-day survivorship increased from 25.7% (9 of 35) in 1994 to 58% (18 of 31) in 1995. In December 1995, a minimum of 28 ferrets (15.13) survived on or near the release site in Montana, and by May, 1996, a minimum of 19 animals were identified in the area. Summer survey in 1996 located a minimum of 10 litters with at least 15, including litters from wild-born females.

Arizona became the recovery program's fourth reintroduction site when 4 male ferrets were released into large (980 m^2) fenced enclosures on a reintroduction site in Aubrey Valley, Coconina County in March, 1996. Thirty-five ferrets (15.20) were later released into the enclosures, including 12.17 four-year-old, 1.1 two-year-old, and 2.2 one-year-old animals. The 10 on-site enclosures were constructed to exclude terrestrial, but not avian ferret predators and each is sub-divided into 4 smaller pens. The state received an additional 15 kits in autumn 1996 and will compare survival and behaviors of kits with those of adults.

South Dakota reintroduced an additional 67 kits and 4 adults and Montana released an additional 43 kits in autum 1996. Concern for maximizing survivorship led the U.S. Fish & Wildlife Service to require pre-conditioning for as many ferrets as possible beginning in fall 1996. Although predator control activities in Montana increased short-term survival, long-term survival was not affected. Pre-release conditioning appears to be the most important factor influencing survival of reintroduced ferrets. Ferrets transferred at an early age to large, dirt filled pens, or born in such facilities, fare best.

PROGRAM ORGANIZATION AND MANAGEMENT

Organization and management of ferret recovery efforts has been the subject of intense research and analysis (May, 1986; Weinberg, 1986; Clark & Harvey, 1988; Clark, 1989, in press; Clark & Westrum, 1987; Thorne & Oakleaf, 1991; Alvarez, 1993; Godbey & Biggins, 1994; Reading & Miller, 1994; Miller *et al.*, 1994b, 1996). Despite broad recognition of many of the program's organizational problems, participants interpreted the underlying reasons for these problems differently. Until recently, little attention was given to addressing these organizational problems, despite many recommendations.

The U.S. Fish & Wildlife Service (hereafter Service) designated Wyoming Game & Fish department the lead agency for ferret recovery soon after discovery of the Meeteetse, Wyoming, population in 1981 (Clark, 1989, 1994). The state agency vigorously managed and controlled the program from 1981-1985, when the Service took the lead in what had become a large, complex, and multi-organizational program. The program has continued to grow as the number of captive facilities and reintroduction sites has grown. At the same time, Congressional allocations for endangered species recovery programs have declined in response to opposition from some sectors (although the general public apparently still strongly supports endangered species conservation).

After 15 years, and because of unresolved organizational problems, an increasingly national (even international) recovery program, and reduced funding, participants requested the Service to assume greater involvement in the ferret recovery program (Miller *et al.*, 1996). This, coupled with Wyoming's financial difficulties and lingering uncertainty of the Wyoming reintroductions, led to several changes in the management of the program by the Service beginning in 1995. In early 1995, the Service formed a committee of agency representatives to oversee ferret recovery efforts. In early 1996, the Service assumed direct responsibility for the captive breeding facility at Sybille, Wyoming. The Service renamed the facility the National Black-footed Ferret Conservation Center and assigned captive breeding and reintroduction specialists to assist a new part-time Recovery Coordinator. Recently, ferrets were allocated to reintroduction sites by the Service, which were required to have detailed proposals and protocols.

In 1995, the Service also contracted the American Zoo and Aquarium Association (AZA) to conduct a programmatic evaluation of the ferret recovery program. The AZA held a series of three Black-footed Ferret Analysis and Action Planning Meetings -on captive breeding, reintroduction and habitat conservation, and program administration and accountability -from late 1995 through early 1996. The working documents produced from these meetings are intended to help the Service improve the program, guide recovery efforts, and draft a recovery plan (Hutchins & Wiese, 1996). To improve coordination and management of recovery efforts, the Service began establishing a formal recovery implementation team in July 1996.

THE FUTURE OF FERRET CONSERVATION

Black-footed ferrets appear to be moving toward recovery, but a variety of challenges remain. Perhaps the largest biological obstacle to recovery is posed by disease epizootics, including canine distemper and plague. Ferrets are highly and fatally susceptible to canine distemper (Williams *et al.*, 1988). A temporary vaccine for canine distemper is now available and a vaccine for lifetime immunity is being researched. Perhaps of greater concern is plague. Until recently, ferrets were thought not to be susceptible to plague; however, the loss of several ferrets at two separate captive facilities has dramatically proven otherwise. In addition, prairie dogs continue to suffer marked declines across most of their range from this introduced, exotic disease and from other causes (e.g. poisoning and shooting). A plague epidemic halted reintroduction in Shirley Basin, Wyoming, after a 50+% decline in prairie dog numbers in one year. Another epidemic has been underway for 3+ years near the Montana reintroduction site, formerly the largest complex of prairie dogs in the United States. Although the rate of decline in Montana has been slower than in Wyoming, the cummulative decline has been similar and threatens that reintroduction. To hamper the spread of plague in Montana, prairie dog burrows were dusted with 2% permethrin dust to kill flea vectors in 1993 and in 1996. Plague epidemics periodically affect most known complexes of prairie dog colonies, with notable exceptions of South Dakota and perhaps Mexico, but it may eventually reach these areas as well. Therefore, combating plague probably poses the most significant biological challenge to the conservation of ferrets and the entire praigered species

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Captive breeding continues to produce kits for reintroduction, but continued inbreeding could lead to problems with fertility, survivorship, and deformities in the future. Unfortunately, options are limited by the extremely small number of founders; only five are represented currently. Resolving issues of relatedness by performing the requisite genetic studies might aid the situation. The recovery program should also develop contingency plans in case inbreeding depression begins to affect the captive population.

Several non-biological challenges also face ferret recovery. Antipathy for prairie dogs remains prevalent among some people, especially relevant groups such as ranchers and many employees of agriculture, wildlife, and public land management agencies (Miller *et al.*, 1990c, 1993; Reading, 1993; Reading *et al.*, in review). Inducing these people to support, or at least not to oppose, ferret and prairie dog conservation programs is crucial to long-term success. Similarly, several groups actively oppose endangered species conservation programs because of real and perceived restrictions associated with the U.S. Endangered Species Act (ESA). Anger and fears associated with several sensitive issues, including private property rights, states'rights versus federalism, and public land management, have produced a strong backlash against the ESA and individual recovery programs (Reading & Kellert, 1993; Reading *et al.*, in review). Successful, long-term conservation requires addressing these concerns effectively.

Organizational challenges to ferret recovery significantly affected program performance in the past and a number of issues remain to be solved. Among the most fundamental of these problems is an inability to "double-loop" learn (Clark, 1996), utilize the potential of high performance teams (Westrum, 1994), and to prototype effectively (Clark *et al.*, 1995). While some issues are being addressed in the current programmatic evaluation and re-organization effort, many important organizational challenges remain (e.g. an effective decision process, see Clark & Brunner, 1996). Several past problems had their origins in differing standpoints of participants -including personality, disciplinary, organizational, parochial, and epistemological biases. These are manifest individually and organizationally in different values sought, organizational cultures, operating philisophies, goals, and control issues over ferrets and other resources and have limited the rationality potentially available to the recovery program. Several of these variables remain unrecognized, undiscussed, or unchanged and must be successfully addressed to reduce further polemics, goal displacement, and unproductive conflict (Miller *et al.*, 1996; Clark, in press). This is especially true as the number of key factors and reintroduction sites increases, as the program increasingly relies on non-governmental sources of funding, and on other key contextual trends and conditions.

On a more positive note, the world's largest prairie dog complex in Chihuahua, Mexico, is being incorporated into a new protected area. Theoretically, this complex could support over 1,200 black-footed ferret families (Ceballos *et al.*, 1993). Currently, biologists from the Universidad Nacional Autonoma de México are assessing the site more fully and government officials from the U.S. and Mexico are preparing the necessary paperwork to permit future reintroductions. In addition, research during reintroductions and captive breeding continues to refine methods, improving chances for future success at lower costs. Finally, many dedicated professionals are commited to the recovery of this charismatic ambassador of the threatened prairie dog ecosystem, substantial progress has been made, and hopes remain high that wild, free-ranging populations of black-footed ferrets will once again roam the prairies of North America.

