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Risk-disturbance overrides density dependence in a hunted colonial rodent, the black-tailed prairie dog *Cynomys ludovicianus*

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Summary

1. Traditional understanding of how hunting affects vertebrate populations emphasizes competitive release and density dependence of vital rates, but more recent thinking has proposed complex non-lethal responses to hunting disturbance and predation risk. Colonial species have been proposed to be more vulnerable than dispersed, solitary species to disturbance and perceived risk from hunting. However, empirical comparisons of density dependence vs. risk disturbance in hunted species are few.

2. To compare density dependence with risk-disturbance effects of hunting on individuals and populations of a colonial species, we tested the response of black-tailed prairie dogs *Cynomys ludovicianus* to shooting in a before–after, treatment–control experiment. We subjected five colonies to a pulse of shooting, and compared individual and colony attributes to those of five control colonies, protected from shooting.

3. Surviving prairie dogs increased alert behaviours eightfold and reduced both aboveground activity and time spent foraging by 66%. Changes in behaviour lowered the body condition of surviving adults by 35%. Survivors of shooting, especially juveniles, exhibited elevated stress levels; faecal corticosterone concentrations increased by 80% among juveniles. Unexpectedly, overwinter survival rates did not increase in response to reduced prairie dog density. Colonies subjected to shooting experienced reproductive near-collapse the summer after shooting; pregnancy rates declined by 50% and reproductive output fell by 82%.

4. Risk-disturbance overwhelmed any possible density-dependent effects of shooting in prairie dogs, which exhibited additive mortality in response to hunting, and reproductive failure 1 year after shooting. Risk-disturbance was the predominant mechanism whereby individuals and colonies were affected by hunting.

5. *Synthesis and applications.* Because of their coloniality, prairie dogs possess certain life-history traits that predisposed them to be particularly susceptible to hunting-associated disturbances, which had cascading effects on population-level processes. Our findings contradict the general belief that small-bodied mammals quickly rebound from hunting exploitation via compensatory mortality and reproduction. Managers should consider measures to reduce recreational shooting intensity and duration in regions where black-tailed prairie dog colony growth and persistence is desired, yet allow shooting in areas where colonies conflict with landowner interests.

Key-words: Allee effect, coloniality, density dependence, hunting, prairie dog, risk–disturbance, Wyoming.

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Introduction

Ecologists increasingly realize that predators, including human hunters, can affect populations of prey in indirect but important ways. Under the risk of predation, animals may alter activity regimes, habitat-use patterns or other behaviours (Lima 1998). Such decision-making occurs when perceived risk of predation constrains other fitness-enhancing behaviours: animals trade-off various kinds of risk – such as starvation, being killed by a predator and not finding a mate – in order to maximize fitness (Lima 1998). These trade-offs have been postulated to result in cascades of effects that can extend to population size, demography and even the structure of ecosystems (Lima 1998; Ripple & Beschta 2004).

The predation–risk paradigm has been applied to animals responding to humans as the risk-disturbance hypothesis (Frid & Dill 2002). In response to hunting or other human disturbance, vertebrates may increase vigilance (Kilgo, Labisky & Fritzen 1998), alter foraging regimes (Roy & Woolf 2001), shift migration routes (Béchet *et al*. 2003) or use resource-poor habitats (Madsen 1998). Such behaviours have been shown to be capable of lowering body condition (Féret *et al*. 2003) or reducing reproductive output (Mainguy *et al*. 2002). Animals unable to avoid risk or disturbance may exhibit other symptoms such as physiological stress (Bateson & Bradshaw 1997). Clearly, these hypotheses and mechanisms have given us a fuller understanding of how animals with adaptive behaviours maximize fitness in the face of human disturbance, or suffer fitness losses in response to unavoidable perceived risk.

At the population level, positive growth ($\lambda > 1$) might counteract the effects of perceived risk, and has been attributed commonly to density dependence. Following hunting, populations limited by resources should enjoy higher survival and reproduction, and such density-dependent responses have been shown for a wide range of hunted taxa (Fowler 1987). Generally, reducing populations below carrying capacity should increase rates of somatic growth, survival and reproduction (Kokko 2001). Physiological stress may decline in response to reduced social interactions, and levels of intraspecies conflict are also expected to decrease. Therefore, human hunting and associated disturbance can be postulated to have contradictory effects on populations, primarily via the two mechanisms of risk-disturbance and density dependence.

Which of these mechanisms is more important might depend on degree of sociality and site fidelity. Gill, Norris & Sutherland (2001) hypothesized that vulnerability to disturbance should be related inversely to capacity to relocate to alternative habitats, and Fitz-Gibbon (1998) reviewed the mechanisms whereby some colonial species are more vulnerable to hunting disturbance than solitary ones. Colonial species cannot relocate to areas away from disturbance, tend to communicate threats to each other and are prone to social disruption (Stephens *et al*. 2002). Such hypothesized vulnerabilities are additive to the fundamental one: that colonies represent high and predictable local concentrations of the species sought. Therefore, the risk-disturbance costs of hunting to surviving animals – perhaps extending to population processes – should be higher among colonial species than solitary, dispersed ones.

In the absence of human hunting, the ecological costs and benefits of colonial living have been well described (Hoogland & Sherman 1976; Hoogland 1979). Colonial animals benefit from cooperative breeding, shared vigilance, decreased predation, increased foraging efficiency and shared habitat enhancement and maintenance. Colony members also pay certain costs: increased disease transmission, intensified intraspecific competition for resources, easier detection by predators and heightened sensitivity to behavioural disturbances. It is unknown, however, how and to what degree an evolutionarily novel perturbation, such as modern human hunting, alters these costs and benefits of coloniality.

The black-tailed prairie dog *Cynomys ludovicianus*, a colonial sciurid rodent of the plains of North America, is an ideal model for examining responses to hunting in a colonial species. Studied intensively throughout their range, in part because of the ecologically pivotal role they play in grassland systems (Miller, Ceballos & Reading 1994), the natural history and coloniality of this species have been well documented (e.g. Hoogland 1995). Prairie dogs have only recently been subject to hunting and, in contrast to most other hunted taxa, are rarely killed for meat or fur but are used as targets by recreational shooters, who typically use high-velocity rifles effective at ≤ 500 m (Reeve & Vosburgh 2005). Most states impose no seasonal restrictions, harvest limits or licensing requirements on prairie dog shooting (Reeve & Vosburgh 2005), and a single shooter can shoot scores of prairie dogs in a single session (Vosburgh & Irby 1998). In recent years, recreational shooters have reported killing > 2 000 000 black-tailed prairie dogs year^{-1} from three states combined (Reeve & Vosburgh 2005). Therefore, shooting is a widespread population influence across the range of *Cynomys*.

Although previous studies (Knowles 1982; Vosburgh & Irby 1998) have described some population and behavioural effects of shooting on prairie dogs, none has evaluated the relative importance of risk-disturbance vs. density-dependent effects. We experimentally tested the response of black-tailed prairie dogs to recreational shooting, and examined some mechanisms that might contribute to the effects hypothesized. We measured population and environmental attributes of 10 colonies, subjected one-half of the colonies to a pulse of shooting, and compared prairie dog attributes between shot and protected colonies over two consecutive summers. Specifically, we quantified shooting-related changes in abundance, survival, reproduction and demography of colonies subjected to vs. protected from shooting. We also compared the behaviours, growth rates and stress levels of the survivors on hunted colonies with those on protected colonies. We predicted effects of both risk-disturbance

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and density dependence, but favoured the former because of the hypothesized vulnerability of colonial species. Specifically, we predicted that surviving prairie dogs would spend less time foraging and allocate more time to vigilance or hiding underground in burrows (Blumstein & Pelletier 2005), and recognized that such effects might cascade to body condition and population-level attributes. At the same time, we expected to observe increased overwinter survival on colonies subjected to shooting, and a pulsed increase in reproduction the following summer as a result of competitive release.

