

Spatial and temporal use of a prairie dog colony by coyotes and rabbits: potential indirect effects on endangered black-footed ferrets

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Abstract

In western North America, endangered black-footed ferrets *Mustela nigripes* are conserved via reintroduction to colonies of prairie dogs *Cynomys* spp., their primary prey. Predation is an important source of mortality; coyotes *Canis latrans* appear to be the most problematic predator, accounting for 67% of known predation events on radio-tagged ferrets. Little is known about what factors affect spatial use of prairie dog colonies by coyotes, or how other animals might affect interactions between coyotes and ferrets. During June–October 2007–2008, we used spotlight surveys to monitor coyotes and ferrets (both years) and rabbits *Sylvilagus* spp. (first year) on a 452-ha colony of black-tailed prairie dogs *Cynomys ludovicianus* in the Conata Basin, South Dakota. Coyotes appeared to select areas of the colony used by rabbits, suggesting coyotes hunted rabbits, a common item in their diet. Between midnight and sunrise, ferrets were most commonly observed during early morning (01:00–03:00 h), whereas coyotes were observed mostly during dawn (04:00 h – sunrise) when ferrets were rarely seen. These temporal differences in the timing of observations suggest ferrets tend to remain underground in burrows when coyotes are most active. Coyotes appeared to be attracted to rabbits in both space and time, suggesting the risk of predation for ferrets might relate to the abundance and locations of rabbits in prairie dog colonies.

Introduction

Early studies of predator–prey interactions concentrated on the proximate causes and ultimate functions of antipredator defenses (Lima & Dill, 1990; Caro, 2005). More recently, ecologists have investigated nonlethal effects of predators on prey (e.g. changes in vigilance or habitat use; Lima, 1998; Creel & Christianson, 2008; Creel, 2011) and the hunting behaviors of predators (Lima, 2002; Sih, 2005). Moreover, it has become apparent that animals can affect predator–prey interactions in which they are not directly involved, providing a springboard for research on ‘interaction modifications’ (Wootton, 1994).

Predator–prey interactions are important from a theoretical perspective, but also in wildlife conservation (Barbosa, Caldas & Riechert, 2005). For instance, predation is an important source of mortality for the endangered black-footed ferret *Mustela nigripes*, a primarily nocturnal carnivore that specializes on prairie dogs *Cynomys* for prey and uses prairie dog burrows for shelter (Henderson *et al.*, 1969; Campbell *et al.*, 1987; Brickner *et al.*, 2014). Numerous species kill ferrets, but coyotes *Canis latrans* appear to be the most

problematic predator, accounting for 67% of known predation events during telemetry studies (Biggins *et al.*, 1998, 1999, 2011a,b; Breck *et al.*, 2006). While coyotes sometimes hamper recovery efforts for *M. nigripes*, little is known about what factors affect space use by coyotes on prairie dog colonies, or how other species might affect interactions between coyotes and ferrets.

In this paper, we advance previous ideas on predator–prey interactions between coyotes and black-footed ferrets and potential interaction modifications caused by *Sylvilagus* rabbits, a common item in the coyote diet (Fichter, Schildman & Sather, 1955; MacCracken & Hansen, 1987). During studies in Colorado, rabbit densities were up to 27 times greater on prairie dog colonies than surrounding grasslands (Dano, 1952; Hanson & Gold, 1977), suggesting rabbits may attract coyotes to prairie dog colonies, thereby elevating the risk of coyote predation for ferrets (Biggins, 2000). At finer scales within prairie dog colonies, rabbits might affect the behavior of coyotes and, in doing so, indirectly affect interactions between coyotes and ferrets (Biggins, 2000; Biggins *et al.*, 2011a), but this possibility requires evaluation.

