Journal of Mammalogy, 92(4):710–720, 2011

Black-footed ferrets and Siberian polecats as ecological surrogates and ecological equivalents

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Ecologically equivalent species serve similar functions in different communities, and an ecological surrogate species can be used as a substitute for an equivalent species in a community. Siberian polecats (*Mustela eversmanii*) and black-footed ferrets (*M. nigripes*) have long been considered ecological equivalents. Polecats also have been used as investigational surrogates for black-footed ferrets, yet the similarities and differences between the 2 species are poorly understood. We contrasted activity patterns of radiotagged polecats and ferrets released onto ferret habitat. Ferrets tended to be nocturnal and most active after midnight. Polecats were not highly selective for any period of the day or night. Ferrets and polecats moved most during brightly moonlit nights. The diel activity pattern of ferrets was consistent with avoidance of coyotes (*Canis latrans*) and diurnal birds of prey. Similarly, polecat activity was consistent with avoidance of red foxes (*Vulpes vulpes*) in their natural range. Intraguild predation (including interference competition) is inferred as a selective force influencing behaviors of these mustelines. Examination of our data suggests that black-footed ferrets and Siberian polecats might be ecological equivalents but are not perfect surrogates. Nonetheless, polecats as surrogates for black-footed ferrets have provided critical insight needed, especially related to predation, to improve the success of ferret reintroductions.

Key words: circadian rhythm, ecological equivalent, ecological surrogate, intraguild predation, moon, *Mustela eversmanii*, *Mustela nigripes*, predator avoidance

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DOI: 10.1644/10-MAMM-S-110.1

Ecologically equivalent species serve similar functions in different communities (Lincoln et al. 1998), especially ecologically similar communities that are widely separated, such as boreal forest or steppe communities in Asia and North America. The literature on ecological equivalence has a long history (Cody 1969; Fisher and Peterson 1964; Fuentes 1976; Simpson 1967). Tests of hypothesized ecological equivalence have been rare and have yielded variable results, although some species pairs do appear to fit the definition (Fuentes 1976; Young et al. 2010).

If 1 member of a truly ecologically equivalent pair is endangered but the other is not, can insight into potential conservation and management approaches for the endangered form be gained through research on the other? Specifically, might one use the nonendangered species as a surrogate for its mate in experimental tests of proposed conservation and management actions? An ecological surrogate species differs from an ecological equivalent species in that the surrogate can be substituted in the community of the endangered species (unfortunately, Lincoln et al. [1998] used the term "ecological equivalent" for both equivalents and surrogates). For example, if species A and species B are ecological equivalents, they serve similar functions in communities A and B. If species B is a surrogate for species A, species B can

be substituted into community A and serve the same ecological function as species A. The use of ecological surrogates also has a long history (Banks et al. 2010; Young et al. 2010), stimulated especially by the need to test toxicities of chemicals on surrogates for endangered species (Banks et al. 2010; Fairchild et al. 2008; Munns 2006; Spromberg and Birge 2005). Whether an ecologically equivalent species can actually be a true surrogate is seldom tested. Managers faced with an endangered species seldom have the luxury of testing the functional equivalence of 2 species in the same community.

Siberian (or steppe) polecats (hereafter, polecats [*Mustela eversmanii*]) and black-footed ferrets (hereafter, ferrets [*M. nigripes*]) have long been considered ecological equivalents (Hoffmann and Pattie 1968). Both are mammalian predators in steppe communities, in Asia and North America respectively, and prey on burrowing mammals. Both are also killed by medium-sized predators (Kydyrbaev 1988; Miller et al. 1996). The 2 forms have been considered conspecific (Heptner et al. 1967), can interbreed in captivity and produce fertile offspring (Davison et al. 1999), and are genetically similar (Davison et al. 1999; O'Brien et al. 1989).