Materials and methods

STUDY SITE AND SELECTION OF COLONIES

We conducted fieldwork in summers 2003–04 on private lands around Thunder Basin National Grassland (TBNG), north-eastern Wyoming (43°45′ N, 105°00′ W). TBNG encompasses > 230 000 ha of federal land in a mosaic of public and private lands. The region is characterized by rolling hills of mixed-grass prairies and sagebrush steppe habitats, dissected locally into small areas of badlands. Dominant plant species included blue grama (*Bouteloua gracilis*), western wheatgrass (*Agropyron cristatum*), needle-and-thread grass (*Stipa comata*), big sagebrush (*Artemisia tridentata*) and pricklypear cactus (*Opuntia polyacantha*). Deciduous trees, primarily plains cottonwood (*Populus deltoides*) and willows (*Salix* spp.), occur along drainages and at some springs. Ponderosa pine (*Pinus ponderosa*) is common at higher elevations. TBNG has hot, dry summers and cold, dry winters. Mean monthly temperatures range from –7 °C in January to 22·8 °C in July Average annual precipitation is about 33 cm, 70% falling during April–August (National Weather Service, Weather Station no. 487810).

We selected 10 black-tailed prairie dog colonies on private land near TBNG for study, excluding colonies that had experienced poisoning, recreational shooting or plague in the previous 10 years. Landowners agreed not to poison or allow shooting on study colonies during our study; we placed signs at each colony prohibiting shooting and monitored for compliance. All colonies were sufficiently isolated that they functioned independently; mean distance to another study colony was 6·5 km (minimum = 2·3 km; see Fig. S1 in Supplementary material) and no dispersals between colonies were detected during fieldwork.

EXPERIMENTAL DESIGN

To control for potentially confounding variation, colonies were paired based on colony area, vegetation attributes, density of prairie dogs and grazing regime in spring 2003 (Appendix S1, see Supplementary material). One colony from each pair was randomly assigned as the treatment and subjected to recreational shooting during midsummer 2003, while the other served as the control, with no shooting.

We entered standardized values (Krebs 1999) of colony area, vegetation, prairie dog density and grazing regime into Horn's (1966) equation to estimate pairwise similarity indices for the 10 colonies. Pairwise distances (PWD) were estimated as $PWD_{i,j} = 1 - PWS_{i,j}$, where $PWS_{i,j}$ is Horn's similarity index for colonies *i* and *j*. We generated a cluster tree using the unweighted pair group method with arithmetic averages (UPGMA). Colonies clustered into distinct clades when analysed with pairwise distances (Fig. S1). We paired colonies sharing the smallest pairwise distance and assigned randomly one colony from each pair as the treatment (Fig. S1). In spring 2004, a plague epizootic reduced prairie dog abundance on one control colony by 95% (Pauli *et al.* 2006). Therefore, data from this colony (5C) and its paired treatment colony (5T) were excluded from analyses requiring data from 2004.

Five volunteers participated in shooting prairie dogs on treatment colonies during 15 June–21 July 2003. Shooters used high-velocity rifles of various models and calibres, with variable-power telescopic sights and various ammunition types, most frequently the 0·223 (5·56 × 45 mm). Shooters (1–2) fired shots opportunistically from positions 15–150 m away from a colony perimeter. An observer recorded the number of prairie dogs killed, the number of rounds fired and the length of each session (Table 1). At the end of our treatment in July 2003, shooters had reduced prairie dog abundance on each treatment colony by our objective of 25–30%. Although invasive, such experimentation was necessary to rigorously quantify prairie dog responses to recreational shooting. Further, mortality rates incurred by our treatment were nominal compared to those on colonies subjected to unregulated shooting and poisoning, which is common on private lands in this region.

We recovered, mapped and determined the sex and age (using the premolar gap method of Cox & Franklin 1990) of 68% ($n = 324$) of shot prairie dogs. Following collection of data from carcasses, we returned them to the colony to mimic typical shooting events. We evaluated whether our treatment was dispersed evenly across each colony by transferring mapped locations of shot prairie dogs to ArcGIS (ESRI, Redlands, CA, USA) where we calculated dispersion using a nearest neighbour algorithm. Nearest-neighbour values of carcasses (1T = 2·33, 2T = 2·70, 3T = 1·15, 4T = 2·21, 5T = 1·79) were > 1·00 (all $Z > 4{\cdot}93$ and $P < 0{\cdot}001$) for all colonies, showing that animals were shot in a spatially uniform pattern (Krebs 1999).

BEHAVIOUR, BODY CONDITION AND STRESS

We randomly established 100 × 100 m marked grids on each colony and recorded prairie dog activity levels and behaviour within each of them twice daily [1·5 h after sunrise and 2 h before sunset, coinciding with peak above-ground activity (Powell *et al.* 1994)] for five consecutive days. Observations were conducted concurrently with trapping, and paired colonies were observed

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Table 1. Number of rounds fired, time spent shooting and number of black-tailed prairie dogs killed by recreational shooters on treatment colonies, Thunder Basin National Grassland, Wyoming, June–July 2003. The percentage of the population killed was estimated by dividing the number killed by the estimated population size

Colony	No. rounds fired	Time spent shooting (person h^{-1})	No. killed	% of population killed
1T	323	8·0	67	31
2T	146	14·3	27	32
3T	697	27·6	209	30
4T	174	9·4	37	30
5T	502	21·2	138	25

simultaneously to control for temporal variation. Observations were postponed during periods of rain or wind speed > 40 km h^{-1}. Observations followed the protocol of scan sampling (Martin & Bateson 1993) and were taken from an elevated position with a 20 × telescope. Following a 20-min delay after assuming our position to allow behaviour to stabilize (Powell *et al*. 1994), we observed and recorded the number and behaviour of prairie dogs on the grid at 10-min intervals for 70 min. We categorized behaviour as: (1) foraging, (2) alert (vigilant or calling), (3) moving, (4) resting, (5) socializing or (6) other. Because few prairie dogs were observed socializing or moving, these two behaviours were pooled with the behavioural category 'other' for subsequent statistical analyses.

Above-ground counts and behaviour were each highly autocorrelated within observation periods (all $r^2 > 0{\cdot}50$). Therefore, we averaged these two variables for each observation period. We expressed behavioural data as the percentage of total time spent in a particular behaviour type. We also expressed above-ground activity as the percentage of animals estimated to occur in a colony (prairie dogs ha^{-1}) above ground at a given time. We used a repeated-measures analysis of variance (RM-ANOVA) to test for the effect of recreational shooting on behaviours over the three trapping sessions and analysed within- and between-subject effects with *post-hoc* comparisons. Prior to each RM-ANOVA, we tested data for normality and homoscedasticity (Zar 1999), transforming non-conforming data using arcsine square-root transformations. In addition, we used Mauchly's *W*-test statistic to test for assumed sphericity (von Ende 2001).

In May–June 2003 (predisturbance), we placed trapping grids randomly on each colony; these same grids were re-established in July–August 2003 and May–June 2004 (post-disturbance). Live traps (Model 203, Tomahawk Live Traps, Tomahawk, WI, USA) were arranged in a 9 × 9 grid, 15 m apart. Paired colonies were trapped simultaneously for 6 consecutive days. During each session, traps were set, wired open and prebaited for 24 h, then baited and set at sunrise and checked and closed at sunset of each day's trapping. We marked captured prairie dogs with fingerling ear tags (National Band and Tag, Newport, KY, USA) and, because we observed during preliminary studies that males tended to lose ear tags, also injected males with subcutaneous passive integrated transponders (Biomark, Boise, ID, USA). We measured weight and hind foot length of each captured animal, using a ratio of the two measurements (g cm^{-1}) as an index of body condition (Krebs & Singleton 1993). Values for an individual were averaged within a trapping session. We tested for changes in the body conditions of juveniles and adults over the study period and between control and treatment colonies with an RM-ANOVA.