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Black-Tailed Prairie Dog Conservation: A New Approach for a 21st Century Challenge

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Abstract

*Black-tailed prairie dog (*Cynomys ludovicianus*) policy is highly contentious. We use the policy sciences to examine how prairie dog conservation became so controversial and suggest ways to increase the prospects for success. We begin by describing the context of prairie dog management — who is involved and how they interact. Stakeholders with diverse values, strategies, sources of power, goals, and demands conflict in their struggle to influence prairie dog management. This conflict stems from the diverse perspectives and interactions of those involved, including ranchers, conservationists, animal rights activists, agency personnel, prairie dog shooters, developers, and the general public. We next examine management and policy responses to the problem. The agencies have begun responding, but are largely offering a replay of old ideas, perspectives, and patterns of interaction that contributed to the decline of prairie dogs. The current mixed federal and state agency program is highly fragmented, and likely will meet with limited success. Progress has been plagued by a narrow focus on biological issues, agency inertia, powerful special interest political forces, and negative attitudes. To improve matters, we suggest keeping participation open and including all stakeholders. We further recommend using adaptive, interdisciplinary, and multi-method approaches. Using a "best practices" approach would capitalize and build on past successes. Only by improving conservation practices can we hope to restore the black-tailed prairie dog to levels that permit it to function as a keystone species across the Great Plains.*

Introduction

The ongoing conflict about black-tailed prairie dog (*Cynomys ludovicianus*) policy is one of the most contentious wildlife conservation issues in the United States. In 1999, the United States Fish and Wildlife Service (USFWS) designated the black-tailed prairie dog as a "candidate species" for listing under the Endangered Species Act (ESA). One journalist said "[S]ome worry that any effort to protect prairie dogs will ignite a range war between endangered species advocates and landowners." Broadly speaking, the overall goal of prairie dog management, and the assemblage of associated species (i.e. the prairie dog ecosystem), is to ensure the ecosystem's viability in well-distributed populations in ways that benefit from broad public support (Clark et al. 1989). Achieving this goal is proving very difficult in practice because "Today's West is at war over natural resources, with wildlife the refugees" (Frasier 1999:A8). How did this issue move to the top of controversies? In this paper we examine this and other questions and suggest ways to achieve prairie dog conservation in a more cooperative, practical way.

We begin by describing the context of prairie dog management — who is involved and how they are interacting. Next we examine management and policy responses to the problem. Finally, we offer recommendations to improve matters. We use the policy sciences in our analysis, which requires that we address both the content (e.g., biology) and procedures (e.g., human interaction) involved (Clark et al. 2001; Clark 2002). We have more than 35 years combined experience in prairie dog management. We seek to contribute constructively to prairie dog conservation, lessen the conflict involved in the current effort, and achieve a successful conclusion in the common interest.

Who is involved? What are their perspectives?

For decades prairie dog policy was characterized by stability. Soon after Europeans began settling the Great Plains to ranch and farm, the U.S. Government embarked on a campaign to eradicate prairie dogs. At that time, around 1900, biologists estimated that prairie dogs inhabited 41 million hectares (Mac et al. 1998). Prairie dogs were classified as agricultural pests. Near consensus existed among scientists (most employed by the United States Department of Agriculture), livestock ranchers, and other appointed and elected government officials that these rodents consumed as much as 50 to 75% of the forage available for cattle and must be diligently controlled (Division of the Biological Survey 1902; Merriam 1902; State of Colorado 1915; Jones 2000).

The prairie dog issue became salient because the situation changed; new players with a new set of demands gained power in the political arena. By 1960, prairie dog populations had dwindled to about 600,000 hectares — a reduction of more than 98%. The 1960s also brought a rise in citizen environmental consciousness with social movements devoted to reducing industrial pollution and saving declining species. The new science of conservation biology emerged and often conflicted with science serving industrial and agricultural constituencies. Though the U.S. had some early wildlife conservation laws on the books (e.g., the Lacey Act of 1900 protected some game animals and the Migratory Bird Treaty Act of 1918 regulated hunting of designated birds), the 1973 Endangered Species Act brought a sea change with sweeping protection for plant and animal species deemed endangered or threatened.

The contemporary prairie dog sociopolitical arena reflects a tension rooted in these shifts. In 1998 black-tailed prairie dogs covered only 280,000 to 320,000 hectares (Biodiversity Legal Foundation 1998; National Wildlife Federation 1998). The further decline of prairie dogs is no longer universally viewed as the success of science and technology to control an agricultural pest, but also as a failure to protect a species important to an entire ecosystem. The data and what they mean for policy are highly disputed among interested groups. The movie *Varmints* captures much of the conflicting views of people involved in contemporary prairie dog management (Hawes-Davis 1998). The complexity, and conflict, stems from the diverse perspectives of people now involved and the way they choose to interact with one another. Currently, many well-organized groups hold deeply-felt, but contradictory views on prairie dog management. To understand the issue requires that we know who is involved and why. Each participant has a unique vantage point, holds special interests, and often "defines" the problem in a narrow and incomplete manner that reflects these interests; thus each viewpoint proposes a different solution (Weiss 1989).

Ranchers

The agricultural industry generally wants prairie dogs eliminated or held at low numbers. Ranchers believe that prairie dogs reduce forage and crops available for their livestock and livelihood. More broadly, they feel a changing economy and culture threaten their traditional lifestyle. They also see that they are losing control over public and private grazing lands, particularly when species are protected under the Endangered Species Act. Ranchers' views of prairie dogs are an outgrowth of a worldview that promotes domination over nature, libertarianism, an endless frontier, and the control of nature for economic gain. Ranchers use their beliefs, the powerful symbol of the American cowboy, and their traditional influence over local politicians to support their interests.

Conservationists

These participants view prairie dogs as a native keystone species and demand their protection. They tend to be motivated to conserve and expand prairie dog populations because of their importance to prairie ecosystems. The root of this viewpoint lies in assumptions and philosophies associated with ecological and conservation thought, the right-to-existence for all organisms, and changing human relationships to the natural world (Kellert 1995). The myth challenges other popular and powerful myths that define quality of life in solely economic terms, instead arguing that society should balance some economic growth for a healthy environment. Powerful symbols include wilderness, endangered species, and charismatic animals. Proponents largely distrust and often vilify big business (e.g., corporate America) and natural resource extractors, including many, if not most, ranchers.

Animal rights activists

Animal rights activists want decreased human impact on the environment and desire an end to pain and suffering to prairie dogs caused by poisoning and other extermination methods. They support extending legal rights to animals that are now reserved for humans (Wise 2000), including prairie dogs. The views of animal rights activists can be traced to the urban animal welfare movement, and developed into a powerfully organized interest in the last few decades (Rudacille 1998). These stakeholders, often in conjunction with conservationists, demand increased involvement in wildlife and public land management and often use lawsuits, media publicity, and appeals to public pressure, including citizen ballot initiatives, to achieve their interests.

Agency personnel
Federal, state, local, and tribal agency personnel hold personal views that vary greatly, but can be quite similar within a single agency. Despite multiple use mandates, most agencies are strongly influenced by a more limited number of special interests (e.g., hunters, loggers, miners, or ranchers), and this influence is manifest in policies that often clash with the common interest (Meier 1993). In extreme cases, this leads to agency "capture" by a special interest group that the agency was created to manage or regulate (Clarke and McCool 1985). There are also struggles for power among the agencies (Fischer 2000). State, local, and tribal government personnel maintain an interest in maximizing power vis à vis the federal government, especially in the western U.S. Despite these differences, some broad generalizations among agencies are possible. Agency personnel generally embrace the "technical rationalist/expert" role (see Clark 1997). In this view, control of nature for human purposes is both possible and desirable, and professional resource managers should be entrusted with making decisions and manipulating nature. With respect to prairie dogs, formal agency policy at all levels resulted in substantial prairie dog declines over past decades. Today, most agencies seek to keep prairie dogs off the endangered species list, and often this goal appears to be more important than species conservation (e.g., see BLM 2000; EDAW 2000; NGPC 2001). In addition, an anti-prairie dog attitude remains strong among wildlife professionals and especially land managers, but this is changing (Reading 1993).

Recreational shooters
Recreational shooters form a small but vocal stakeholder group. They want prairie dogs to be abundant enough to serve as live targets for their shooting. Shooters view themselves as highly skilled agents of control for agricultural pests and identify with the agricultural community. They mostly embrace a libertarian view, one that is an offshoot of the frontier/cowboy worldview. Prairie dog shooters want free access to public lands for hunting with minimal government regulation, and they support continued shooting opportunities provided on many public lands and Indian reservations. They influence prairie dog management by actively promoting their interests and enlisting support of ranchers, gun rights activists, and local businesses that benefit from their pursuits.


Black-tailed prairie dog (*Cynomys ludovicianus*) by Richard P. Reading.

Developers
Developers play a restricted role in the prairie dog management debate, but they are key stakeholders along Colorado's Front Range, for example. Developers focus on generating wealth for themselves and view prairie dogs as pests that interfere with urban development. As housing tracks are put in, prairie dogs are killed or relocated. Developers are searching for inexpensive solutions to the prairie dog management challenge that will permit them to continue developing land (e.g., exterminate or move animals in the way of development).

General Public
The American public is diverse, and most citizens are unaware of the prairie dog conservation problem. However, public support for conserving wildlife is strong. For example, a survey by Czech and Krausman (1997) found 84% of the public support the current ESA or would like it strengthened. Some publics, such as homeowners living near urban prairie dog colonies, are a part of the development debate. Zinn and Andelt (2001) found that support for prairie dogs increased with the distance respondents lived from prairie dog colonies in the city of Fort Collins, Colorado. Alternatively, some of the most vocal supporters of prairie dogs in urban environments are people living near the colonies who like to watch the animals or recognize their ecological importance (Prairie Dog Coalition 2002). Fox-Parrish (2002) found that antagonism toward prairie dogs increased as their exposure to and experience with prairie dogs increased among the general public in rural Kansas. Many Native Americans with traditional cultural beliefs consider prairie dogs to be a species with which they are intimately interconnected. They demand that everyone can and should be more connected to nature, that all species are important, and that therefore the tribes are obligated to protect and restore native communities on reservation lands.