Ferrets nearly became extinct in 1985 when epizootics of canine distemper (caused by *Morbillivirus*) and plague (caused by *Yersinia pestis*) struck the last known wild population (Forrest et al. 1988; Williams et al. 1988). The population was reduced to 10 adults (Miller et al. 1996), after which all remaining individuals of this species, including their wild-born progeny, were captured for a captive-breeding program. Because ferrets became extinct in the wild and numbers in captivity were low, polecats and ferret–polecat hybrids were used repeatedly as research surrogates (Biggins 2000). Nonetheless, the steppes of Asia and North America are geographically separated and environmentally different, leading to adaptive divergence between polecats and ferrets. Ferrets and polecats are distinguishable by hair length and coloration (Anderson et al. 1986). Polecats prey on diverse ground squirrels (*Spermophilus*), other burrowing rodents, and pikas (*Ochotona*—Denisov 1984; Heptner et al. 1967; Zhou et al. 1994b), and ferrets have evolved as specialists on prairie dogs alone (*Cynomys*—Miller et al. 1996).

Examination of data suggests that these mustelines differ also in their predator-avoidance behaviors. Reintroduced ferrets suffer significant predation mortality (57 of 137 radiotagged animals—Biggins et al. 2006a) yet captive-reared polecats released onto ferret habitat suffer even higher rates of predation (Biggins 2000; Biggins et al. 2011). Predator avoidance includes activity patterns that reduce encounters with predators, which could be partly heritable and could involve active decision-making (Lima and Dill 1990). Thus, interpretation of the results of polecat–ferret surrogate studies (Miller et al. 1990a, 1990b; Powell et al. 1985; Williams et al. 1991) would be enhanced by an improved understanding of the ecological and behavioral similarities and differences between black-footed ferrets and Siberian polecats; that is, understanding whether their ecological equivalence implies that they are ecological surrogates.

Members of the genus *Mustela* can time their activity to coincide with active periods of their prey (Zielinski 1986, 1988). Although ferrets are predominantly nocturnal (Biggins et al. 1986; Hillman 1968), both ferrets and polecats have tremendous flexibility of foraging times. Both species hunt and kill prey in burrows and above ground during day and night (Eads et al. 2010). Consequently, their circadian patterns might have been molded more to avoid predation than to procure food. Fear of predation is a powerful agent in shaping realized niches, social behaviors, movement, circadian patterns, and even community structure (Brown et al. 1988; Gilbert and Boutin 1991; Lockard and Owings 1974; Ripple and Beschta 2004; Terborgh et al. 1999). Other carnivores (Korpimäki and Norrdahl 1989; Latham 1952; Mukherjee et al. 2009), including other members of the genus *Mustela* (Debrot et al. 1985), are prey for larger predators. Predation by other predators, predominantly coyotes (*Canis latrans*), is the greatest source of mortality for reintroduced ferrets (Biggins et al. 2006a). Intraguild predation (Polis et al. 1989) benefits the larger predator through both nutrition and reduced competition. The common failure of coyotes to eat small carnivores they kill (including San Joaquin kit foxes [*Vulpes macrotis*]—Cypher and Spencer 1998) suggests that reducing competition is more important for coyotes than obtaining these animals as food. Stable coexistence of 2 predators involved in asymmetrical, intraguild predation requires the victim to be the better exploitative competitor (Holt and Polis 1997; Polis et al. 1989). Ferrets, with their abilities to hunt prairie dogs above and below ground, appear to be more effective than coyotes at exploiting prairie dogs. If possible, small predators should avoid being active when the prey of midsized predators are active, even if the predators share prey. Densities of medium-sized carnivores on prairie dog colonies can be nearly 6 times higher than densities of these carnivores on grassland habitats away from colonies (Krueger 1986), making temporal avoidance of midsized predators critically important to ferrets.