We collected scat samples from trapped prairie dogs in 2003 for analysis of faecal corticosterone concentration, a metric of physiological stress (Harper & Austad 2000). Although trapping and handling elevates corticosterone levels, faecal corticosterone levels reflect stress experienced about 6–12 h before defecation (Harper & Austad 2000). Therefore, we collected scat samples only from animals that had been held in traps < 5 h, and that had not been captured the previous day. Scat samples were air-dried in the field and stored at –20 °C. Corticosterone was extracted from faeces using methods described by Monfort *et al*. (1998) and assayed using a radioimmunoassay kit (ICN Biomedical Inc., Costa Mesa, CA, USA) and scintillation counter. The inter- and intra-assay coefficients of variation were 10% and 8%, respectively, and the detection threshold of the assay was 2·6 ng g^{-1}. We analysed variation in corticosterone levels for two age groups (adults and juveniles), before and after shooting, and on control and treatment colonies with two-way ANOVAs.

DENSITY, DEMOGRAPHY AND VITAL RATES

We determined the reproductive status of adult females in May and June at first capture. Females were considered to have been reproductively active earlier in the year if their nipples were enlarged and turgid. We entered capture histories into program CAPTURE to estimate juvenile, adult female and adult male abundances for each colony and trapping session. We estimated densities by dividing abundance estimates by the effective area trapped (Wilson & Anderson 1985), using half the mean maximum distance moved (averaging the maximum distance between recaptures for captured animals) and adding it to the perimeter of the trapping grid. Separate values were calculated for each age–sex group (juvenile, adult female, adult male), colony and trapping session, and variances for densities were calculated using the approach of Otis *et al*. (1978). We analysed changes in the densities of each prairie dog age–sex group over the study period and between control and treatment colonies with RM-ANOVA.

We evaluated changes in the proportions of juveniles, adult males and adult females in each colony with log-likelihood ratios. We compared the proportion of males and females that were yearlings and adults, and the proportional number of reproductively active females

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Table 2. Mean percentage and standard error of prairie dogs foraging, alert and resting on control ($\bar{x}_C$) and treatment ($\bar{x}_T$) colonies from three sampling periods, Thunder Basin National Grassland, Wyoming, 2003–04. Prior to testing, percentages were converted using the arcsine transformation (Zar 1999) and compared between control and treatment colonies for each sampling period with paired *t*-tests (d.f. for all tests = 39). Treatment colonies were subjected to intensive shooting in June–July 2003

	Foraging						Alert						Resting					
Date	$\bar{x}_C$	SE	$\bar{x}_T$	SE	*t*	*P*	$\bar{x}_C$	SE	$\bar{x}_T$	SE	*t*	*P*	$\bar{x}_C$	SE	$\bar{x}_T$	SE	*t*	*P*
May–June 2003 (pre-disturbance)	76·2	1·3	78·7	1·3	–1·23	0·23	7·4	1·2	3·7	1·0	1·65	0·11	6·0	1·1	6·8	1·5	0·60	0·55
July–August 2003 (post-disturbance)	91·1	1·0	66·1	1·2	14·5	<0·001	3·2	0·7	29·2	1·1	–22·1	<0·001	2·7	0·9	0·7	1·1	3·55	0·01
May–June 2004 (post-disturbance)	74·7	1·4	71·0	1·4	1·20	0·24	10·3	1·1	15·6	1·2	–3·45	0·001	1·1	1·1	0·7	1·1	0·85	0·40

between control and treatment colonies in 2003 and 2004 with log-likelihood ratios, corrected for continuity. Indices of reproductive rate (juveniles × adult female^{-1}) were compared between control and treatment colonies in 2003 and 2004 with a paired *t*-test.

Using the robust design model in program MARK (White & Burnham 1999), we modelled apparent survival ($\hat{S}_i$), temporary immigration (γ_i') and emigration (γ_i''), conditional capture ($\hat{p}_{ij}$) and recapture ($\hat{c}_{ij}$) probabilities. Parameter estimates in MARK are maximum likelihood estimates with 95% confidence intervals. To remove the estimates of population size from the likelihood, we used Huggins' estimator (Huggins 1991). We developed a series of 12 *a priori* models based on a number of factors that we believed would influence one or more of the parameter estimates. Factors that we hypothesized would affect parameter estimation included the intervals between trapping occasions, the dates of capture, age and sex of animals, colony, colony pair and experimental status (control, treatment). Because we assumed that temporary immigration and emigration were not occurring on any of the colonies, the parameters γ_i' and γ_i'' were set at 0.

We ranked models of survival rate using Akaike's information criterion corrected for small samples (AIC_c; Burnham & Anderson 2002). We ranked AIC_c values relative to the model with the lowest AIC_c value. Comparisons among models were made using ΔAIC_c (Burnham & Anderson 2002). Normalized Akaike weights (w_i) were also computed for each model as an additional assessment of the strength of evidence for each model.

Results

BEHAVIOUR, BODY CONDITION AND STRESS

Behaviour and time spent above ground were not influenced by the time (morning or evening) of observations (all $F_{2,39} < 0{\cdot}70$, $P > 0{\cdot}65$); therefore, morning and evening observations were pooled. Before shooting, prairie dog behaviour did not differ between control and treatment colonies (Table 2); most behaviour was foraging (76%), followed by resting (7%) and alertness (5%). Shooting caused several behaviour types to differ (foraging: $F_{2,39} = 39{\cdot}5$, $P < 0{\cdot}001$; resting: $F_{2,39} = 2{\cdot}90$, $P = 0{\cdot}033$; alertness: $F_{2,39} = 89{\cdot}7$, $P < 0{\cdot}001$) between control and treatment colonies. Shortly after shooting, alertness on treatment colonies increased to 29%, while on control colonies it decreased to 3% over the same period (Table 2). This coincided with reduced foraging (to 66%) and resting (to < 1%). By contrast, on control colonies foraging increased to 91%, while resting decreased slightly to 3% (Table 2). In 2004, the year after shooting, behaviours on treatment colonies returned to control levels for foraging (73%) and resting (1%), but alertness remained slightly elevated (Table 2). Time spent above ground was also affected by recreational shooting. Activity indices did not differ between control and treatment colonies prior to shooting ($t_{39} = 0{\cdot}69$, $P = 0{\cdot}50$), but diverged after shooting ($F_{2,39} = 5{\cdot}95$, $P = 0{\cdot}003$; Fig. 1). Above-ground activity on treatment colonies declined later the same summer by 66%, while corresponding values on control colonies declined by only 22% ($t_{39} = 8{\cdot}72$, $P < 0{\cdot}001$). The summer after shooting, above-ground activity recovered on treatment colonies, so that it did not differ ($t_{39} = 0{\cdot}65$, $P = 0{\cdot}52$; Fig. 1) from control-colony values.

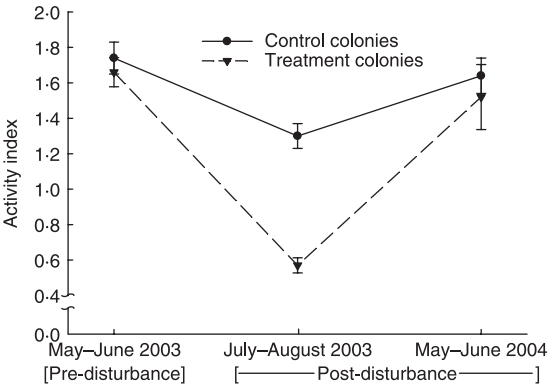


Fig. 1. Mean above-ground activity indices (± 1 SE) for black-tailed prairie dogs on control and treatment colonies, Thunder Basin National Grassland, Wyoming, 2003–04. Activity indices were calculated by dividing the number of prairie dogs above ground (prairie dogs ha^{-1}) by density estimates (prairie dogs ha^{-1}) for that colony. Prior to shooting, activity indices did not differ between control and treatment colonies. Following shooting in June–July 2003, activity on treatment colonies was lower than on control colonies. Above-ground activity on treatment colonies rebounded to control levels in 2004.