Prairie dogs
Black-tailed prairie dogs are participants in this issue too, as are a myriad of other associated species. Prairie

dogs are one-kilogram ground squirrels that live in colonies of strongly defended family groups, known as "coteries" (Hoogland 1995). One of five species of prairie dogs, the black-tailed form is the only species that inhabits the Great Plains, ranging over most of the short and mid-grass prairies from southern Canada to northern Mexico. Because they are colonial and live in burrows they excavate, and constantly clip tall vegetation, prairie dogs alter the grassland ecosystem's structure, processes, and composition (Kotliar et al. 1999). To ecologists, these changes indicate their importance as a "keystone species" that enriches ecosystem function in a unique and significant way disproportionate to their abundance (Miller et al. 2000). Their interest, to the extent their interest can be known, appears to be for continuation of their species and individual well-being. Miller and Reading (2002) list eight threats facing black-tailed prairie dogs: continued habitat destruction; uncontrolled recreational shooting; introduced diseases (especially plague); inadequate regulatory mechanisms by government agencies; continued and widespread poisoning; the inability of prairie dogs to respond evolutionarily to present threats; lack of adaptive management; and negative attitudes toward prairie dogs.

Right or wrong, humans will decide the prairie dogs' fate. The categories delineated above provide a general characterization of the players involved in prairie dog policy. Many participants fall into more than one category; much variance exists within categories. Intensity of belief and the degree to which individuals are willing to work with other groups vary as well. However, conflict and polarization largely typify interactions between groups in the prairie dog policy arena that have included lawsuits, arrests of activists at protests, and even threats of violence (Gutierrez 1998; Proskocil 1999; Fong 1999). While some debate can be constructive, unmanaged conflict can erode trust in government institutions and lead to policy failure.

Prairie dogs as a policy problem

Defining the prairie dog "problem" practically is a challenge. As Weiss (1989:97) noted, "problem definition is a package of ideas that includes, at least implicitly, an account of the cause and consequences of undesirable circumstances and a theory about how to improve them." Key questions include: "Just what is the problem?;" "How big is it?;" and "Who is it a problem for?;" as well as "What might be done about it?" Prairie dog conservation is about making choices, like "How will the prairie dog ecosystem be managed?" and "Who gets to decide?" In other words, it is largely a human value problem in decision-making, although many technical elements are involved. In fact, much of the behind-the-scenes politics is masked by technical discussions. The answers to the last two questions are determined by who has authority and, especially, control of the management process. Authority means having the right to make a decision, and control means having the power to carry out an action in the face of opposition.

Prairie dogs on the political agenda

Black-tailed prairie dogs made it onto the U.S. political agenda as a conservation issue in 1998 when several conservationists petitioned the USFWS to list the species as threatened under the ESA (National Wildlife Federation 1998; Biodiversity Legal Foundation et al. 1998). The USFWS had rejected an earlier petition filed by Biodiversity Legal Foundation and Sharps (1995).

Following the second petition, all participants positioned themselves either for or against the petition and utilized their resources to substantiate or refute its claim that prairie dogs were or were not in need of special help. In some cases, participants recognized that prairie dogs needed protection, but stated that they favored local control over federal listing as the best way to manage the species. Persuasion as well as coercion were used to influence the evolving definition of the prairie dog conservation "problem," shape a preferred "solution," and control the overall decision-making process to the maximum extent possible (see Clark 1997). Attention during this phase focused on the USFWS. Ranchers and government agencies, especially state agencies, largely opposed listing. The states, in particular, banded together to form an anti-listing coalition.

Caught between savvy conservationists, ranchers, and state governments, often backed by their representatives in the U.S. Congress, the USFWS took the most risk-averse path. The agency decided to designate the species as "warranted" for listing as threatened under ESA, but "precluded" it from listing because of other, higher priority species that needed attention first (USFWS 1999). The USFWS appeared reluctant to grant prairie dogs candidate species status, and so far has abdicated its responsibility to protect a species it accepts as meeting the requirements for ESA protection. The USFWS's 90-day and 12-month findings supported a definition of the problem as articulated in the petitions, that prairie dog populations had indeed declined by as much as 99% due to threats including habitat loss, plague, inadequacy of existing regulatory mechanisms, and long-term rodent control (USFWS 1999; USFWS 2000). This move sent shock waves through the Western cattle and real estate industries (Matthews 1999:8). The "warranted, but precluded," or candidate species, designation focused the controversy that had been brewing for years and fueled great activity by agricultural interests, government land and wildlife management agencies, nongovernmental conservation organizations, scientists, and others (e.g., Predator Conservation Alliance 2001; Thacker 2001; Prairie Dog Coalition 2002).

The agencies respond

In response to the candidate species designation, federal land management agencies made some prairie dog management changes. The U.S. Forest Service declared a temporary moratorium on poisoning prairie dogs within National Grasslands. The U.S. Bureau of Land Management also ceased poisoning prairie dogs on land it manages, and both agencies began more active prairie dog conservation, such as temporary shooting bans. The USFWS recommended including incentives for landowners in the 2002 farm bill to pay landowners for helping to conserve prairie dogs. But the USFWS basically turned prairie dog management over to the states that had lobbied for control of implementation, moving the states to center stage. A directive to them that "doing nothing" was not a policy option accompanied delegation of authority to the states. The USFWS retains oversight of states' efforts and reviews the status of candidate species each year.

The states have begun responding to the USFWS's "warranted, but precluded" ruling, but progress toward prairie dog conservation has been slow. The 11 states within the range of the black-tailed prairie dog formed the Interstate Black-tailed Prairie Dog Conservation Team and produced a conservation plan, the "Black-tailed Prairie Dog Conservation Assessment and Strategy" with subsequent draft addendums, to conserve the species and address factors causing its decline (Van Pelt 1999; Luce 2001a, 2002). The draft interstate plan's main goal appears to be to prevent listing prairie dogs under the ESA and the associated loss of control over management (Miller and Cully 2001). That goal arguably takes precedence over recovery of the species — a classic case of goal substitution driven by competition for power. Throughout the draft plans, recovery is never discussed as such; instead, the plans refer to prairie dog conservation with respect to precluding the need for listing under the ESA (Luce 2002).

The objectives of the draft interstate plan ". . . set an adaptive management strategy target to increase occupied acreage [of prairie dog colonies] to exceed 1% of historic range in the next 10 years (by 2011)," while stating that present acreage figures are "slightly less than 1% of historic (Luce 2002:13)." Thus, the plan is striving for a vague goal that is just marginally better than the status quo. In addition, the plan never clarifies how success or failure in adaptive management will be assessed, or how the plan will be adapted or terminated. The draft interstate plan goes on to call for conducting additional research and monitoring, identifying focal areas that contain high densities of prairie dogs, creating financial incentives for cooperating landowners who conserve prairie dogs, and increasing regulation of and oversight over prairie dog shooting and poisoning (Luce 2001c, 2002). The draft plan also permits unrestricted shooting and calls for providing money to cooperating landowners for poisoning, even if a state remains below its target objectives for prairie dog acreage.

After three years, the interstate plan remains in draft form, but all states are developing conservation plans and some states have begun taking action (Luce 2001b). For example, a few states have removed "pest" species designations from prairie dogs and others are working toward that end (Predator Conservation Alliance 2001). A number of state agencies have also started regulating prairie dog poisoning and shooting, which were formerly unlimited (Luce 2002). Arizona, Colorado, and South Dakota have already banned shooting for part or all of the year, primarily on public land (Luce 2002). In 2002, Colorado started a $600,000 pilot program that uses lottery money to provide financial incentives to landowners that conserve prairie dogs (Davis 2002). Other initiatives include developing education programs and exploring the use of regulatory amendments to the ESA to encourage participation by landowners, tribes, and state agencies, such as Candidate Conservation Agreements with Assurances.

Annual reviews by the USFWS and states claim the agencies are making adequate progress (USFWS 2001; Luce 2001b). Indeed, some progress has been realized at the federal and state level, but it has been slow to arrive. Conservation efforts thus far have been largely evaluated by the agencies themselves; a task ideally conducted by an external organization with no stake in the outcome (Kleiman et al. 2000). Montana, North Dakota, South Dakota, and Wyoming already claim that they exceed the target figures laid out in their individual state plans. (Luce 2002). Colorado and Wyoming suggest they already exceed the draft interstate plan's target figures (CDOW 2002; Luce 2002).

What the states have so far proposed and carried out is necessary for prairie dog conservation, but far from sufficient. Calls for more research, frequent meetings, and regular revising of the draft plan give the impression that the states are working toward conservation goals, but these activities are not substitutes for effective policy and real action. The draft interstate plan promotes traditional decision-making, without fully addressing how the states will reverse their lack of success in protecting the prairie dog ecosystem to date. Instead, the interstate plan, the perspectives behind it, and the interests it serves, offer a replay of old ideas and patterns of interaction that have for decades contributed to the decline of prairie dogs. As a result, current prairie dog conservation efforts are plagued by a narrow focus on biological issues, agency inertia, powerful special interest political forces, and negative human attitudes toward prairie dogs. In addition, agencies have dominated conservation planning, with little input from other important stakeholders.