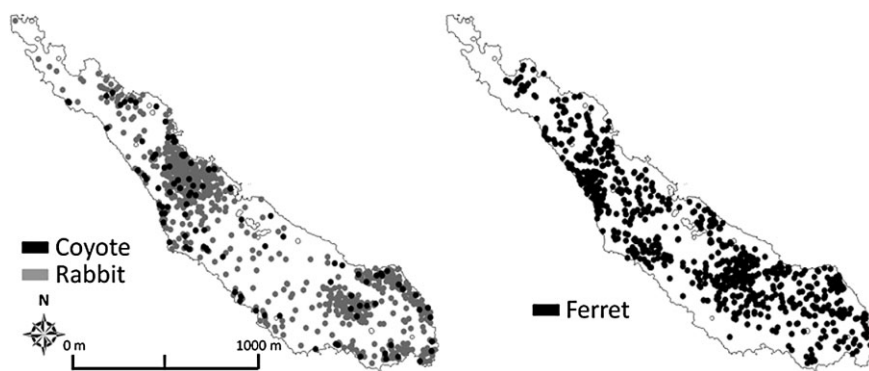


Figure 1 Locations for detections of coyotes *Canis latrans*, cottontail rabbits and black-footed ferrets *Mustela nigripes* on colony SC07, the South Exlosure, a 452-ha colony of black-tailed prairie dogs in the Conata Basin, South Dakota (43°45'N, 102°18'W). We monitored coyotes and black-footed ferrets via spotlight surveys during June–October 2007 and 2008; rabbit locations were approximated during 2007. Locations of active openings to prairie dog burrows are depicted in Eads *et al.* (2011).

Three questions are relevant to fine-scale interactions between coyotes and ferrets: (1) Does coyote spatial activity on prairie dog colonies correlate with space use by rabbits? (2) Does rabbit spatial activity correlate with space use by ferrets in areas with high prairie dog density (Eads *et al.*, 2011)? (3) What is the temporal pattern of coyote activity on prairie dog colonies relative to rabbits and ferrets? We evaluate these questions using data on relationships among prairie dogs, rabbits, coyotes and ferrets during nighttime periods in a colony of black-tailed prairie dogs *Cynomys ludovicianus*.

Prairie dogs typically remain in burrows and, consequently, are mostly inaccessible to coyotes at night (Hoogland, 1995). Thus, we hypothesized that coyotes would not exhibit selection for areas where prairie dogs were abundant. As a corollary, we hypothesized that coyotes would not select areas used by black-footed ferrets, because ferrets selectively use areas where prairie dogs are abundant (Eads *et al.*, 2011); further, in most cases, coyotes do not eat the ferrets they kill, suggesting predation relates mostly to interspecific competition, and less to acquisition of food (Biggins *et al.*, 2011a). We hypothesized that coyotes would select areas used by rabbits.

We also evaluate how rabbits might indirectly affect spatial interactions between coyotes and ferrets. We expected that rabbits would not exhibit selection for areas where prairie dogs were abundant because the two herbivores may compete for food (Hanson & Gold, 1977) and prairie dogs exhibit agonistic behaviors toward rabbits (Eads *et al.*, 2015). Instead, we posited that rabbits would select areas with reduced prairie dog densities. In doing so, rabbits might reduce competition for forage, while also luring coyotes away from areas inhabited by ferrets.

Coyotes often exhibit increased rates of movement during crepuscular periods (Arias-Del Razo *et al.*, 2011). Thus, during our primary sampling period, from midnight to dawn, we posited that we would most commonly observe coyotes around sunrise. As suggested by radio-tracking data (Biggins *et al.*, 1986, 2011a) and previous spotlight surveys (Clark *et al.*, 1986; Paunovich & Forrest, 1987), we hypothesized that spotlight observations of ferrets would be most common during 01:00–04:00 h, a period when rabbits and coyotes typically exhibit low rates of activity.

Materials and methods

We conducted our study in the Conata Basin, South Dakota, on a 452-ha colony of black-tailed prairie dogs that has been referred to as the ‘South Exlosure’ or ‘SC07’ (Fig. 1). The colony is situated primarily in Buffalo Gap National Grasslands but the northern tip extends to Badlands National Park. Cottontail rabbits are commonly observed on prairie dog colonies in the general area, whereas *Lepus* jackrabbits are not (see also Dano, 1952). Research was completed under University of Missouri Animal Use and Care Committee Protocol 6839 and met guidelines of the American Society of Mammalogists for the use of mammals in research (Sikes *et al.*, 2011).