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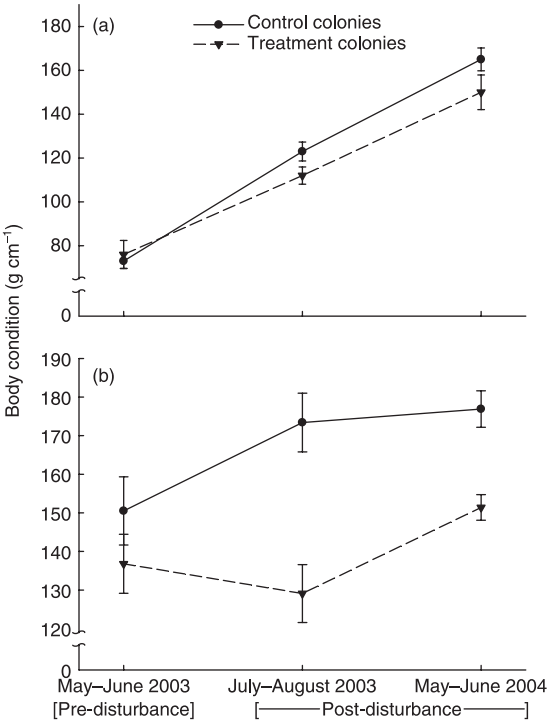


Fig. 2. Mean body condition (± 1 SE) for (a) juvenile and (b) adult black-tailed prairie dogs on control and treatment colonies over three sampling periods, Thunder Basin National Grassland, Wyoming, 2003–04. Treatment colonies were subjected to intensive recreational shooting in June–July 2003. On both control and treatment colonies, juveniles exhibited improved body condition over the course of the study. After shooting, adult body condition on treatment colonies declined, while adults on control colonies exhibited improved body condition. In 2004, adult body condition on treatment colonies partially recovered, but remained lower than on control colonies.

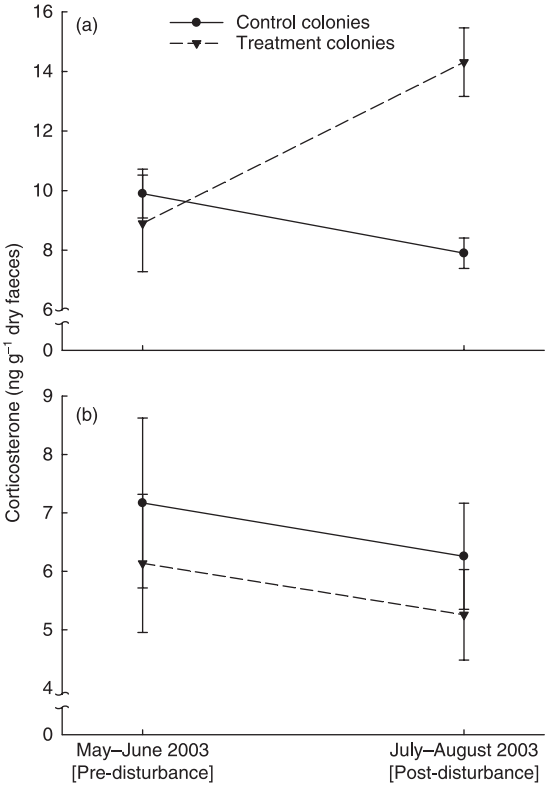


Fig. 3. Mean faecal corticosterone concentrations (± 1 SE) from (a) juvenile and (b) adult black-tailed prairie dogs on control and treatment colonies before and after treatment colonies were subjected to recreational shooting, Thunder Basin National Grassland, Wyoming.

Recreational shooting did not affect body condition of surviving juveniles ($F_{2,56} = 2{\cdot}37$, $P = 0{\cdot}11$). On both control and treatment colonies, body condition of animals that were juveniles in 2003 increased approximately linearly from May–June 2003–04 ($F_{2,56} = 176{\cdot}1$, $P < 0{\cdot}001$; Fig. 2a). In contrast, recreational shooting altered the body condition of surviving adults ($F_{2,38} = 3{\cdot}23$, $P = 0{\cdot}050$; Fig. 2b). Before shooting, adult body condition did not differ between control and treatment colonies ($t_{18} = 0{\cdot}46$, $P = 0{\cdot}65$). After shooting, adult body condition decreased on treatment colonies and increased on control colonies, resulting in a 35% difference in body condition between control and treatment colonies later in the summer of shooting ($t_{18} = 2{\cdot}78$, $P = 0{\cdot}012$). By the following summer, body condition of adults on treatment colonies had recovered somewhat, to 17% below control values ($t_{18} = 3{\cdot}00$, $P = 0{\cdot}008$; Fig. 2b).

Stress responses to shooting depended on age (Fig. 3). For adults, recreational shooting did not affect stress; corticosterone levels were 10·8 ± 0·7 (± 1 SE) ng g^{-1} dry faeces for both control and treatment colonies, before and after shooting ($F_{1,27} < 0{\cdot}001$, $P = 0{\cdot}99$). Also for adults, corticosterone levels did not change from May–June 2003 to July–August 2003 ($F_{1,27} = 0{\cdot}60$, $P = 0{\cdot}45$). In contrast, juveniles exhibited elevated stress in response to shooting ($F_{1,41} = 7{\cdot}42$, $P = 0{\cdot}009$); before shooting, corticosterone levels did not differ between control and treatment colonies ($t_8 = 0{\cdot}47$, $P = 0{\cdot}65$). After shooting, however, values increased on treatment colonies to levels 80% higher than those on control colonies ($t_{33} = 4{\cdot}95$, $P < 0{\cdot}001$; Fig. 3).

DENSITY, DEMOGRAPHY AND VITAL RATES

Prior to shooting in 2003, prairie dog densities were similar between control and treatment colonies for juveniles ($t_3 = -0{\cdot}33$, $P = 0{\cdot}76$), adult females ($t_3 = 0{\cdot}26$, $P = 0{\cdot}81$) and adult males ($t_3 = 1{\cdot}17$, $P = 0{\cdot}33$; Fig. 4). Densities of all three age–sex groups on treatment and control colonies diverged following our shooting treatment (juveniles: $F_{2,7} = 11{\cdot}83$, $P = 0{\cdot}001$; adult females: $F_{2,7} = 4{\cdot}54$, $P = 0{\cdot}034$; adult males $F_{2,7} = 6{\cdot}43$, $P = 0{\cdot}013$; Fig. 4). After shooting in 2003, densities of juveniles born in 2003 did not differ between treatment and control colonies ($t_3 = -2{\cdot}27$, $P = 0{\cdot}11$), but 10 months later the 2004 cohort on treatment colonies was 85% smaller than that of the previous year, and 89% smaller than the 2004 cohort on control colonies ($t_3 = -4{\cdot}96$, $P = 0{\cdot}016$; Fig. 4a). Shooting reduced adult female densities by 40% in the short term, to values lower than those on control colonies at the same time ($t_3 = -3{\cdot}40$, $P = 0{\cdot}042$). Ten months later, densities of adult females on treatment

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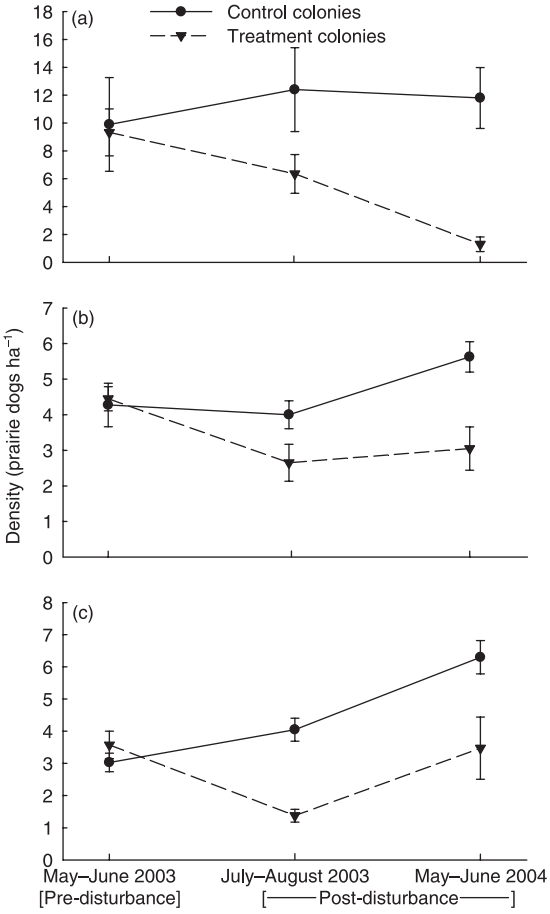