One of the most significant deficiencies of the interstate and individual state plans are their failure to provide mechanisms for addressing the sociopolitical factors affecting prairie dog conservation policy. The plans fail to establish how the states will manage their political environments, such as powerful conservative governors, agricultural lobbies, urban and suburban developers, and conservation interest groups. For example, how will the interstate plan address the fact that politically powerful stakeholders (e.g., ranchers) hold strongly negative attitudes toward prairie dogs that leads them to continue fighting conservation initiatives and arguing for continued poisoning (e.g., see Reeder 2002). Both state and federal agencies have pitched simplistic solutions to this problem. For example, the agencies advocate landowner incentives as a primary tool to protect the species. While potentially helpful, incentives are insufficient, as they do little to address the underlying negative attitudes toward prairie dogs held by many stakeholders (Reading et al. 1999; Lamb et al. 2001; Fox-Parrish 2002). Ranchers are already resisting voluntary measures, even financial incentives that reward prairie dog protection on private land (Omaha-World Herald 2002). Indeed, an incentive program in Colorado was largely unsuccessful in finding ranchers willing to participate, possibly because they dislike prairie dogs for far more than financial reasons (e.g., prairie dogs are seen as symbols of poor land stewardship, a loss of control over public and private land, outsiders telling them what to do, and threats to their lifestyles; Reading and Kellert 1993; Reading et al. 1999). There is a also risk of non-compliance to new rules, especially poisoning and shooting restrictions that are difficult to monitor on huge swaths of private and public land.

Overall, the draft plan currently offers little that is new, creative, and helpful in maximizing cooperation among stakeholders. The plan offers no recognition of these complex and contentious sociopolitical variables and no methods to provide policy-relevant information about them. This is not surprising, given the traditional, biological focus of the training that most conservationists and wildlife and land managers receive (Clark 2001). However, the states ignore sociopolitical variables at their own peril.

Inattention to the relevant social context can lead to increased tension and ultimately policy failure. Problems exist that impede prairie dog conservation. Some states face hostile state legislatures and commissions. For example, in 2001 the Wyoming Game and Fish Commission voted to bar the state from endorsing the states' conservation plan. And recently, Wyoming joined North Dakota and Colorado in withdrawing from the official interstate effort, calling into question the new organization's ability to coordinate effective regional conservation. In addition, animal rights and conservation groups have sued to gain protection for prairie dogs resulting in resource intensive court battles for federal and state agencies (McCullen 2000).

Currently, the prairie dog program is on a fixed course and there seems to be no effort by either the federal or state agencies involved to seek out more effective management in the common interest. The program chosen is the most conservative and the closest to the status quo as possible. Moreover, it is failing to advance the common interest in ensuring the survival of prairie dogs and the viability of prairie dog ecosystems in ways that benefit from broad public support.

How can prairie dog conservation be improved?

The prairie dog conservation challenge is complex and contentious and it likely will not yield to more government bureaucracy. The practical problem at hand now is to decide what can be done to improve matters.

One of the biggest challenges is convincing the key participants that achieving broad public support for and realizing prairie dog conservation is in the common interest and in their own interest. For example, how will ranchers, who see prairie dogs and prairie dog conservation as threatening to their livelihood and lifestyle, ever tolerate prairie dog protection policies? Why should conservationists care if enacted policies receive broad support when for many the goal is conservation using science not public opinion as indicators, regardless of the level of coercion needed to achieve it? Opponents resistant to popular conservation proposals risk provoking more coercive regulations — such as ESA measures — which they despise. They also risk losing some popular support for agricultural programs that are increasingly contested by the conservation community. On the flip side, even strict prairie dog protection codified by the ESA is likely to fail without the political will needed to effectively implement and enforce enacted policies. It is the state and federal agencies, those formerly charged with eradicating prairie dogs that will have discretion over the application of prairie dog conservation measures.

We recommend building new cooperative relationships and expanding on successful practices to date — "practice-based" approaches. Practice-based conservation is adaptive management at its best. It involves finding and taking advantage of opportunities that exist or can be created to address problems. Practice-based conservation involves three steps, each of which requires on-going evaluation (Kleiman et al. 2000). First, participants identify the "best practices" being employed. Second, these are adapted and applied to similar circumstances elsewhere in the prairie dog's range. Finally, the most effective practices are diffused as widely as possible, where professionals continue to adapt, refine, and upgrade them relying on their own experience. Such adaptive management should be carried on endlessly. Thus, the prudent way for conservation to proceed is to find and continually upgrade performance in the light of experience (Clark and Brunner 1996). Independent evaluations of policies and practices are essential to prevent self-serving appraisals. "Watch dogging" the agencies and helping them to learn and upgrade their performance is necessary. We have chosen to highlight a few of what we consider "best practices," each of which could be improved through evaluation and refinement.

Outcome-driven initiatives

While the federal and state governments have not considered alternatives to the interstate prairie dog plan, some bottom-up approaches are worth considering. Several private individuals and organizations have initiated conservation projects for black-tailed prairie dogs in recent years. For example, several recently created land trusts focus on conserving wildlife and ecosystems. With respect to the prairie dog ecosystem, the Southern Plains Land Trust was founded in 1998 to capitalize on the relatively low price of land in and around southeastern Colorado. They focus on land inhabited by prairie dogs and located close to large blocks of public land. Their experience has much to offer others involved in prairie dog conservation. Similarly, other non-profit organizations, such as The Nature Conservancy, and for-profit organizations, such as Turner Enterprises, Inc., are purchasing land and working to restore prairie dogs and their associated species. They and their collaborators have taken an experimental approach to restoring the prairie dog ecosystem that promises to benefit similar restoration efforts throughout the range of prairie dogs (Truett et al. 2001).

Process-focused initiatives

Opening up a dialogue between traditional antagonistic stakeholders holds the promise of reducing unproductive conflict and stimulating discussions that can help dispel inaccurate myths and build bridges for conservation. Such dialogues must occur in "safe-harbor" situations, where people feel safe to come together and freely state their true opinions without resorting to rhetoric (i.e. opening "real" dialogue among stakeholders). For example, in 1999 the Denver Zoological Foundation and the Northern Rockies Conservation Cooperative held a daylong workshop at the Denver Zoo on prairie dog conservation. Participants included representatives from the Western Governor's Association; ranching, animal rights, environmental, and conservation organizations; and tribal, city, county, state, and federal government agencies. Many of these individuals and groups had never met in such a setting before. Although the workshop was a modest beginning, it succeeded in bringing together diverse interests, in sharing values, concerns, and strategies for addressing prairie dog management, and in opening a dialogue for future collaboration, coordination, or at least communication. Unfortunately, this process was discontinued, but it serves as a model that could be duplicated and expanded in the future.

Process/outcome initiatives

Montana was the first state to set up a prairie dog working group to seek appropriate conservation and management of prairie dogs within the state. The group recently put together a management plan (Montana Prairie Dog Working Group 1999), which involved state and federal agencies, tribal representatives, conservation organizations, and private interests and builds on the Montana Prairie Dog Management Guidelines developed in 1988 by the Montana Black-footed Ferret Working Group (1988). Focusing on both prairie dog species (black-tailed and white-tailed) that inhabit Montana, its goal is "for the state of Montana to provide for management of prairie dog populations and habitats to ensure long-term viability of prairie dogs and associated species." Five objectives follow and a strategy to meet each objective is outlined. Annual review is required. Although lacking in some areas, the plan is the product of a cooperative effort among diverse interests over several years and is arguably the best state plan currently addressing prairie dog management. More importantly, it provides a basis for upgrading conservation planning and implementation in the future.

Several other best practices should be identified, adapted, and spread among participants in prairie dog conservation efforts. Particularly important areas for analysis include federal agricultural policies (including both working to halt perverse agricultural subsidies that encourage prairie dog eradication and creating incentives for landowners that manage their properties for prairie dog conservation), initiatives on tribal lands, actions undertaken at the city and county levels, federal land management (including national grasslands, wildlife refuges, parks, and monuments, as well as lands managed by the BLM), and applied research, especially on managing introduced diseases. We suggest holding well-mediated, problem-oriented workshops on each of these issues to facilitate the process.

Finally, prairie dog conservation requires sound leadership at all levels. Leaders should strive for a strong, open, objective, fair, and competent leadership style. Westrum (1994) refers to such competent, dynamic leaders as "maestros." Maestro coordinators could greatly improve both social and decision processes in prairie dog conservation efforts by facilitating information flow, communication, coordination, efficient use of resources, the identification and dissemination of best practices, and more. Quality leadership at state levels is also required for similar reasons.

Conclusions

Black-tailed prairie dog populations have declined dramatically and become increasingly fragmented over the past century. That decline has important implications for the entire ecosystem because of the prairie dog's role as a keystone species. The USFWS recognized the plight of the prairie dog in 1999 by declaring the species warranted for listing under the ESA. However, the USFWS also precluded such listing, stating the need to focus on other, higher priority species. Prairie dog conservation is highly contentious, wherein stakeholders with diverse values, strategies, sources of power, goals, and demands conflict in their struggle to influence the prairie dog management process. The current mixed federal and state agency program is highly fragmented, especially among the federal and state governments. The current program likely will meet with limited success. We recommend a more innovative response.