During nonday periods (i.e., crepuscular periods and night) coyotes in the high plains are generally most active during evening twilight (0.5 h before sunset to 0.5 h after sunset) and least active after 0000 h (Andelt and Gipson 1979; Gese et al. 1989; Laundré and Keller 1981; Woodruff and Keller 1982). Leporids constitute a large part of coyote diets in steppe and shrub–steppe habitats in North America (Clark 1972; Fichter et al. 1955; MacCracken and Hansen 1987), and North American leporids are predominantly crepuscular (Mech et al. 1966; Rogowitz 1997). During daylight several raptors (e.g., ferruginous hawks [*Buteo regalis*] and golden eagles [*Aquila chrysaetos*]) hunt prairie dogs and are, likewise, threats to ferrets (Biggins et al. 1999). By generally avoiding the activity periods of their diurnal prey, ferrets decrease the probability of encountering other predators that hunt those prey.

Perhaps the hazard of predation during daylight induced a niche shift (Hutchinson 1957) to nocturnality by ferrets, as has been suggested for some birds (Carothers and Jaksic 1984; Watanuki 1986). We predict ferrets will avoid activity peaks

of coyotes during night, will be most active when coyotes are least active, and will be most active when moonlight is dim.

Polecats in Asia, with more diverse prey and different predators, could face more complex problems of optimization than ferrets. Trade-offs for them in foraging and predator avoidance must vary as diverse prey and their other predators change in relative abundances. Across their range and over decades polecats show no consistent circadian patterns (Brom 1954; Denisov 1984; Heptner et al. 1967; Serrebrennikov 1929; Stroganov 1962; Sviridenko 1935; Zhou et al. 1994b). Nonetheless, in central Asia polecats are often nocturnal during winter and spring but diurnal in summer and autumn. Where the main prey of polecats is diurnal prey with small burrows, polecats can be forced to hunt above ground, elevating their risk of predation by diurnal predators (T. Katzner, University of Pittsburgh, pers. comm.) in exchange for reduced risk of starvation, as shown for European polecats (*Mustela putorius*—Lodé 1995). Red foxes (*Vulpes vulpes*) appear to be an important, or the most important, predator of polecats in fall and winter (Zhou et al. 1994a, 1994b, 1995), and polecats did appear to avoid periods of fox activity in 1 study in China (Zhou et al. 1994b). Before sunset, activity of polecats diminished as activity of foxes increased. The time of highest nocturnal polecat activity (after midnight) corresponded to the time of lowest nocturnal fox activity, although foxes were quite active during all periods of night. By 2 h after sunrise polecat activity ceased, but foxes remained somewhat active until noon. Polecats resumed moderate activity in early afternoon, when foxes were inactive. Foxes are smaller than coyotes and might not exact the selective pressures on polecats that coyotes do on ferrets. Nonetheless, as with ferrets, we predict polecats will avoid activity peaks of foxes, be most active when foxes are least active, and be most active when moonlight is dim.

Materials and Methods

Study sites and subjects.—To gain insight into how to reestablish ferrets we released 55 captive-born and wild-born polecats (Biggins et al. 2011) during September–October onto colonies of black-tailed prairie dogs (*Cynomys ludovicianus*) near Veteran, Wyoming, in 1989 and 1990 and near Hasty, Colorado, in 1990 (Fig. 1). To prevent polecats from reproducing we sterilized them >3 weeks prior to release (removal of oviducts or removal of vasa deferentia and epididymides). Similar surgery as a placebo treatment was not possible with endangered ferrets. We released 37 ferrets onto white-tailed prairie dog (*C. leucurus*) colonies in Shirley Basin, Wyoming, in 1991 (Fig. 1). We provided all ferrets and 14 polecats with postrelease food and release cage refugia (Biggins et al. 2011). Research was done humanely and in accordance with guidelines of the American Society of Mammalogists that were published later (Gannon et al. 2007). Animal handling and monitoring procedures were approved by Animal Care and Use Committees at the National Zoo in Washington, D.C., and the Fish and Wildlife Service National Ecology Research Center in Fort Collins, Colorado.