Fig. 4. Density estimates (± 1 SE) for (a) juvenile, (b) adult female and (c) adult male black-tailed prairie dogs on control and treatment colonies during three trapping occasions, Thunder Basin National Grassland, Wyoming, 2003–04. Treatment colonies were subjected to intensive recreational shooting in June–July 2003. For juveniles, shooting did not immediately reduce their densities, but 1 year later juvenile densities fell by 85%. Shooting reduced female densities by 40% in the short term and these densities remained lower 1 year later, in 2004. Adult males were most susceptible to shooting, exhibiting a 62% decline in densities, but were capable of rebounding to predisturbance and control-level densities in 2004.

colonies remained marginally lower than on control colonies ($t_3 = -2{\cdot}99$, $P = 0{\cdot}058$; Fig. 4b). For adult males the pattern differed; densities declined by 62% in short-term response to shooting ($t_3 = -9{\cdot}05$, $P = 0{\cdot}003$), but recovered by 10 months later, when densities did not differ from those on control colonies ($t_3 = -2{\cdot}23$, $P = 0{\cdot}11$; Fig. 4c). Changes in the density of each age–sex group is explained partially by the selectivity of shooting: juveniles represented 59% of animals shot, a value proportional to their abundance (Appendix S2), while adult females were the least vulnerable, composing only 15% of animals shot, but 22% of the colony members. Adult males were the most susceptible age–sex group, constituting 26% of animals shot, but only 19% of the animals on the colony (Appendix S2).

Age structure did not differ between control and treatment colonies before shooting ($G2 = 2{\cdot}46$, $P = 0{\cdot}88$); juveniles dominated age–sex groups (53% of animals),

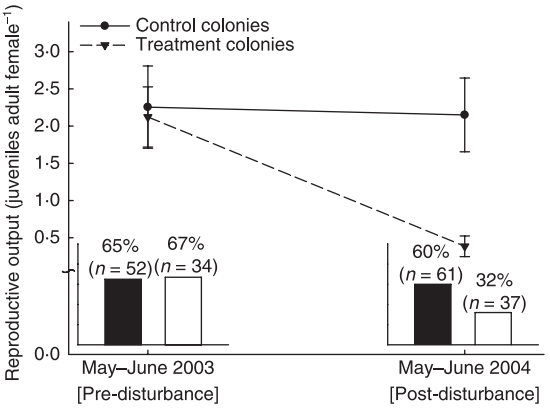


Fig. 5. Mean reproductive output (± 1 SE; main graph) and pregnancy rates (inset bar graphs) for adult female black-tailed prairie dogs on control (solid shading, inset bar graphs) and treatment colonies (open shading, inset bar graphs), Thunder Basin National Grassland, Wyoming, 2003–04. After shooting treatment colonies in June–July 2003, pregnancy rates fell by 50% and reproductive output fell by 82%.

followed by adult females (27%) and adult males (20%). Immediately after shooting, age structure did not differ between control and treatment colonies ($G_2 = 3{\cdot}10$, $P = 0{\cdot}21$). However, 10 months after shooting, age structure had changed ($G_2 = 11{\cdot}7$, $P = 0{\cdot}003$), with juveniles (born in 2004) less prevalent on treatment colonies (16% vs. 49% on control colonies). The proportion of the population that was adult female (39% treatment, 24% control) and adult male (45% treatment, 27% control) increased, reflecting the major decline in proportional abundance of juveniles.

Before shooting, age structure for prairie dogs > 1 year of age did not differ between control and treatment colonies for females ($G_1 = 2{\cdot}47$, $P = 0{\cdot}12$) or males ($G_1 = 0{\cdot}14$, $P = 0{\cdot}71$); 31% of adult females and 30% of adult males were yearlings. One year after shooting, the percentage of yearling females increased (53%), but did not differ between control and treatment colonies ($G_1 = 0{\cdot}01$, $P = 0{\cdot}94$). For males in 2004, however, age structure diverged between control and treatment colonies ($G_1 = 4{\cdot}89$, $P = 0{\cdot}027$); on control colonies, the percentage of yearlings increased to 54%, while on treatment colonies the percentage of yearlings more than doubled, to 76%.

In 2003, reproductive output was 2·2 juveniles × adult female^{-1}, similar between control and treatment colonies ($t_3 = -0{\cdot}41$, $P = 0{\cdot}71$; Fig. 5). The summer following shooting reproductive output remained similar on control colonies, but fell by 82%, to 0·4 juveniles × adult female^{-1}, on treatment colonies ($t_3 = 3{\cdot}33$, $P = 0{\cdot}044$; Fig. 5). This reduction reflected a concomitant decline in pregnancy rates, which did not differ between control and treatment colonies in 2003 ($G_1 < 0{\cdot}01$, $P = 0{\cdot}96$); 66% of females showed evidence of recent reproduction (Fig. 5). In 2004, however, 60% of females on control colonies gave birth, in comparison with just 32% of females on treatment colonies ($G_1 = 6{\cdot}62$, $P = 0{\cdot}010$; Fig. 5).

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Table 3. Twelve a priori models from survival analyses using program MARK (White & Burnham 1999) for black-tailed prairie dogs from eight paired study colonies, Thunder Basin National Grasslands, captured in Wyoming, 2003 and 2004. We modelled capture ($\hat{p}$) and recapture probabilities ($\hat{c}$) from five variables: age (juvenile, adult), date (date of capture or recapture), session (primary trapping session), colony (the eight colonies) and treatment (control vs. treatment colonies). We modelled prairie dog survival ($\hat{S}$) from six variables: interval (period between trapping sessions), age (juvenile, adult), age/sex (juvenile, adult male, adult female), block (colony pairs), shot-acute (shooting effects on treatment colonies from May–August 2003) and shot-chronic (shooting effects on treatment colonies from August 2003 to May 2004). For all models temporary emigration (γ'') and immigration (γ') were set at 0 and therefore not depicted below. Models were ranked using Akaike's information criterion (AIC_c). Also provided with each model are ΔAIC_c (the difference between the best model's AIC_c and subsequent models), w_i (weight of evidence in favour of each model), K (number of parameters) and log (L) (maximum log-likelihood)

Model	AICc	ΔAICc	w_i	K	log(L)
$\hat{S}$ (interval, age, shot-acute) $\hat{p}$ (age,date*session, colony,treatment) $\hat{c}$ (age,date*session,colony)	7952·6	0	0·410	29	–3945·9
$\hat{S}$ (interval,age/sex,shot-acute) $\hat{p}$ (age,date*session, colony,treatment) $\hat{c}$ (age,date*session,colony)	7954·2	1·6	0·184	30	–3945·6
$\hat{S}$ (interval,age,shot-acute,shot-chronic) $\hat{p}$ (age,date* session,colony,treatment) $\hat{c}$ (age,date*session,colony)	7954·6	2·0	0·151	30	–3945·8
$\hat{S}$ (interval,age,block,shot-acute) $\hat{p}$ (age,date* session,colony,treatment) $\hat{c}$ (age,date*session,colony)	7955·5	2·9	0·095	32	–3944·0
$\hat{S}$ (interval,age/sex,shot-acute,shot-chronic) $\hat{p}$ (age,date *session,colony,treatment) $\hat{c}$ (age,date*session,colony)	7956·3	3·7	0·064	31	–3945·5
$\hat{S}$ (interval,age/sex,block,shot-acute) $\hat{p}$ (age,date* session,colony,treatment) $\hat{c}$ (age,date*session,colony)	7957·2	4·7	0·040	33	–3943·8
$\hat{S}$ (interval,age,block,shot-acute,shot-chronic) $\hat{p}$ (age,date* session,colony,treatment) $\hat{c}$ (age,date*session,colony)	7957·2	4·7	0·040	33	–3943·8
$\hat{S}$ (interval,age/sex,block,shot-acute,shot-chronic) $\hat{p}$ (age,date* session,colony,treatment) $\hat{c}$ (age,date*session,colony)	7959·1	6·5	0·016	34	–3943·6
$\hat{S}$ (interval,age,block) $\hat{p}$ (age,date*session,colony, treatment) $\hat{c}$ (age,date*session,colony)	7968·4	15·8	0·000	31	–3951·6
$\hat{S}$ (interval,age) $\hat{p}$ (age,date*session,colony,treatment) $\hat{c}$ (age,date*session,mix*adult,colony)	7968·0	15·4	0·000	28	–3954·7
$\hat{S}$ (interval,age/sex,block) $\hat{p}$ (age,date*session,colony,treatment) $\hat{c}$ (age,date*session,colony)	7970·3	17·7	0·000	32	–3951·4
$\hat{S}$ (interval,age/sex) $\hat{p}$ (age,date*session,colony,treatment) $\hat{c}$ (age,date*session,colony)	7969·8	17·2	0·000	29	–3954·5