During July to mid-September 2007, we used Trimble CMT MC-V global positioning system (GPS) receivers (Trimble Navigation Limited, Sunnyvale, CA, USA) to record the Universal Transverse Mercator (UTM) locations of openings to prairie dog burrows (Eads *et al.*, 2011). An opening was classified as ‘active’ if fresh prairie dog scat (greenish, black or dark brown) was present within 0.5 m of the opening, and the opening was at least 7 cm wide. Densities of active burrow openings provide an index of prairie dog densities (Biggins *et al.*, 1993). The proportionate activity of burrow openings was the same in 2007 and 2008 in 177 of 192 circular plots (20 m radius) distributed throughout the colony, suggesting some consistency in the distribution of active burrows during our study (Eads *et al.*, 2011).

During 13 June–10 October 2007 and 11 June–27 September 2008, we used spotlight surveys to monitor coyotes, black-footed ferrets and rabbits (Eads, 2009; Eads *et al.*, 2011, 2012; Eads & Biggins, 2012). The survey route was established as a loop that helped maximize coverage of the colony, while minimizing overlap (Eads *et al.*, 2011). During a survey, the loop was repeatedly traversed at 8–16 km h⁻¹, with each circuit lasting about 45 min to 1 h. Observers conducted spotlight surveys during 78% of nights in the study ($n = 93/120$ in 2007; 86/109 in 2008); surveys were not feasible during nights with intense rainfall or fog, or when soils were too muddy for efficient travel.

Data within this study are limited to adult ferrets (Eads *et al.*, 2011), adult coyotes and adult rabbits, the latter two classified by size. *Sylvilagus* rabbits tend to inhabit home ranges that are about 3–4 ha in size (Swihart, 1986), suggesting we may have monitored many resident individuals in the 452-ha colony. In contrast, coyotes can inhabit home ranges that are three times or more larger than our 452-ha study colony (Schroeder, 2007). This suggests that our observations probably include a small number of resident coyotes (Andelt, 1985) whose home range included the prairie dog colony, and transient coyotes that moved through the colony on occasion.

We devised a procedure to reduce repeat observations of the same coyote or rabbit during a circuit through the colony. Upon collecting a location for a coyote in a portion of the colony, another coyote location was not recorded for that portion of the colony (~200 m radius) until the area was sampled during the next circuit. We rarely collected >1 coyote observation per circuit. The criterion was slightly modified for rabbits; two or more rabbit locations could be collected in the same area (~100 m) during a circuit if >1 animal was observed in the same area at the same time. These criteria, although somewhat arbitrary, may have reduced the number of repeat observations of individual coyotes and rabbits during a circuit through the colony, but would not have reduced the occurrence of resighting during separate circuits within a night or during different nights.

We collected locations of coyotes and ferrets via handheld GPS units as UTM coordinates (Garmin GPS 12XL Personal Navigator units, error ≤ 15 m; Garmin International, Inc., Olathe, KS, USA) and noted the time of each observation using a satellite clock (Eads *et al.*, 2011, 2012; Eads & Biggins, 2012). Coordinates were collected at the location where an animal was first observed.

Rabbits were observed much more frequently than ferrets and coyotes, which inhibited collection of all coordinates for rabbits because such data collection could have compromised the carnivore surveys. Instead, in 2007, we drew rabbit locations (time not recorded) on printed maps of features that assisted in estimating locations, including the colony boundary, fences and wooden posts. In ArcGIS® 9.2 (Environmental Systems Research Institute, Redlands, CA, USA), we transferred the rabbit locations to a georeferenced map of the colony and calculated UTM coordinates for each observation.

To evaluate the accuracy of the rabbit locations, we used GPS units in the field to estimate UTM coordinates for a subset of 15 rabbit observations that were plotted on the maps. We calculated the Euclidean distance between the GPS field estimates and those derived from mapped approximations. The locations differed by an average of 90.87 m ($SD = 18.95$). Errors of this sort would introduce nuisance variation that would weaken our ability to detect relationships between coyotes and rabbits, but the errors would not be expected to bias our results.

We did not estimate locations of rabbits in 2008 but spotlight surveys suggested rabbits concentrated their crepuscular and nighttime activities in the same portions of the colony during both years of study (D. A. Eads, pers. obs.). Between-

year changes in space use by rabbits should have weakened our ability to detect relationships between coyotes and rabbits when the 2007–2008 data were combined (we analyzed the 2007 and 2007–2008 data).