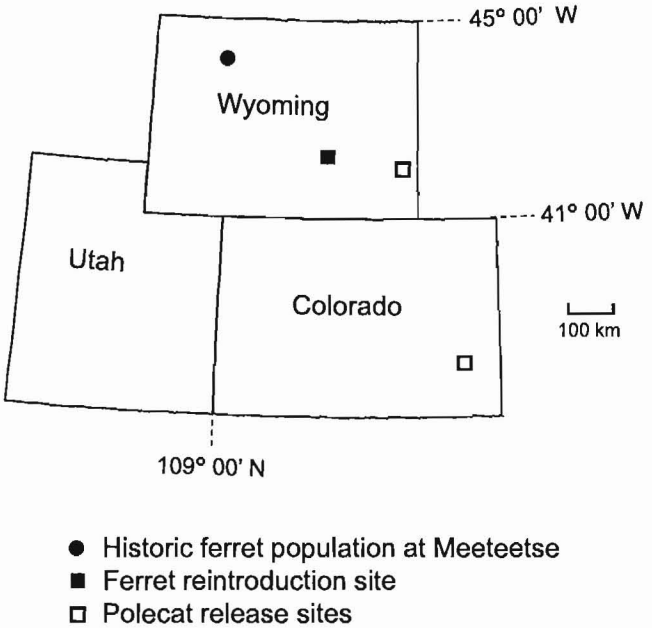

Fig. 1.—Locations of release sites for Siberian polecats (*Mustela eversmanii*) near Hasty, Colorado, and Veteran, Wyoming, and for black-footed ferrets (*M. nigripes*) in Shirley Basin, Wyoming (1st reintroduction for that species). Prairie dog colonies near Meeteetse, Wyoming, were home to the historic population of ferrets ancestral to all captive and released animals.

Rearing and releasing of ferrets was conducted under endangered species permit PRT-704930.

To limit our analyses to animals that behaved most naturally we used only those data collected >3 days after artificial support had ended. This restriction, plus mortality and collar loss, eliminated data for 44 polecats and 17 ferrets radio-monitored at the time of release, resulting in a sample of 11 polecats and 20 ferrets for this assessment.

Radiotelemetry.—We radiotagged polecats and ferrets using 10-g transmitter packages with activity monitors affixed to degradable wool collars and 20-cm whip antennas (Biggins et al. 2006c). Pulse rates of motion-sensitive transmitters (4–11 individual radiosignals emitted per 10 s) were proportional to the rate that a motion-sensitive mercury switch in each collar was actuated.

We radiotracked primarily using triangulation from pairs of fixed stations fitted with 11-element, dual-beam yagi antennas on 6.1-m masts, operated continuously from sunset to sunrise (Biggins et al. 1999, 2006c). We estimated polecat and ferret locations at about 15-min intervals. Radiotracking during day was a mixture of triangulation from multiple stations and monitoring from single stations to collect data on activity only. Nonpositional monitoring documented changes in presence or absence of radiosignal and pulse rate when a signal was present. Automated strip chart recording was used to monitor some animals whose transmitters were not simultaneously audible from at least 2 fixed stations.

Radiotracking error is a nuisance variable that can confound interpretation of effects of primary treatments. We estimated

the angular error of each fixed tracking station (Biggins et al. 2006c) and used intersecting error arcs to calculate areas of error quadrangles (hereafter, error quads—White and Garrott 1990) that accompanied each location estimate for an animal. An error quad variable was retained in all linear models involving movements (Biggins et al. 2006c) to control for effect of telemetry error (regardless of its statistical significance in those models). We used multiple beacon transmitters to reference stations (Biggins et al. 2006c).