Table 4. Survival estimates and associated standard errors for black-tailed prairie dog age–sex groups in Thunder Basin National Grassland, Wyoming, 2003–04. Modelling was performed in program MARK. Treatment colonies were subjected to a pulse of recreational shooting in June–July 2003; control colonies were protected from shooting. Shown, in order, are estimates from the three most competitive models ranked by AIC_c. For details on models and model ranking see Table 3

	June–August 2003				August 2003–June 2004			
	Control		Treatment		Control		Treatment	
Age–sex group	$\hat{S}$	SE	$\hat{S}$	SE	$\hat{S}$	SE	$\hat{S}$	SE
Model 1								
Juvenile	0·725	0·047	0·438	0·06	0·423	0·042	–*	–*
Adult	0·677	0·055	0·383	0·06	0·368	0·044	–*	–*
Model 2								
Juvenile	0·726	0·047	0·438	0·06	0·423	0·042	–*	–*
Adult male	0·647	0·069	0·351	0·07	0·337	0·057	–*	–*
Adult female	0·697	0·06	0·404	0·07	0·390	0·054	–*	–*
Model 3								
Juvenile	0·727	0·048	0·438	0·06	0·450	0·071	0·414	0·045
Adult	0·678	0·055	0·381	0·06	0·392	0·069	0·358	0·048

*Survival estimates and standard error did not differ from those computed for control colonies.

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Variation in survival was best explained by a model (Table 3) that included parameters for trapping sessions, age–sex group and shooting ($\Delta AIC_c = 0·0$, $w_i = 0·410$; Table 3). Estimates of survival from June to August 2003 on control colonies were 0·73 for juveniles and 0·68 for adults. Corresponding estimates for treatment colonies (juvenile: 0·44; adult: 0·38) were about 30% lower (Table 4). Overwinter survival (August 2003–

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June 2004), however, was not affected by shooting; our best model estimated juvenile survival as 0·42 and adult survival as 0·37 for both control and treatment colonies (Table 4).

We found less, and approximately equal, support for two other models (Table 3) that, in addition to accounting for short-term effects of shooting, also (1) differentiated survival rates among sexes ($\Delta AIC_c = 1{\cdot}6$, $w_i = 0{\cdot}184$); and (2) accounted for shooting reducing overwinter survival on treatment colonies ($\Delta AIC_c = 2{\cdot}0$, $w_i = 0{\cdot}151$). However, both models appeared suboptimal because log-likelihood estimates remained similar even though the number of estimable parameter increased (Table 3). Further, uncertainty associated with the survival estimates from these suboptimal models resulted in considerable overlap between survival estimates, making their utility ambiguous (Table 4). As predicted, models that did not account for changes in survival from shooting fitted our data poorly (ΔAIC_c range = 15·8–17·2, all $w_i < 0{\cdot}0001$; Table 3).

Discussion

Prairie dogs subjected to hunting exhibited risk-disturbance effects that overwhelmed and obscured any possible density-dependent ones. As observed in some other hunted vertebrates, surviving prairie dogs altered behaviour to reduce their vulnerability to shooting at the expense of other fitness-enhancing activities. They increased their alertness and decreased above-ground activity, time spent foraging and time spent resting above ground. In general, these behavioural responses were transient, returning to preshooting and control-colony levels the summer after shooting. However, alert behaviours remained slightly elevated on treatment colonies 10 months later. This persistently elevated alertness may reflect a confounding influence, however. Loughry (1992) showed that adult prairie dogs exhibited higher alertness than juveniles, so the increase in alertness we observed could be attributable to changes in age structure. Although qualitatively similar behavioural responses have been reported for hunted waterfowl (Madsen & Fox 1995; Féret *et al*. 2003) and ungulates (Kilgo *et al*. 1998), prairie dog responses to shooting were particularly dramatic.

Behavioural responses of prairie dogs to shooting may have been influenced by factors in addition to risk-avoidance. First, prairie dogs exhibit complex social networks and deaths due to shooting could have disrupted important social interactions and individual behaviour. Indeed, Shier (2006) showed that among translocated prairie dogs, group cohesion strongly affected foraging efficiency: intact family groups foraged more and were vigilant less than those composed of mostly unrelated individuals. Shier (2006) found that these changes extended to survival and reproductive output, as did we. Secondly, in contrast to more traditional forms of hunting, recreational shooting involves many rounds fired over hours (Table 1; Vosburgh & Irby 1998). Such a disturbance contributed presumably to the dramatic behavioural responses we observed in prairie dogs. Thus, the behavioural sensitivity of prairie dogs to shooting seems a combination of their coloniality, low mobility and sensitivity to social disruption as well as the duration and intensity of the disturbance.

Reduced foraging and above-ground activity resulted in lowered body condition of surviving adult prairie dogs, which had body conditions 35% poorer than those of control animals. Although adult body condition on treatment colonies improved the following year, it remained 17% lower than on control colonies. So, effects of shooting on body condition via foraging persisted into the next growing season for adults. In contrast, shooting did not affect the body condition of surviving juveniles, for reasons that are suggested by our stress-response data. Unlike adults, juveniles exhibited a distinct stress-response to shooting, but no response of body condition. We hypothesize that juveniles tended to remain above ground and forage during and after shooting, unlike adults. Prairie dogs survive winter on somatic stores (Lehmer & Van Horne 2001), and with especially limited stores, juveniles must increase body mass rapidly in the first summer of life to survive their first winter (Rayor 1985). Therefore, juveniles may need to forage during times of increased risk, including during shooting, more than do adults, thereby exposing them to disturbance and resulting physiological stress (Lima 1998). Despite the adaptiveness of corticosterone in managing short-term stressors, chronically high levels can lead to reproductive failure, immune suppression and poor body condition (Sapolsky 1992). Therefore, chronically elevated corticosterone levels could cascade to reduced survival and recruitment.

Such cascades have been shown for other hunted species. Féret *et al*. (2003) and Roy & Woolf (2001) found that game birds subjected to intensive hunting increased the time spent flying and decreased the time spent foraging, with negative consequences for body condition. Hjeljord & Histøl (1999) found that the body mass of moose (*Alces alces*) in Norway was correlated negatively with hunting intensity. The changes reported by these studies were less dramatic than those we describe here for prairie dogs. Again, the coloniality and low mobility of prairie dogs and the intense and disruptive nature of recreational shooting seem to account for this difference.