We suggest that prairie dog conservation is more likely to succeed if participation remains open and includes the full range of stakeholders. This requires movement toward adaptive, interdisciplinary, and multi-method approaches. We provide recommendations for using a "best practices" approach that capitalizes and builds on activities that have already proven successful in prairie dog conservation. Using workshops and a more representative, open, and flexible organizational structure offers a better chance for resolving the conflict of values currently dominating prairie dog conservation and moving more quickly toward more effective and efficient practices that are acceptable to more stakeholders. Despite recent attention to the plight of the black-tailed prairie dog, the species continues to decline across most of its range. We must improve conservation practices if we hope to restore the black-tailed prairie dog to levels that permit it to function as a keystone species across the Great Plains.

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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, January 28-29, 2004

Edited by James E. Roelle, Brian J. Miller, Jerry L. Godbey, and Dean E. Biggins

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Shooting Prairie Dogs

By Archie F. Reeve[1,2] and Timothy C. Vosburgh[3]

Abstract

Recreational shooting of prairie dogs (*Cynomys* spp.) has occurred for many years, but interest and intensity have increased dramatically in the past decade. Shooting can cause prairie dogs to change their behavior and can affect sex and age groups differently. Prairie dog populations are capable of recovering from shooting or other reductions, but time to full recovery depends on demographic parameters (survivorship and fecundity). Simple population growth models with demographic variability demonstrate less risk of population extinction when shooting is regulated by effort rather than by quotas on numbers shot. Landowners might consider allowing shooting as a source of income, but, if not closely managed, shooters potentially can eliminate small colonies. Predation by black-footed ferrets (*Mustela nigripes*) probably does not significantly depress prairie dog populations. Prairie dog mortality caused by unregulated recreational shooting can vastly exceed predation by black-footed ferrets, affecting prairie dog survivorship and potentially affecting fecundity and recruitment. Until effects of shooting prairie dogs as prey for black-footed ferrets are better understood, shooting closures on reintroduction sites are appropriate.

Keywords: black-footed ferret, *Cynomys* spp., *Mustela nigripes*, prairie dog, recreational shooting

Introduction

Many long-time residents of western States recall spending summer vacations “plinking” prairie dogs (*Cynomys* spp.), whether by wrist rocket, air gun, or .22 caliber rifle. For over 100 years, shooting black-tailed prairie dogs (*C. ludovicianus*) in rural Kansas, for example, was common on Sunday afternoons by self-styled “varmint hunters” and by after-school target shooters (Smith, 1967). Shooting prairie dogs has been and continues to be primarily for sport but now involves marksmen who utilize high-technology rifles while practicing their shooting skills. To hone their skills, many shooters use a variety of rifles, scopes, range finders, shooting benches, and reloading equipment. Indeed, shooting prairie dogs at distances >450 m entitles one to membership in the 500 Yard Club, sponsored by the Varmint Hunters Association, and some members have registered successful shots >1,350 m.

Many shooters come from out of State (Vosburgh, 2000; South Dakota Prairie Dog Work Group, 2001), but this appears to be a recent phenomenon. In North Dakota, for example, nonresidents must purchase either a nongame license or a combination nongame and furbearer license to shoot prairie dogs; residents are exempt (North Dakota Game and Fish Department, 2001). The number of nonresident nongame licenses sold increased from 36 in 1975 to 625 in 2001, while nonresident nongame and furbearer license sales increased from 163 in 1989 to 1,326 in 2001 (S. Hagen, written commun., 2003). The recent increase in license sales to nonresidents in North Dakota indicates the rise in recreational shooting of prairie dogs by people from out of State. Similarly, in South Dakota over 35 percent of the estimated 16,011 prairie dog shooters on nontribal land in 2001 were nonresidents (Gigliotti, 2001).

Shooting Intensity

Available information indicates that substantial numbers of prairie dogs have been shot. In 2000, recreational shooters killed 1,186,272 prairie dogs on nontribal lands in South Dakota (South Dakota Prairie Dog Work Group, 2001). The number killed on nontribal lands increased to 1,516,174 in 2001 (Gigliotti, 2001). Shooters spent a total of 75,059 recreation days to kill that many prairie dogs: 54,849 by residents and 20,210 by nonresidents (Gigliotti, 2001).

During 1998 in Nebraska, 7,100 shooters spent 33,400 recreation days killing 301,000 prairie dogs; in 1999, fewer shooters (5,970) spent less time (28,300 recreation days) to kill more prairie dogs (356,000) (Nebraska Game and Parks Commission, 2001). The Colorado Division of Wildlife (2002) estimated (with ±95 percent confidence interval) that 6,070 shooters (±629) killed 418,412 prairie dogs (±75,234) during 64,674 recreation days (±825) in the 1998–99 reporting period. Based on these data, shooter success rates (number killed per recreation day) appear similar among reporting States: 6.5 killed per day in Colorado (between 5.2 and 7.7), 12.6 killed per day in Nebraska in 1999, and 20.3 killed per day in South Dakota in 2001.

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Estimates of prairie dogs killed in individual States depend on shooters' responses to survey questionnaires, which are possible only when shooters are licensed, such as in South Dakota and Colorado (South Dakota Prairie Dog Work Group, 2001; Colorado Division of Wildlife, 2002, 2003). On the other hand, nontribal recreational shooters on some tribal lands are required to be accompanied by a guide and must fill out a questionnaire that includes the number of days spent shooting, number of rounds fired, and estimated number of prairie dogs killed. In 2000, 936 shooters fired 156,307 rounds to kill 57,848 prairie dogs on the Rosebud Indian Reservation (T. Vosburgh, unpub. data, 2002). That rate of one prairie dog killed per 2.7 rounds fired is similar to an observed rate of one prairie dog killed per 3.0 shots fired on the Fort Belknap Indian Reservation in northern Montana during 2001 (Vosburgh, 2000).

The Lower Brule Indian Reservation in central South Dakota has collected 9 years of black-tailed prairie dog harvest data (table 1). From 1993 to 2001, an average of 121 licensed recreational shooters killed an average of 14,200 prairie dogs per year while spending an average of 372 recreation days on the reservation (Lower Brule Sioux Tribe, 2002). Each shooter averaged 118 prairie dogs shot per year or about 38 shot per day. That level of success is comparable to nonresident shooters on nontribal lands in South Dakota who, in 2001, spent an average of 3.5 days per shooter to kill 36 prairie dogs per day (Gigliotti, 2001). The average success rate was higher than reported above by Nebraska or Colorado. Relatively high levels of shooter success may be due to tribes' interest in recreational shooting as a source of revenue with concomitant monitoring of shooting effects on prairie dog populations. Also, out-of-State shooters may be especially diligent in pursuit of their quarry. During 2001, residents of South Dakota shot an average of 14 prairie dogs per day, considerably fewer than the 36 prairie dogs per day reported shot by nonresidents (Gigliotti, 2001).

Shooter success rates appear related to prairie dog densities. Typical densities of black-tailed prairie dogs exceed those of white-tailed prairie dogs (*C. leucurus*) (Tileston and Lechleitner, 1966), whereas densities of Gunnison's prairie dogs (*C. gunnisoni*) are intermediate or overlap those of the other two species (Fitzgerald and others, 1994). All three species are shot in Colorado, but harvest estimates are not reported by species, only by county (Colorado Division of Wildlife, 2003). Based on species' distributions (Fitzgerald and others, 1994), we estimated harvest for the three species (table 2). Although ranges of shooting success rates overlap, shooters in 2002–03 killed more prairie dogs per recreation day in counties with black-tailed prairie dogs than in counties inhabited by Gunnison's and/or white-tailed prairie dogs (table 2).

Effects of Shooting on Individual Prairie Dogs

Prairie dogs subjected to shooting change their behavior. In Montana, black-tailed prairie dogs in colonies with recreational shooting spent less time above ground than did prairie dogs in colonies with no shooting. When above ground, the former devoted less time to feeding and more time to scanning than the latter (Vosburgh and Irby, 1998). Prairie dogs in colonies with recreational shooting are more likely to escape when approached on foot or by vehicle, retreating to burrows sooner than prairie dogs not subjected to shooting (Vosburgh and Irby, 1998; Keffer and others, 2000). Increased alertness and early escape by prairie dogs are potential problems for recreational shooters, though some shooters may by more interested in shooting skill and firearm accuracy than in numbers of prairie dogs killed.

The timing of shooting prairie dogs may affect reproduction and mortality of various sex and age groups. Shooting from March to May is likely to kill pregnant or lactating females so that neither they nor their offspring will reproduce the following year (Knowles, 1988). Shooters generally cannot distinguish between male and female prairie dogs and, except during early summer, between adults and juveniles. Juvenile prairie dogs are more susceptible than adults to low levels

Table 1. Data from 9 years of shooting black-tailed prairie dogs (*Cynomys ludovicianus*) on the Lower Brule Indian Reservation, S. Dak.[a]

	Year								
Statistic	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**
Number of licenses sold	115	146	139	127	157	97	114	130	64
Estimated total killed	17,700	28,000	4,600	10,700	15,300	16,700	12,100	14,800	8,069
Total recreation days	367	503	334	486	372	392	363	319	211
Harvest/day/shooter	48	56	14	22	41	43	33	46	38
Average days/shooter	3.2	3.6	2.4	3.8	2.8	2.9	3.2	2.5	3.3

[a] Lower Brule Sioux Tribe (2002).