In ArcGIS, we combined the coyote and ferret locations (2007 or 2008 separately) and the 2007 rabbit locations with the map of active burrow openings (Fig. 1). We buffered all coyote locations by a 20 m radius circular plot (0.13 ha; Eads & Biggins, 2012; Eads *et al.*, 2013) and counted the numbers of active burrow openings, rabbit locations and ferret locations in each plot. The 0.13-ha plot size was selected because small plots would seemingly include fewer rabbit or ferret locations than larger plots, which could make it more difficult to detect a relationship between coyotes and rabbits or ferrets.

We implemented a use-availability design to investigate habitat selection by coyotes (Johnson, 1980). Used locations were those at which a coyote was observed via spotlight. We generated available locations (one per coyote location; Eads *et al.*, 2013) as random locations restricted to the area of the colony, which was delineated by Eads *et al.* (2011). This approach assumes the entire colony was available to coyotes, which seems reasonable for a far-ranging carnivore. We buffered each available location by a circle of 20-m radius and counted the numbers of active burrow openings, rabbit locations and ferret locations in each plot. Most plots contained 0–1 rabbit locations and 0–1 ferret locations, so we converted those counts to binomial variables (presence/absence).

During analysis of the coyote data, we compared the rank values for numbers of active burrow openings in used and available plots using Mann–Whitney U -tests ($\alpha = 0.05$) in Program R version 2.11.1 (R Development Core Team, 2010). We compared the presence or absence of rabbits or ferrets in used and available plots using χ^2 tests of independence.

We also evaluated the habitat selection by rabbits. If rabbits selected particular areas of the prairie dog colony, coyotes might have frequently used those areas, thus increasing predation risk for nearby ferrets. We used the same type of analysis described above but restricted the assessment to numbers of active burrow openings in 0.13-ha circular plots centered on rabbit (used) and available locations.

To evaluate the potential differences in temporal activity by coyotes and ferrets during our primary survey period, which was assessed during >90% of surveys (midnight – 06:59 h), we categorized the timing of observations ($n = 792$ ferrets, 74 coyotes) into seven hourly intervals and compared frequencies of observations in the intervals using a χ^2 test of independence in Program R. This test used spotlight detection data as an index of activity, and assumed monitoring effort was the same for ferrets and coyotes, which seems plausible because we monitored ferrets and coyotes during the same surveys. The amount of time devoted to searching was sometimes reduced when we (1) collected and recorded locations for animals; (2) trapped ferrets during August–September to assess population size; (3) counted ferret kits with adult females to index offspring production; (4) observed behaviors of individual animals. Nevertheless, these factors equally reduced the amount of time devoted to finding coyotes, ferrets and rabbits.

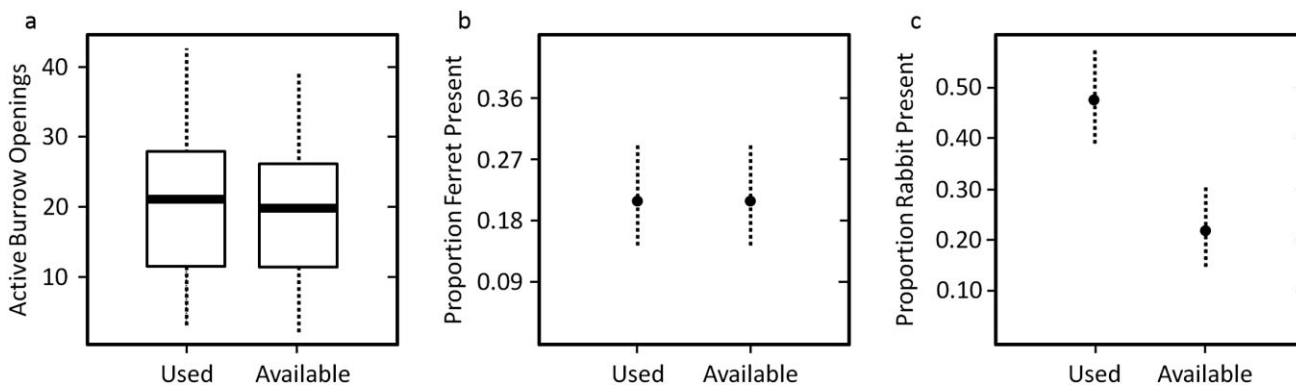


Figure 2 Numbers of active burrow openings within 20 m of coyote *Canis latrans* locations and random locations (a, presented as median box plots) and proportions (means \pm 95% CIs) of 20-m radius circle plots centered on coyote locations and random locations containing one or more black-footed ferret *Mustela nigripes* location (b) and one or more cottontail rabbit location (c).