Animal activity.—In general, receiving a signal from an animal's transmitter at 2 or more stations indicated that the animal was above ground; signals emanating from below ground could usually be heard only from short distances (<200 m), and stations were separated by 1–8 km. A bout of activity contained ≥2 consecutive telemetric observations classified as active and separated by <1 h. Some bouts were truncated by cessation of monitoring. A few partial bouts are assumed to be in the data set. Because of the maximum of 1 h between observations, we did not consider a bout to be complete unless an animal emerged ≥1 h after monitoring began and became inactive ≥1 h before monitoring ended. Measures used in analyses were cumulative distances traveled per bout (location-based bouts, as defined below) and numbers of bouts. We classified each bout according to moon condition and time period when the bout began, even if the bout continued into other periods. Statistical methods included preference analyses (use compared to availability) and general linear modeling.

We derived 2 indexes of activity based on presence or absence of radiosignal in combination with either the pulse rate of the motion-sensitive transmitters or the lengths of activity bouts based on triangulated location estimates. We used data based on pulse rate for comparisons of day and night because these data could be derived equally well from tracking from single or multiple stations, increasing the quantity of data available. Bouts derived from location estimates were preferred when available because they were most likely generated by aboveground signals, allowing us to compare activity above ground between species. Classifying activity based on pulse rate provided assurance that an animal was active but not necessarily that it was above ground. We accumulated pulse rate–based monitoring time for an animal whenever the animal's transmitter could produce a signal of sufficient quality for receiving equipment to time pulses from at least 1 station. Pulse rate–based bouts began when an observation had a pulse rate > 5 pulses per 10 s and ended when an observation of pulse rate was ≤5 pulses per 10 s, when an interobservation span exceeded 1 h, or when we ended monitoring.

A nested series of questions guided the strategy for data analysis, and different subsets of data were required to address each (Appendix I). We 1st tested for overall differences in activity rates between species. Second, we tested for differences in activity by time of day (diurnal, nocturnal, or crepuscular), followed by a finer-grained test of differences during blocks of nonday times (Table 1, combinations of categories 1–6). Third, we tested for differences in activity depending on the presence of moon. Finally, when the moon was present, we tested for effects of amount of illumination on nocturnal activity.

TABLE 1.—Categories into which the calendar day was divided, used for summarizing cumulative telemetric monitoring time and activity of black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmanii*) in Wyoming and Colorado.

Period no.	Name	Begin	End
0	Day	0.5 h after sunrise	0.5 h before sunset
1	Dusk	0.5 h before sunset	1.0 h after sunset
2	Evening twilight	1.0 h after sunset	2.0 h after sunset
3	Premidnight	2.0 h after sunset	Midnight
4	Postmidnight	Midnight	2.0 h before sunrise
5	Morning twilight	2.0 h before sunrise	1.0 h before sunrise
6	Dawn	1.0 h before sunrise	0.5 h after sunrise

We defined location-based monitoring time for each individual animal as time spent radiotracking from multiple stations so that we could estimate locations of that animal when it was above ground. Location-based monitoring included time when the subject was not located because it was below ground but did not include time when the subject was not within signal-receiving range from at least 2 stations. Location-based bouts began when an animal was 1st located and continued as long as subsequent locations were separated by <1 h, or until the monitoring session ended. Estimates of moves and their elapsed times based on consecutive relocations also were assigned lunar and time periods that were present during the 1st location defining the move but without respect to classification of bouts (which was based on conditions at the beginning of each bout). For these estimates we split movements and times that spanned >1 period. The 2 periods each accumulated a portion of the elapsed time between relocations determined by the time of change in category, and distance was segregated in proportion to the split in time.

We obtained times of sunrise, sunset, moonrise, and moonset, and moon illumination values from United States Naval Observatory data (United States Navy 2011) for Lamar, Colorado (25 km east of the Hasty site), Torrington, Wyoming (22 km northeast of the Veteran site), and Medicine Bow, Wyoming (25 km south of the site in Shirley Basin, Wyoming). The calendar day was divided into 7 periods (Table 1), which were recombined into 2–5 periods, depending on the type of analysis.