Table 2. Harvest estimates for three species of prairie dogs (*Cynomys*)—white-tailed (*C. leucurus*), Gunnison's (*C. gunnisoni*), and black-tailed (*C. ludovicianus*)—in Colorado during 2002–03 with rates and ranges of number killed per recreation day.

Species[a]	Number of counties in distribution[a]	Number of hunters[b]	Recreation days spent[b]	Total prairie dogs killed[b]	Shooter kill rate (number/day)	Range (number/day) for counties
White-tailed	5	1,063	13,197	30,943	2.34	0.78–5.51
White-tailed with Gunnison's	2	394	12,153	66,772	5.49	4.76–5.71
Gunnison's	12	827	9,278	31,533	3.40	0.00–6.44
Gunnison's with black-tailed	3	197	1,083	3,762	3.47	3.25–3.65
Black-tailed	20	1,948	17,845	170,867	9.58	1.42–101

[a] Counties within species' distributions as described by Fitzgerald and others (1994).

[b] Colorado Division of Wildlife (2003).

of shooting (Keffer and others, 2000). For example, when a colony having 35 percent juveniles was subjected to a 10 percent harvest during early to mid-summer, 53 percent of the animals killed were juveniles. On the same colony, adult females and adult males (39 percent and 26 percent of the population, respectively) were killed proportionately less than their occurrence in the population. Higher shooting pressure (>20 percent mortality) on another colony also targeted juveniles disproportionately (Keffer and others, 2000).

Adult females, including yearlings, appear more vulnerable to shooting than do adult and yearling males (Vosburgh and Irby, 1998; Keffer and others, 2000). During early summer 1995 in Montana, for example, the ratio of adult males to females was 92:100 on nine colonies (Vosburgh and Irby, 1998). In late summer, after an average of 8.5 hours of shooting per colony, the ratio of adult males to adult females was 167:100 on the same nine colonies. Survivorship of adult females during shooting was only 57 percent of the survivorship of adult males. On eight control colonies with no shooting, adult female survivorship was 122 percent of adult male survivorship between early and late summer in the same year (Vosburgh and Irby, 1998), which is similar to differential survival of unhunted black-tailed prairie dog populations elsewhere (Hoogland, 1995). Greater vulnerability of females probably exacerbates the impact of shooting by diminishing future reproduction.

Reproduction by adult and yearling female prairie dogs may be suppressed on colonies that are subject to continual recreational shooting. In North Dakota, only 32 percent of yearling female black-tailed prairie dogs on colonies disturbed by >20 years of heavy shooting reproduced (based on placental scars and evidence of ovulation) compared with 90 percent of yearling females on colonies relatively undisturbed by shooting (Stockrahm and Seabloom, 1988). Counts of placental scars in adult females (≥2 years old) examined from the disturbed colonies were significantly lower than in adult females on relatively undisturbed colonies, indicating depressed reproduction on the disturbed colonies. These observations do not demonstrate that continual shooting was solely responsible for depressed reproduction because the disturbed colonies were spatially confined and not growing, whereas the undisturbed colonies were not spatially restricted and had doubled in size during the previous 5 years (Stockrahm and Seabloom, 1988). Depressed reproduction in the disturbed though confined colonies, especially by yearling females, may indicate density-dependent processes similar to those observed by Garrett and others (1982) in South Dakota.

Effects of Shooting on Prairie Dog Populations

Populations increase with birth and immigration of individuals but decrease with their death or emigration. For species such as prairie dogs that reproduce once a year (Hoogland, 1995) but die from various sources throughout the year, information about the rate of population increase (sometimes called the "finite rate of increase" and symbolized here by R; others often use lambda, λ) is important to understanding potential effects of recreational shooting on colonies. The equation $N_t = N_0 R^t$ can be used to compute population size at time t, N_t, if the initial population size, N_0, and R are known.

Finite rates of increase in prairie dog colonies with no shooting vary from year to year. For example, at one black-tailed prairie dog colony in Wind Cave National Park, S. Dak., colony size increased in some years but declined in others. Population finite rates of increase at this colony averaged 1.03 (1 standard deviation = 0.25), with minimum R = 0.70 and maximum R = 1.45 (Hoogland, 1995, table 16.1). Because this colony was surrounded by unsuitable habitat, its area remained constant, so the observed R = 1.0 might have been expected. Stationary populations often increase in response to factors such as addition of food, increase in habitable area, and population reduction (Caughley and Sinclair, 1994). Population reduction decreases competition, usually for food. With more food per individual, reproduction increases, mortality decreases, and the population grows (Caughley and Sinclair, 1994).

Limited experimental evidence demonstrates that removing prairie dogs, by shooting or other means, enhances population growth rates. After 2 consecutive years of shooting at two small black-tailed prairie dog colonies, populations were reduced or eliminated; in the year after shooting ceased, portions of both colonies were still inactive (Knowles, 1988). Five years after the shooting program ended, the larger of the two shot colonies had expanded to cover 140 percent of its preshooting area, and the smaller had grown to cover 90 percent of its former area (Knowles, 1988). Spatial growth of these treatment colonies resulted from increased numbers of prairie dogs, but details of population increase—whether by immigration from neighboring colonies or as a demographic response of the surviving prairie dogs—are unavailable. Data on active versus inactive burrow entrances indicate a similar response to cessation of shooting at larger black-tailed prairie dog colonies in South Dakota. Less than 45 percent of total burrows were active while recreational shooting was allowed, but, after 4 years without shooting, 74 percent of burrow entrances were active (B. Perry, unpub. data, 2000).

Rates of population increase have been documented under other conditions that reduce prairie dog populations. Knowles (1986) studied the effects of a toxicant, zinc phosphide, on several black-tailed prairie dog colonies by different treatment regimes and then observed the population recoveries for up to 5 years following the treatments. Knowles computed instantaneous growth rates for each year during population recovery. The instantaneous growth rate, r, is related to the finite rate of increase, R, by $R = e^r$, (Akçakaya and others, 1999) and is employed to predict population growth in continuous time rather than in discrete time, by the equation $N_t = N_0 e^{rt}$. One month after treatments that attempted to completely eradicate two colonies, Knowles (1986) estimated a reduction of 95 percent caused by the treatments. By continuing to monitor population recovery, Knowles computed average r = 0.916 (R = 2.499) after 1 year, r = 1.069 (R = 2.912) from the first to the second year and r = 0.350 (R = 1.419) from the second to the fifth year. For the five colonies that received partial toxicant treatment, which reduced target populations to an average of 19 percent of pretreatment levels, average r = 1.339 (R = 3.815) after 1 year and r = 0.148 (R = 1.160) from the first to the second year (Knowles, 1986).

Values for R reported by Knowles (1986) were higher for both study groups after the first year following treatments than values observed on a prairie dog colony in Wind Cave National Park, S. Dak. That colony expanded from 0.47 ha to 1.86 ha over a 3-year period (Garrett and Franklin, 1988) when colony size in June increased from 51 to 134 adults and juveniles (average R = 1.38). Similarly, a black-tailed prairie dog colony near Nunn, Colo., with no population reduction treatment, expanded from 2.1 ha to 3 ha in 1 year as the colony size in June grew from 28 to 82 animals (Koford, 1958, p. 10, table 1). For that colony in that 1-year period, R = 2.93, but in the previous year the colony had declined from 50 to 28 animals (R = 0.56).

Population responses were also tracked following reduction of two colonies in South Dakota by translocating live-trapped black-tailed prairie dogs (Radcliffe, 1992). After intensive removal during June of the first study year, 6 prairie dogs remained in one of the colonies, but 10 were present by June of the following year. By June of the second year following removal, the population had increased to 51 prairie dogs, but the increase was mostly attributed to immigration (Radcliffe, 1992). The second colony also grew substantially after the population was reduced to 10 individuals in June of the treatment year. By the next June that colony had grown to 23 and by June of the second year had grown to 80 prairie dogs; the extraordinary growth rate during the second year was R = 3.48. In this second colony, immigration played a minor role (three immigrated annually). Population growth mainly resulted from increased litter size and higher juvenile survivorship (Radcliffe, 1992).

These data support our earlier generalization that populations can be stimulated to grow by reducing the number of animals that compete for a limited resource. Similar population responses were noted in colonies of Gunnison's prairie dog during and after a sylvatic plague epizootic in Moreno Valley, N. Mex. Cully (1997) found that after plague killed more than 99 percent of the population, the few surviving prairie dogs formed two colonies in areas that were previously unoccupied. Using Leslie matrix analysis involving demographic parameters (survivorship and fecundity), Cully found that the population would be nearly tripling each year. The key to this high rate of population growth was found to be yearling females reproducing at a rate similar to that of adults and having a relatively high survival rate (Cully, 1997). Similarly, the survival rate of juveniles (90 percent) in a young, expanding black-tailed prairie dog colony in South Dakota was significantly higher than juvenile survivorship (49 percent) in an older, nonexpanding colony (Garrett and others, 1982). In addition, yearling females on the younger colony were more likely to produce and wean a litter than were those on the older colony. These two demographic characteristics of juveniles and yearlings appear consistent in rapidly growing prairie dog populations.