Results

We collected 101 coyote locations and 979 ferret locations in 2007–2008. We collected 707 rabbit locations in 2007. Ferrets were individually identifiable (9 F, 3 M in 2007; 9 F, 5 M in 2008). On average, we collected 38 observations per ferret in 2007 (range = 12–47) and 30 per ferret in 2008 (range = 2–55). A total of 56 633 active burrow openings were mapped in 2007.

Rank values for numbers of active burrow openings were similar in plots used by or available to coyotes (Fig. 2: $U = 5480$, $P = 0.36$) and similar proportions of used and available plots encompassed a ferret location (Fig. 2: $X^2_1 = 0.00$, $P = 1.00$). Coyotes were observed to be in areas with rabbits more often than areas without rabbits; the plots used by coyotes were about two times more likely to contain a rabbit location than plots deemed available to coyotes (Fig. 2: $X^2_1 = 14.78$, $P < 0.01$). The same results were found when the data were limited to 2007, the year in which rabbit locations were collected ($X^2_1 = 6.77$, $P < 0.01$).

In the assessment of habitat selection by rabbits in 2007, rank values for numbers of active burrow openings were 1.2 times higher in available plots ($U = 77\ 176$, $P < 0.01$). Thus, in contrast to ferrets (Eads *et al.*, 2011), rabbits might have avoided areas with an abundance of prairie dogs.

Between midnight and sunrise during 2007–2008, the timing of ferret and coyote observations differed ($X^2_6 = 254.46$, $P < 0.01$). We most commonly located ferrets during 01:00–03:00 h and coyotes during 04:00 h – sunrise (Fig. 3).

Discussion

Some limitations of our sampling approach

Spotlight surveys have proven valuable in monitoring ferrets (Biggins *et al.*, 2006; Eads *et al.*, 2012) but less is known about the effectiveness of spotlight surveys for rabbits and coyotes in prairie dog colonies. When illuminated under

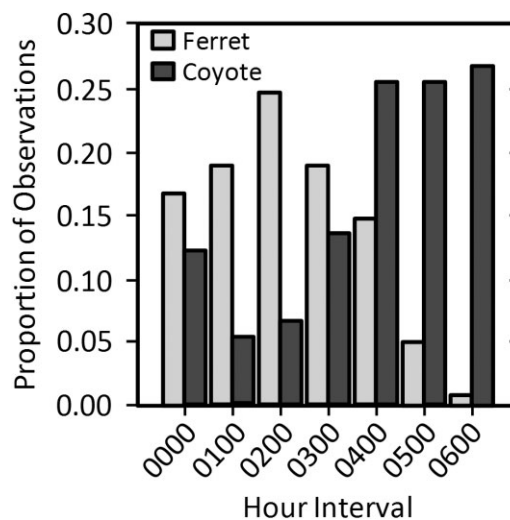


Figure 3 Proportion of coyote *Canis latrans* and black-footed ferret *Mustela nigripes* observations collected in hourly intervals during midnight – 06:59 h.

spotlight, rabbits did not exhibit overt escape responses, but either ‘froze’ (Caro, 2005) or moved to a nearby burrow opening and monitored the survey vehicle. In contrast, coyotes sometimes moved away from the vehicle (Matchett, Breck & Callon, 2013). Although such avoidance is undesirable from a sampling perspective, the coyotes would not be expected to preferentially escape into areas with high or low densities of ferrets, rabbits or active burrow openings.

Coyotes and rabbits were not individually identifiable during our study. The clustering of coyote and rabbit sightings (Fig. 1) could partly reflect sightings of the same individuals. In particular, the coyote data may relate to a small number of residents that consistently occupied our study site, and transients that moved through the area. Thus, inference for *C. latrans* should be interpreted with caution.