Analysis of use and availability.—A common problem arising in selection studies using radiotelemetry is nonindependence of consecutive data points (Aebischer et al. 1993; Swihart and Slade 1985). Individual estimates of location in our study were correlated serially, but we summarized series of such estimates in bouts. Bout summaries (in contrast to summaries by animal) gave greatest weight to the most successful animals; longer survival times provided increased sample sizes of bouts monitored. To evaluate further the

assumption of independence of bouts we used the Durbin–Watson test (R^2) for 1st-order autocorrelation (Neter et al. 1996). Also, we examined serial correlation plots of residuals in general linear models with multiple animals and for simpler models for each of the 5 individual animals with largest sample sizes (17–48 bouts).

Definitions of availability can have profound effects on conclusions regarding selection and avoidance (Johnson 1980; McClean et al. 1998). We defined availability as proportionate monitoring time for an animal within each time period (relative to total monitoring time for that animal) and measured it without variation. This design allowed us to apply the selectivity analysis of Neu et al. (1974), involving a chi-square (χ^2) test for goodness of fit to evaluate overall differences in proportionate use (proportion of bouts) and availability (proportion of monitoring time) between or among $\geq$2 periods. Although sample sizes met minimum criteria for the traditional chi-square test (Alldredge and Ratti 1986, 1992), we used the less restrictive exact chi-square procedure (Berry and Mielke 1985). These omnibus tests, if significant, were followed by calculation of Bonferroni-adjusted confidence intervals based on the Z-statistic, with $\alpha = 0.05$, to evaluate selection and avoidance in individual periods (Neu et al. 1974).

Pulse rate–based data facilitated comparisons of bout counts between day and nonday periods (Table 1). During nonday (periods 1–6; Table 2) we monitored movements by telemetric locations and used location-based bouts to characterize activity. For evaluation of diel patterns we combined periods 1 and 2 (Table 1) into a crepuscular period for evening and combined periods 5 and 6 into a morning crepuscular period. To compare ferrets and polecats regarding their use of the crepuscular periods (1 + 2 + 5 + 6) and night periods (3 + 4), we used a chi-square test of independence (Berry and Mielke 1985). To assess overall correspondence between activity and monitoring time (availability) for the 4 periods of night (2 + 3 + 4 + 5) we used the omnibus chi-square test, followed by calculation of Bonferroni-adjusted confidence intervals to assess the selection or avoidance of individual periods.

We used the periods of night (2 + 3 + 4 + 5; Table 1) to assess moon effect, assuming that the sun had no influence from 1 h after sunset until 1 h before sunrise. For each bout at night we recorded a moon influence value that was the proportion of the moon lit by the sun, or 0 if the moon was below the horizon or was in the new moon phase. The moon influence value was >0 if the moon provided primary illumination and was present at any time during the bout. Moon illumination values indicate potential brightness. Atmospheric conditions such as clouds and ground conditions such as snow cover and type of vegetation affect light levels but were not considered.

For evaluating the effect of moon presence on ferret and polecat activity we grouped nights based on moon presence, moonrise, and moonset. Dark nights were those with <1.5 h of moonlight available, moonlit nights had <1.5 h without moonlight, and mixed nights were the remainder. Because moon phase and moonrise cycles are monthly and synchronous, dark nights are associated with low moon illumination, moonlit nights with nearly full illumination, and mixed nights with partial illumination. We used the method of Neu et al. (1974) to examine selection for moonlight. We compared numbers of bouts and availability for moonlit nights and dark nights and conducted a similar comparison for moonlit and dark periods within the mixed night period.

To examine further the effect of brightness when the moon was present we assessed distances moved per bout during nights when moon illumination was $\geq$20% (including all of the moonlit nights and part of the mixed nights), using general linear modeling in the MINITAB 8 statistical package (Addison-Wesley Publishing Co., Reading, Massachusetts). If the moon was present during any portion of a bout, we assigned its illumination value to the entire bout.