Simulated Effects of Different Shooting Strategies

In many of these studies, prairie dog populations appear to exhibit density-dependent growth; crowding with concomitant diminishing resources available to each individual leads to increased mortality (decreased survival), decreased reproduction, and/or increased emigration. An assumption of density-dependent population growth is that when a population approaches carrying capacity (K) the growth rate declines and eventually reaches R = 1.0 when N = K. The value of R at time t, R_t, depends on the population size N_t relative to K according to the equation, $R_t = R_{max}^{(1 - Nt/K)}$. When the population N_t is small, the exponent $(1 – N_t/K)$ is close to 1 and the population's growth rate R_t is close to the maximum possible, or R_{max}. As the population grows and approaches its carrying capacity, the growth rate R is much less than R_{max}, and when the population reaches carrying capacity, R = 1.0 because the exponent $(1 - N_t/K) = 0$.

If prairie dogs are viewed as an economic resource, the best strategy is to manage colonies for a sustained yield. A landowner or wildlife manager hoping to capitalize on prairie dog harvest might allow shooters to kill as many prairie dogs in a year as are produced. With density-dependent growth (R_{max} = 2.00, K = 1,000), a population growing from 20 to 1,000 animals produces the maximum number of animals (maximum yield) when it is approximately at half of carrying capacity (Peek, 1986). In this example, maximum yield = 209 when the population reaches 438 after 5 years of growth.

Harvesting the population at maximum productivity maximizes yield, but managing for maximum yield is difficult (Caughley and Sinclair, 1994). Removing animals from a population reduces the base population. The difficult task is determining what base population produces the best yield for the next year. If the harvest exceeds maximum yield and continues over time, the population will eventually decline to zero (Caughley and Sinclair, 1994).

Two common approaches to control harvest are (a) imposing a quota on numbers harvested and (b) regulating harvesting effort (Caughley and Sinclair, 1994). Regulating harvest by quotas is conceptually attractive: once the quota is attained, shooting stops. Determining when quotas for prairie dogs are reached might be problematic, however. If shooters consistently record prairie dogs killed and number of rounds fired, wildlife managers can estimate the number killed from the number of shots. Figure 1 demonstrates the problem with fixed annual harvest quotas. An initial population of 1,000 eventually stabilizes at 585 animals in 24 years if 195 prairie dogs are shot each year, but if the annual harvest exceeds 209 animals (the maximum yield when R_{max} = 2.00 and K = 1,000), then the population declines to extinction, doing so faster with larger harvests.

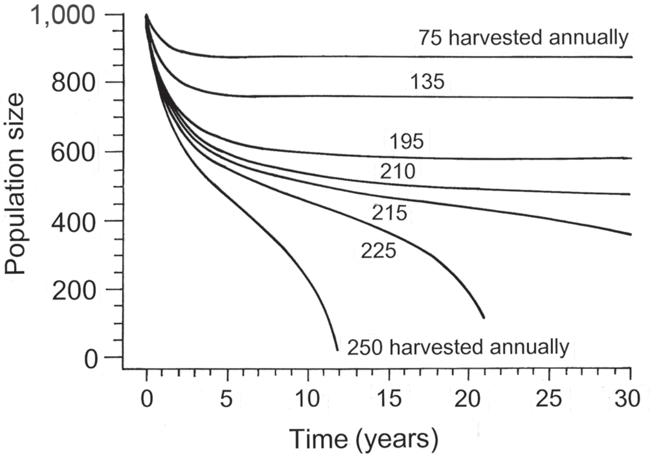

Figure 1. Effects of constant annual harvest quotas on a population with density-dependent growth (R_{max} = 2.00, K = 1,000) but no random variation in R_t. Annual harvest >209 animals (maximum yield) cannot be sustained, and the population eventually declines to zero.

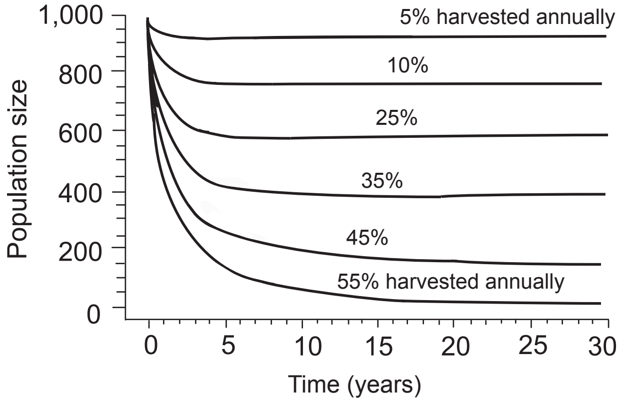

Figure 2. Deterministic predictions of a population with density-dependent growth (R_{max} = 2.00, K = 1,000) subject to different levels of proportional harvest annually.

Theoretically, controlling harvest effort removes some proportion of the population over time rather than a fixed number of animals each year. One way to control harvest effort is to limit the timing and duration of the harvest. Another way is to limit the number of shooters (Caughley and Sinclair, 1994). Figure 2 shows the outcome of various annual harvest levels as percentages of the current population. At an annual harvest rate of 25 percent, the population stabilizes at 585 animals, but in only 13 years, while the long-term average harvest (from t = 0 to t = 30) is approximately 199 animals.

To this point, population growth was assumed to be deterministic with no uncertainty in birth or death rates. Environmental variation from year to year, or day to day, and from one locale to another causes fluctuations in prairie dog populations' birth and death rates (Hoogland, 1995). In addition, individual animals in the same population have different reproductive capabilities or chances of survival. Recreational shooting of prairie dogs introduces additional uncertainty in population demographic parameters since age groups and sexes may be affected differently. Levels of variability might be measured at some point in time but cannot be predicted in the future. Stochastic population models provide for such uncertainty.

In the simulation examples provided so far, the finite rate of increase at time t, R_t, is equal to $R_{max}^{(1-Nt/K)}$. Annual variation in rates of birth, immigration, death, and emigration all contribute to variability of R_t. Annual variation in carrying capacity also causes variation in R_t. We introduce variation by increasing or decreasing the computed value of R_t by a random amount but within some defined limits, for example within ±20 percent of the computed value for R_t, which includes demographic variation as well as random variation in carrying capacity.

This simple approach was applied in 100 simulations to project population growth from an initial population of 20 animals with $R_{max} = 2.0$ and $K = 1{,}000$. The simulations show that the average population size stabilizes at approximately 1,000 animals (fig. 3) but, because of random variability of R_t, the population at $t = 15$ could range from 797 to 1,230 animals in any one simulation.

Random variation, now limited to only ±15 percent of the computed value for R_t, for example, is used to predict how an initial population of 1,000 ($N_0 = K$) with $R_{max} = 2.0$ responds to an annual quota of 195 animals harvested. The results (fig. 4) are different from those generated by the deterministic model (fig. 1). After 1,000 simulations, the stochastic model predicts a population of 406 (ranging from 0 to 819) at the end of 30 years with average annual harvest of 183. The model also predicts a 23 percent chance that the population will become extinct by $t = 30$. Risk of extinction increases with level of random variation in R_t. For example, with random variation ±10 percent of R_t, extinction within 30 years occurred in 1 percent of the trials, but a 46 percent chance of extinction is expected with random variation ±20 percent of R_t (after 1,000 simulations with an annual quota of 195).

Alternatively, an annual harvest rate of 25 percent produces an expected population of 580 animals (ranging from 439 to 744 animals) after 30 years of simulation with average annual harvest of 197 animals but poses no risk of extinction (fig. 5), unlike the risk observed with fixed quota harvest (fig. 4). With demographic and environmental uncertainty, sustainable populations are more likely if harvested proportionally rather than by fixed quota. Implicit in modeling these two harvest strategies, however, is intensity of harvest management. Once set, the quota of 195 harvested did not change over time even though the population may have been declining

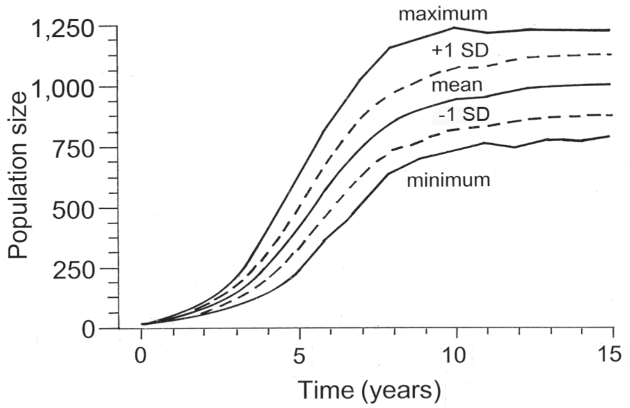

Figure 3. Results of 100 simulations of density-dependent population growth ($R_{max} = 2.00$, $K = 1{,}000$), but with random variation in the population growth rate each year (within ± 20% of R_t after computation as $R_t = R_{max}^{(1-Nt/K)}$).