Age–sex groups differed in their vulnerabilities and responses to shooting. Adult females were not particularly susceptible to shooting, but failed to recover to preshooting densities the summer after the treatment. Conversely, adult males were susceptible to shooting, but recovered to preshooting and control-colony densities the following summer. Juvenile proportional abundances were not affected in the short term, but were reduced by 85% the following summer. Juveniles, the dominant age group (54%) on colonies before shooting, were the smallest age group (< 20%) the following year. This delayed effect, of shooting on juvenile abundance the following summer, was mediated largely

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by reproduction. On colonies subjected to shooting, reproductive output decreased by 82% from 2003 to 2004, whereas control colonies showed little change over the same period. The proportion of females producing young on treatment colonies declined by ~0·5. Knowles (1987) found a fairly constant 0·66 of females giving birth, similar to values from our control colonies.

Two mechanisms could explain reduced pregnancy and reproductive rates on treatment colonies. First, reduced body condition of surviving adult females could have reduced litter production. We found that the body condition of prairie dogs > 1 year of age decreased by 35% in response to shooting. Somatic stores are important for both survival and reproduction among ground squirrels (Woods & Armitage 2003), and female prairie dogs must accumulate sufficient reserves to reproduce successfully (Seabloom & Theisen 1990). At northern latitudes, black-tailed prairie dogs copulate in February–March (Hoogland 1995), when prairie dogs have the lowest body masses and are most stressed nutritionally (Lehmer & Van Horne 2001). Therefore, adult females on colonies subjected to shooting could have been physiologically unable to carry a litter to parturition, as a result of foraging opportunities lost (Knowles 1987). Secondly, changes in age–sex structure could have reduced the availability of reproductively competent males. The summer after shooting abundance of males rebounded, but ages were lower than before shooting; most mature males had been replaced by presumably immigrant, yearling males. As in larger mammals (Wielgus & Bunnell 1994), yearling male prairie dogs are less competent breeders than older males (Seabloom & Theisen 1990). This form of Allee effect, resulting from reduced availability to breeding-age females of competent adult males (Stephens & Sutherland 2000), could be an important consequence of male-biased hunting, particularly among polygynous, colonial animals for which females are mate-selective (Halliday 1983). Thus, nutritional deficiencies in adult females or the influx of yearling males after shooting – or both – might have contributed to the reproductive near-collapse that we observed the summer following shooting.

Surprisingly, shooting did not improve overwinter survival. If anything, we saw evidence for decreased survival among treatment animals. One top-ranked model accounted for reduced overwinter survival on treatment colonies, but those survival estimates overlapped considerably with values for control colonies. None the less, the importance of incorporating a parameter for shooting was apparent; models that accounted for an effect of shooting in reducing survival were competitive, while models that did not do so performed poorly.

COMPARATIVE ASPECTS

Generally, populations of small-bodied mammalian herbivores, such as lagomorphs (Rose 1977) and squirrels (Mosby 1969), recover quickly from hunting via density-dependent vital rates. In contrast, prairie dogs in our study showed no evidence of density dependence in overwinter survival or next-year natality. Rather, we found that for prairie dogs, hunting induced not only additive effects on survival, but also led to reproductive near-collapse the summer following the shooting. We attribute these remarkable effects to costs represented by shooting to a highly colonial species: shooting reduced the usual benefits and increased some of the common costs of coloniality. In unperturbed colonies, animals benefit from cooperative vigilance, allowing a relaxation of individual vigilance, which increases foraging efficiency and reduces susceptibility to predation (Hoogland 1981). Coloniality also facilitates adult reproduction and juvenile survival through enhanced mate-finding and cooperative breeding (Jennions & MacDonald 1994). These common benefits of coloniality, however, appeared to be reduced by recreational shooting. Intense, prolonged shooting increased alertness at the expense of foraging, so that a primary benefit of coloniality was reduced. Coloniality presumably facilitates reproduction by providing easy access to mates, and some communal care of neonates. However, the effects that we observed suggest a shift in the net fitness costs and benefits of coloniality.

Among costs, coloniality causes all above-ground animals to be disturbed by a single shot that is fired; animals that escape to below ground forego foraging opportunities. Under most circumstances, access to mature male mates is not limiting to female prairie dogs (Hoogland & Foltz 1982), but shooting selectively removed adult males, so that female access to competent mates may have been reduced. This may have contributed to the reproductive near-collapse the summer after shooting. Thus, coloniality appears to make prairie dogs more sensitive to hunting than other small mammalian herbivores.

CONSERVATION IMPLICATIONS

Prairie dogs are ecologically pivotal members of North American grassland systems (Miller *et al*. 1994), supporting predators, including the obligate prairie dog predator, the endangered black-footed ferret (*Mustela nigripes*). Prairie dog burrows also provide habitat structure for burrowing owls (*Athene cunicularia*), prairie rattlesnakes (*Crotalus viridis*) and various small mammals. Through herbivory, prairie dogs alter vegetation and cycle nutrients (Holland & Detling 1990). Therefore, the population biology of prairie dogs and the viability of their colonies have broad implications for North American grassland communities. Future research needs to elucidate the large-scale effects of shooting on prairie dog populations and colony viability as well as its effects on other species that depend on prairie dog colonies. Wildlife managers should consider measures to reduce recreational shooting intensity and duration in regions where black-tailed prairie dog colony growth

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and persistence is desired, such as recovery sites for the black-footed ferret, yet allow shooting to continue in areas where colonies conflict with private-landowner interests.

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References

Bateson, P. & Bradshaw, E.L. (1997) Physiological effects of hunting red deer (*Cervus elaphus*). *Proceedings of the Royal Society of London, Series B*, **263**, 1707–1714.

Béchet, A., Giroux, J.-F., Gauthier, G., Nichols, J.D. & Hines, J.E. (2003) Spring hunting changes the regional movements of migrating greater snow geese. *Journal of Applied Ecology*, **40**, 553–564.

Blumstein, D.T. & Pelletier, D. (2005) Yellow-bellied marmot hiding time is sensitive to variation in costs. *Canadian Journal of Zoology*, **83**, 363–367.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: a Practical Information-Theoretical Approach*, 2nd edn. Springer-Verlag, New York, NY.

Cox, M.K. & Franklin, W.L. (1990) Premolar gap technique for aging live black-tailed prairie dogs. *Journal of Wildlife Management*, **54**, 143–146.

von Ende, C.N. (2001) Repeated-measures analysis: growth and other time-dependent measures. *Design and Analysis of Ecological Experiments*, 2nd edn (eds S.M. Scheiner & J. Gurevitch), pp. 134–157. Oxford University Press, New York, NY.

Féret, M., Gauthier, G., Béchet, A., Giroux, J.-F. & Hobson, K.A. (2003) Effect of a spring hunt on nutrient storage by greater snow geese in southern Quebec. *Journal of Wildlife Management*, **67**, 796–807.

FitzGibbon, C. (1998) The management of subsistence harvesting: behavioral ecology of hunters and their mammalian prey. *Behavioral Ecology and Conservation Biology* (ed. T. Caro), pp. 449–473. Oxford University Press, New York, NY.

Fowler, C.W. (1987) A review of density dependence in populations of large mammals. *Current Mammalogy* (ed. H. H. Genoways), pp. 401–441. Plenum Press, New York, NY.

Frid, A. & Dill, L.M. (2002) Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6**, 11. Available at: http://www.consecol.org/vol6/iss1/art11 (accessed 1 January 2005).

Gill, J.A., Norris, K. & Sutherland, W.J. (2001) Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation*, **97**, 265–268.

Halliday, T.R. (1983) The study of mate choice. *Mate Choice* (ed. P. Bateson), pp. 3–32. Cambridge University Press, Cambridge, UK.

Harper, J.M. & Austad, S.N. (2000) Fecal glucocorticoids: a noninvasive method of measuring adrenal activity in wild and captive rodents. *Physiological and Biochemical Zoology*, **73**, 12–22.

Hjeljord, O. & Histøl, T. (1999) Range–body mass interactions of a northern ungulate – a test of a hypothesis. *Oecologia*, **119**, 326–339.

Holland, E.A. & Detling, J.K. (1990) Plant response to herbivory and below ground nitrogen cycling. *Ecology*, **71**, 1040–1049.

Hoogland, J.L. (1979) Aggression, ectoparasitism, and other possible costs of prairie dog (Sciuridae, *Cynomys* spp.) coloniality. *Behaviour*, **69**, 1–35.