We produced an overall summary of combined effect of moon and periods of night on activity of ferrets and polecats by summing all movements within 4 temporal periods. We grouped these periods so that 2 of them (2 + 3 and 4 + 5) covered all time lacking effect of sun (1 h after sunset to 1 h before sunrise), then split each of these 2 periods into subperiods of moon present and moon absent. We summarized cumulative movements relative to cumulative monitoring time for the additional 2 periods (1 and 6, dusk, and dawn; Table 1), lasting 1.5 h each and encompassing the remainder of the nonday period. For all statistical tests we set $\alpha = 0.05$.

Results

We used telemetric data from 11 polecats monitored for 1,371 h ($\bar{X}$ = 123.6 h per polecat) and 20 ferrets monitored for 5,245 h ($\bar{X}$ = 262.3 h per ferret). Polecats averaged longer moves than ferrets, 1.26 km per bout in 89 bouts compared to 0.61 km per bout in 201 bouts in ferrets (Table 2), and polecats moved >2 km in 18% of their bouts compared to 5% for ferrets. The overall rate of movement for ferrets ($\bar{X} \pm SE$), adjusted for error quad, was 544.6 ± 96.7 m/h, significantly less ($F_{1,22} = 8.92$, $P = 0.007$) than the adjusted rate of movement for polecats of 1,016.5 ± 119.8 m/h. Estimates for each animal were derived from total cumulative distances and elapsed times between consecutive relocations (separated by <1 h). Error quads were a noteworthy control variable in this statistical model ($F_{1,22} = 6.50$, $P = 0.018$). One polecat that established movement extremes engaged in numerous moderate bouts of activity during her first 9 days postrelease, followed by no aboveground moves for 12 consecutive days, the longest continuous period below ground we documented for a ferret or polecat. She then abandoned the prairie dog colony and moved to a nearby area with yellow-faced pocket gophers (*Cratogeomys castanops*), later making the 2 longest cumulative aboveground movements recorded for this study (10.4 and 11.2 km).

Bouts could be considered statistically independent observations because residual variation, which should be most evident in analyses of individual animals, was not serially

TABLE 2.—Summary of cumulative monitoring time, length of cumulative movements, and number of bouts of activity during various periods of day and night (Category) for black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmanii*) released during 1989–1991 on prairie dog colonies in Wyoming and Colorado. Parenthetical numbers refer to periods defined in Table 1.

	Black-footed ferrets			Siberian polecats		
	Monitor (h)	Movement (km)	Bouts (*n*)	Monitor (h)	Movement (km)	Bouts (*n*)
Category						
Day (0)	2,284	0.8	2	425	31.5	15
Evening (1 + 2)	549	9.2	20	150	14.2	17
Premidnight (3)	968	34.0	68	342	24.1	18
Postmidnight (4)	905	62.5	98	308	28.5	27
Morning (5 + 6)	539	16.2	13	146	13.4	12
Total	5,245	122.7	201	1,371	111.7	89
Moon (at night, periods 2–5)						
Moonlit nights	445	30.9	55	91	23.5	8
Dark nights	551	18.9	46	120	3.1	5
Mixed nights	1,350	62.8	85	564	41.6	45

correlated in regression models with error quad and moon illumination as predictors and cumulative movement per bout as the response ($R^2 < 0.03$, $P > 0.05$). Plots of higher order autocorrelations also lacked predictable patterns. In final multivariable models with all animals autocorrelation was small ($R^2 < 0.001$, $P > 0.05$).