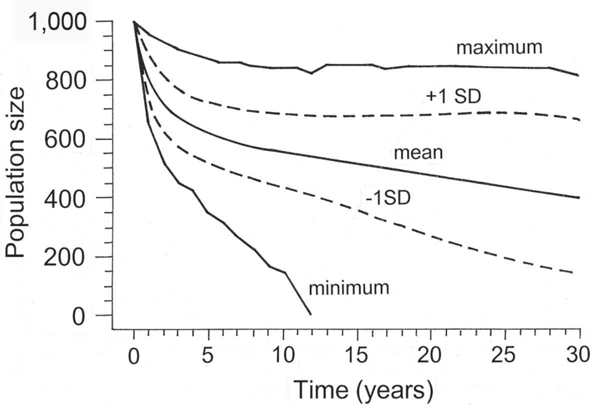

Figure 4. Results of 1,000 simulations with an annual harvest quota of 195 animals, an initial population of 1,000 animals, density-dependent population growth ($R_{max} = 2.00$), and random variation in the population growth rate each year (within ±15% of R_t after computation as $R_t = R_{max}^{(1-Nt/K)}$).

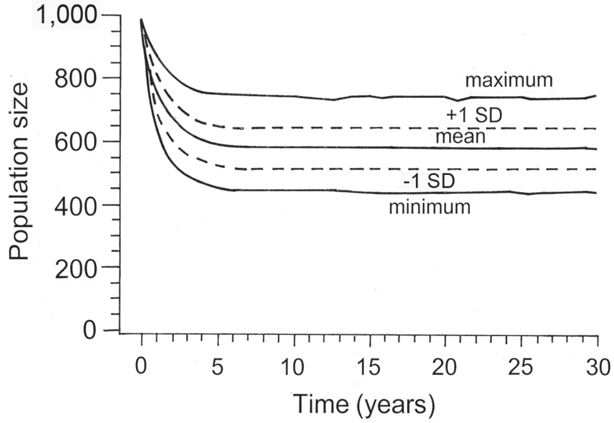

Figure 5. Results of 1,000 simulations with an annual harvest rate of 25%, an initial population of 1,000 animals, density-dependent population growth with $R_{max} = 2.00$, and random variation in the population growth rate each year (within ±15% of R_t after computation as $R_t = R_{max}^{(1-Nt/K)}$).

in a given simulation. Alternatively, numbers harvested were continuously adjusted when a harvest rate of 25 percent was applied. To ensure a sustainable population while realizing a desired annual harvest, the manager must monitor the dynamics of the target population and respond accordingly.

Proper application of either harvest strategy, whether by regulating harvest quota or by regulating harvesting effort, requires knowledge of the target population's carrying capacity and the species' R_{max}. Seldom are these parameters known with any certainty. A population at approximately K/2 is expected to yield the maximum number of animals that, in theory, could be harvested each year as a maximum sustained yield (MSY). Nevertheless, stochastic events in the environment and variability among individuals in a population can lead to substantial population fluctuations, and harvest should always be well below the estimated MSY (Caughley and Sinclair, 1994).

A third approach involves harvesting only when a population exceeds some threshold level, above which excess animals are taken (Lande and others, 1997). Threshold harvesting requires specific knowledge about population levels but produces high annual variation in harvest because populations below the threshold are not harvested (Lande and others, 1997). Threshold harvesting might be possible if a manager or landowner had never attempted to control prairie dogs and had monitored population levels under various environmental conditions so that average K could be estimated.

Recreational Shooting on Private Land for Prairie Dog Conservation

Of >660 livestock and agricultural operators surveyed in eastern Wyoming (Wyoming Agricultural Statistics Service, 2001), 23 percent expressed interest in a program of financial compensation for allowing prairie dogs on their land. The survey posed four types of management programs to respondents who expressed interest in financial compensation: (a) a shooting management program, (b) a cooperative shooter placement program to direct shooters to landowners willing to allow shooting, (c) a program to develop markets for prairie dogs as pets or for nature photography, and (d) a banking program in which other States would compensate Wyoming landowners for conserving prairie dogs (Wyoming Agricultural Statistics Service, 2001). Of these, prairie dog banking was the most popular (59 percent interested), a cooperative shooter placement program (57 percent interested) was second, followed by interest in shooting management (51 percent of respondents).

Respondents who expressed interest in programs with financial compensation considered $74–$86/ha annually to be reasonable ($30–$35/acre, median value). Generally, interest in maintaining or increasing the number of acres of prairie dog colonies on their land varied directly with the level of financial compensation. To attain $74–$86/ha in potential income from shooting, a landowner with 405 ha (1,000 acres) of prairie dog colonies, for example, could charge four shooters $79–$92 per person per day to shoot during the period between Memorial Day and Labor Day (approximately 95 days). Four shooters during that period are equivalent to 380 recreation days. Applying data from the Fort Belknap Indian Reservation (average of 38 prairie dogs shot per recreation day), the annual toll would be 14,440 prairie dogs killed, whereas 2,470 killed would be expected in a year at the rate of 6.5 prairie dogs per recreation day estimated in Colorado.

Densities of black-tailed prairie dogs in Conata Basin, S. Dak., range from 8/ha to 41/ha (Severson and Plumb, 1998). If that range of densities is applied to the simple example of a 405-ha colony on private land, then the population, estimated between 3,240 and 16,605 prairie dogs, could eventually be eliminated by recreational shooting under either the shooter success rate on Fort Belknap Indian Reservation or in Colorado. To ensure a future income, the private landowner would have to significantly decrease the number of recreation days spent shooting, which should concomitantly decrease the number of prairie dogs shot. In addition, to attain the desired income, the landowner would have to substantially increase fees charged per shooter.

Managing prairie dogs on private land for recreational shooting might be appropriate for some landowners and not others. Still, when faced with the apparent need or desire to control prairie dogs, opening land to shooters can provide landowners with an additional source of income and thus an incentive to support some level of occupied habitat that they otherwise would not tolerate.

Recreational Shooting on Black-footed Ferret Reintroduction Sites

Recreational shooting of prairie dogs has been totally or partially restricted on black-footed ferret (*Mustela nigripes*) reintroduction sites (Colorado Division of Wildlife and others, 2002), although there are few instances where effects of shooting closures on prairie dog populations have been monitored. In some instances, shooting closures coincided with changes in statewide prairie dog management practices following States' adoption of the Black-tailed Prairie Dog Conservation Assessment and Strategy and addendum (Luce, 2001). Closures to shooting have also been applied to other species of prairie dog, as in Arizona where black-footed ferrets were introduced in Gunnison's prairie dog colonies (B. Van Pelt, oral commun., 2003). In other cases, shooting closures were initiated to improve habitat for introduced black-footed ferrets and to ensure that ferrets, especially kits, would not be inadvertently shot (B. Perry, oral commun., 2003). Other wildlife, burrowing owls (*Athene cunicularia*) in particular, can be killed during recreational shooting of prairie dogs. Though not documented as a consequence of shooting prairie dogs, there are instances of substantial burrowing owl mortality by shooting (Haug and others, 1993; James and Espie, 1997).

In its review of a petition to list the black-tailed prairie dog under the Endangered Species Act, the U.S. Fish and Wildlife Service (1999) evaluated effects of recreational shooting, concluding in part that shooting may be a compensatory source of mortality in large populations with substantial reproduction. Where small prairie dog populations are depressed by other factors such as disease, shooting may be an additive source of mortality. Compensatory mortality, where one source of mortality offsets or replaces another source (Mackie and others, 1990), whether caused by harvest or predation, is most likely to occur in populations near their ecological equilibrium or carrying capacity (Peek, 1986; Bartmann and others, 1992; Boyce, 2000). In such density-dependent regulated populations, when density is high so are mortality rates, and a population decrease by whatever means results in higher survivorship in the remaining population, as long as removal of animals does not adversely affect reproduction the following year. When removal by harvest and/or predation is high enough to affect reproduction in subsequent years, mortality from those sources is likely to be additive and, if extreme, can force the target population to extinction.

By most accounts, ferret predation does not significantly depress prairie dog populations (Fagerstone, 1987) and would seem a source of compensatory mortality. Biggins and others (1993) estimated annual consumption of 109 prairie dogs by one black-footed ferret family group (1 adult female, 3.3 young, and 0.5 adult male) while recognizing the potential for substantial prairie dog predation by other species. Assuming moderate levels of mortality by other sources, Biggins and others (1993) estimated that a stable population of 763 prairie dogs would sustain a ferret family group for 1 year. Using an age-dependent predation model of ferrets and prairie dogs, Klebanoff and others (1991) concluded that as many as 2,000 prairie dogs per ferret may be necessary to sustain a stable predator-prey system. A stable system can also be attained with fewer prairie dogs—though not as few as 763—but only if prairie dog survivorship or fecundity rates increase (Klebanoff and others, 1991). We are not aware if either estimation approach has been field tested.

Prairie dog mortality by unregulated recreational shooters can vastly exceed predation by black-footed ferrets, thus affecting prairie dog survivorship and potentially affecting fecundity and recruitment. Recreational shooting can be additive mortality, potentially more so on black-tailed prairie dog colonies than on Gunnison's or white-tailed colonies (table 2). Management agencies have recognized that, even with closures of specific areas, recreational shooting has continued and that enforcement of shooting closures is problematic (V. Kopcso, oral commun., 2003). Until more is known about effects of recreational shooting on prairie dogs that are the primary prey resource for black-footed ferrets, managers are wise to restrict shooting and enforce closures, particularly on ferret reintroduction sites inhabited by black-tailed prairie dogs.

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