Individual marking of rabbits, coyotes and black-footed ferrets (via radio tags or visual means) would allow for estimation of variation due to repeated reobservations of individuals over time. Radio telemetry in particular provides the benefit of potentially providing fine-scale data on spatial and temporal relationships among the animals (Creel, Winnie & Christianson, 2013). On the other hand, costs of telemetry include increased monetary outlays, potential impacts of radio tags on welfare and behaviors of the subjects, and spatial error due to remote tracking methods (Biggins *et al.*, 2006).

While potential limitations of the spotlight surveys should be kept in mind when interpreting our results, the rabbits, coyotes and ferrets at our study site behaved in ways that suggest rabbits could modify interactions between coyotes and ferrets.

Potential interactions between coyotes, rabbits and black-footed ferrets

Coyotes appeared to select areas of the prairie dog colony that were commonly used by rabbits. Perhaps the risk of coyote predation is heightened for black-footed ferrets in areas of prairie dog colonies where rabbits are abundant. While this relationship is perhaps not intuitive, it is supported by field data from a coarse spatial scale at other sites. When Siberian polecats *Mustela eversmannii* were released to two prairie dog colonies as investigational surrogates for ferrets, survival rates were 17 times higher at the colony with 11-fold fewer sightings of rabbits (Biggins *et al.*, 2011b). During that study, the abundance of jackrabbit and cottontail sightings was positively correlated with the abundance of coyote sightings.

In contrast to ferrets during our study (Eads *et al.*, 2011), rabbits did not appear to select areas of the colony with high densities of active burrow openings. This potential difference in resource selection by rabbits and ferrets, and the possible attraction of coyotes to rabbits, may collectively suggest *Sylvilagus* draw coyotes away from ferrets. If so, elevated risk of coyote predation for ferrets at a coarse scale on prairie dog colonies (Biggins, 2000) may be attenuated by the locations of rabbits away from areas with high prairie dog densities.

Between midnight and sunrise at our study site, coyotes were most commonly observed near sunrise, suggesting coyotes exhibited increased rates of movement during dawn. These results correspond with multiple studies in western North America, where coyotes exhibited increased rates of movement during crepuscular periods (e.g. Andelt, 1985; Laundré & Keller, 1981; Young *et al.*, 2006; Arias-Del Razo *et al.*, 2011). The timing of coyote observations in our study also corresponds with high rates of aboveground activity by rabbits during crepuscular periods (Fichter *et al.*, 1955; Mech, Heezen & Siniff, 1966; MacCracken & Hansen, 1987; Young *et al.*, 2006; Arias-Del Razo *et al.*, 2011). Thus, in our study, it seemed coyotes were attracted to rabbits in space and time on a prairie dog colony, as hypothesized by Biggins (2000) and Biggins *et al.* (2011a).

Spotlight observations of ferrets were concentrated during 01:00–03:00 h, an hourly interval in which we rarely observed coyotes. Conversely, we rarely observed ferrets during the

periods when we most commonly observed coyotes (Fig. 3). These temporal differences in the timing of observations suggest ferrets exhibit reduced rates of aboveground activity when coyotes are most active. Such behavior would correspond with a plethora of studies in which animals avoided movements when their most lethal predators were hunting (Caro, 2005).

Recommendations for future research

Our results suggest rabbits may indirectly modify interactions between coyotes and ferrets in space (by affecting space use by coyotes and the 'landscape of fear' for ferrets; Laundré, Hernandez & Altendorf, 2001) and time (by affecting rates of activity by coyotes). If possible, during future studies, large proportions of coyotes, rabbits and ferrets should be monitored intensively at multiple study sites and colonies throughout the year, and individuals should be tracked, for instance using GPS collars (Creel *et al.*, 2013). It would be useful to conduct a multivariate analysis with a suite of ecological variables that are hypothesized to influence the behaviors of these mammals (e.g. vegetation, water sources and other predators). In addition, it might be possible to experimentally manipulate the spatial distribution of rabbits (e.g. Rebollo *et al.*, 2013) in a sample of prairie dog colonies and determine if monitored coyotes respond to the treatment, compared with controls. With continued study, the coyote, rabbit and ferret system might be added to the growing list of wildlife communities in which interaction modifications occur (Wootton, 1994; Morin, 2011).

Acknowledgments

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