Hoogland, J.L. (1981) The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus and C. ludovicianus*). *Ecology*, **62**, 252–272.

Hoogland, J.L. (1995) *The Black-Tailed Prairie Dog: Social Life of a Burrowing Mammal*. University of Chicago Press, Chicago, IL.

Hoogland, J.L. & Foltz, D.W. (1982) Variance in male and female reproductive success in a harem-polygynous mammal, the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). *Behavioral Ecology and Sociobiology*, **11**, 155–163.

Hoogland, J.L. & Sherman, P.W. (1976) Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecological Monographs*, **46**, 33–58.

Horn, H.S. (1966) Measurement of 'overlap' in comparative ecological studies. *American Naturalist*, **100**, 419–424.

Huggins, R.M. (1991) Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics*, **47**, 725–732.

Jennions, M.D. & Macdonald, D.W. (1994) Cooperative breeding in mammals. *Trends in Ecology and Evolution*, **9**, 89–93.

Kilgo, J.C., Labisky, R.F. & Fritzen, D.E. (1998) Influences of hunting on the behavior of white-tailed deer: implications for conservation of the Florida panther. *Conservation Biology*, **12**, 1359–1364.

Knowles, C.J. (1982) *Habitat affinity, populations, and control of black-tailed prairie dogs on the Charles M. Russell National Wildlife Refuge.* MS Thesis, University of Montana.

Knowles, C.J. (1987) Reproductive ecology of black-tailed prairie dogs in Montana. *Great Basin Naturalist*, **47**, 202–206.

Kokko, H. (2001) Optimal and suboptimal use of compensatory responses to harvesting: timing of hunting as an example. *Wildlife Biology*, **7**, 141–150.

Krebs, C.J. (1999) *Ecological Methodology*, 2nd edn. Addison-Wesley Longman, Inc., Menlo Park, CA.

Krebs, C.J. & Singleton, G.R. (1993) Indices of condition for small mammals. *Australian Journal of Zoology*, **41**, 317–323.

Lehmer, E.M. & Van Horne, B. (2001) Seasonal changes in lipids, diet, and body condition of free-ranging black-tailed prairie dogs (*Cynomys ludovicianus*). *Canadian Journal of Zoology*, **79**, 955–965.

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Lima, S.L. (1998) Stress and decision making under the threat of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior*, **27**, 215–290.

Loughry, W.J. (1992) Ontogeny of time allocation in black-tailed prairie dogs. *Ethology*, **90**, 206–224.

Madsen, J. (1998) Experimental refuges for migratory waterfowl in Danish wetlands. II. Tests of hunting disturbance effects. *Journal of Applied Ecology*, **35**, 398–417.

Madsen, J. & Fox, A.D. (1995) Impacts of hunting disturbance on waterbirds – a review. *Wildlife Biology*, **1**, 193–207.

Mainguy, J., Bêty, J., Gauthier, G. & Giroux, J.-F. (2002) Are body condition and reproductive effort of laying greater snow geese affected by the spring hunt? *Condor*, **104**, 156–161.

Martin, P. & Bateson, P. (1993) *Measuring Behaviour: an Introductory Guide*, 2nd edn. Cambridge University Press, Cambridge, UK.

Miller, B., Ceballos, G. & Reading, R. (1994) The prairie dog and biotic diversity. *Conservation Biology*, **8**, 677–681.

Monfort, S.L., Mashburn, K.L., Brewer, B.A. & Creel, S.R. (1998) Evaluating adrenal activity in African wild dogs (*Lycaon pictus*) by fecal corticosteroid analysis. *Journal of Zoo and Wildlife Medicine*, **29**, 129–133.

Mosby, H.S. (1969) The influence of hunting on the population dynamics of a woodlot grey squirrel population. *Journal of Wildlife Management*, **33**, 59–73.

Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978) Statistical inference from capture data on closed animal populations. *Wildlife Monographs*, **62**, 1–135.

Pauli, J.N., Buskirk, S.W., Williams, E.S. & Edwards, W.H. (2006) A plague epizootic in the black-tailed prairie dog (*Cynomys ludovicianus*). *Journal of Wildlife Diseases*, **42**, 74–80.

Powell, K.L., Robel, R.J., Kemp, K.E. & Nellis, M.D. (1994) Aboveground counts of black-tailed prairie dogs: temporal nature and relationship to burrow entrance density. *Journal of Wildlife Management*, **58**, 361–366.

Rayor, L.S. (1985) Effects of habitat quality on growth, age of first reproduction, and dispersal in Gunnison's prairie dogs (*Cynomys gunnisoni*). *Canadian Journal of Zoology*, **63**, 2835–2840.

Reeve, A.F. & Vosburgh, T.C. (2005) Recreational shooting of prairie dogs. *Conservation of the Black-Tailed Prairie Dog* (ed. J.L. Hoogland), pp. 139–156. Island Press, Washington, DC.

Ripple, W.J. & Beschta, R.L. (2004) Wolves and the ecology of fear: can predation risk structure ecosystems? *Bioscience*, **54**, 755–766.

Rose, G.B. (1977) Mortality rates of tagged adult cottontail rabbits. *Journal of Wildlife Management*, **41**, 511–514.

Roy, C. & Woolf, A. (2001) Effects of hunting and hunting-hour extension on mourning dove foraging and physiology. *Journal of Wildlife Management*, **65**, 808–815.

Sapolsky, R.M. (1992) Neuroendocrinology of the stress-response. *Behavioral Endocrinology* (eds J.B. Becker, S.M. Breedlove & D. Crews), pp. 287–324. Massachusetts Institute of Technnology Press, Cambridge, MA.

Seabloom, R.W. & Theisen, P.W. (1990) Breeding biology of the black-tailed prairie dog in North Dakota. *Prairie Naturalist*, **22**, 65–74.

Shier, D.M. (2006) Effect of family support on success of translocated black-tailed prairie dogs. *Conservation Biology*, **20**, 1780–1790.

Stephens, P.A., Frey-Roos, F., Arnold, W. & Sutherland, W.J. (2002) Sustainable exploitation of social species: a test and comparison of models. *Journal of Applied Ecology*, **39**, 629–642.

Stephens, P.A. & Sutherland, W.J. (2000) Vertebrate mating systems, Allee effects and conservation. *Vertebrate Mating Systems* (eds M. Apollonio, M. Festa-Bianchet & D. Mainardi), pp. 186–213. World Scientific Publishing, London, UK.

Vosburgh, T.C. & Irby, L.R. (1998) Effects of recreational shooting on prairie dog colonies. *Journal of Wildlife Management*, **62**, 363–372.

White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46** (Supp**l.**), 120–138.

Wielgus, R.B. & Bunnell, F.L. (1994) Dynamics of a small, hunted brown bear *Ursus arctos* population in southwestern Alberta, Canada. *Biological Conservation*, **67**, 161–166.

Wilson, K.R. & Anderson, D.R. (1985) Evaluation of two density estimators of small mammal population size. *Journal of Mammalogy*, **66**, 13–21.

Woods, B.C. & Armitage, K.B. (2003) Effect of food supplementation on juvenile growth and survival in *Marmota flaviventris*. *Journal of Mammalogy*, **84**, 903–914.

Zar, J.H. (1999) *Biostatistical Analysis*, 4th edn. Prentice Hall, Inc., Upper Saddle River, NJ.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Attributes of 10 black-tailed prairie dog colonies, Thunder Basin National Grassland, Wyoming, summer 2003.

Appendix S2. Mean standardized selection indices and associated standard errors for prairie dog cohorts shot on treatment colonies, Thunder Basin National Grassland, Wyoming, 2003.

Fig. S1. (a) Locations of 10 black-tailed prairie dog colonies used in an experimental study of recreational shooting around Thunder Basin National Grassland (TBNG), Wyoming, 2003-2004. (b) Cluster tree depicting the relative similarity of colonies using the unweighted pair group method with arithmetic averages.

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