Ferrets were consistently more nocturnal than were polecats. Although 43% of monitoring time was during day, only 5% of pulse rate–based bouts of activity for ferrets were during day ($\chi^2_1 = 222.65$, $P < 0.001$). For polecats the 31% of monitoring time during day contained 25% of their bouts of activity, insufficient to demonstrate avoidance ($\chi^2_1 = 3.28$, $P = 0.082$). Both ferrets and polecats were active above ground 7.5% of the time they were monitored during nonday periods, but comparing distribution of bouts between periods, polecats were more crepuscular than were ferrets ($\chi^2_1 = 16.24$, $P < 0.001$; Fig. 2). The difference could not be explained by availability because crepuscular monitoring (periods 1 + 2 + 5 + 6; Fig. 2) was 36.7% of total monitoring time for ferrets and 31.2% of total monitoring for polecats. Selection for the 4 nonday periods by ferrets varied ($\chi^2_3 = 45.49$, $P < 0.001$; Fig. 2), with the Bonferroni-adjusted confidence intervals suggesting significant selection for postmidnight periods and avoidance of the 2 crepuscular periods. Use of the 4 nonday periods by polecats did not differ significantly from availability ($\chi^2_3 = 5.66$, $P = 0.128$).

Both species were most active during moonlight (Fig. 3), but the patterns differed by species and time of night. Unlike ferrets, polecats tended to move less during dark periods of the night than during crepuscular periods when the sun's effect remained, but night moves exceeded crepuscular moves when the moon was present.

During mixed nights (nights having a combination of >1.5 h with and without moonlight), polecats made significantly more bouts of movement when the moon was present ($\chi^2_1 = 8.16$, $P = 0.005$; Fig. 4) than when the moon was absent; a trend was not obvious for ferrets ($\chi^2_1 = 2.09$, $P = 0.159$). Ferrets tended to engage in more bouts of movement during moonlit than dark nights ($\chi^2_1 = 3.91$, $P = 0.057$), but the pattern for polecats, although similar, was not significant ($\chi^2_1 = 1.79$, $P = 0.262$; Fig. 4). In the multivariable model of distances moved during bouts (treating moon illumination $\geq 20\%$ as a continuous variable) species effects ($F_{1,131} = 18.55$, $P < 0.001$), moon illumination effects ($F_{1,131} = 31.24$, $P < 0.001$), and a species by moon illumination interaction ($F_{1,131} = 25.82$, $P < 0.001$) were significant. Because of the

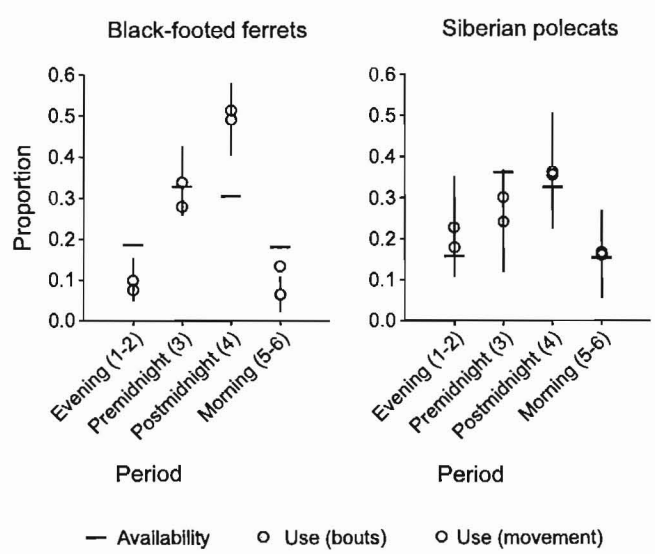

FIG. 2.—Use of 4 nonday periods (proportions of bouts of activity and proportions of distances moved) by black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmanii*) compared to availability (cumulative telemetric monitoring time) within those periods. Vertical bars through symbols for bouts indicate 95% (Bonferroni-adjusted) confidence intervals; intervals below horizontal lines of availability indicate significant avoidance of that period; and intervals above the horizontal lines indicate significant selection for activity during that period. Consecutive periods are delimited by 0.5 h before sunset, 2.0 h after sunset, midnight, 2.0 h before sunrise, and 0.5 h after sunrise. Parenthetical numbers refer to periods defined in Table 1.

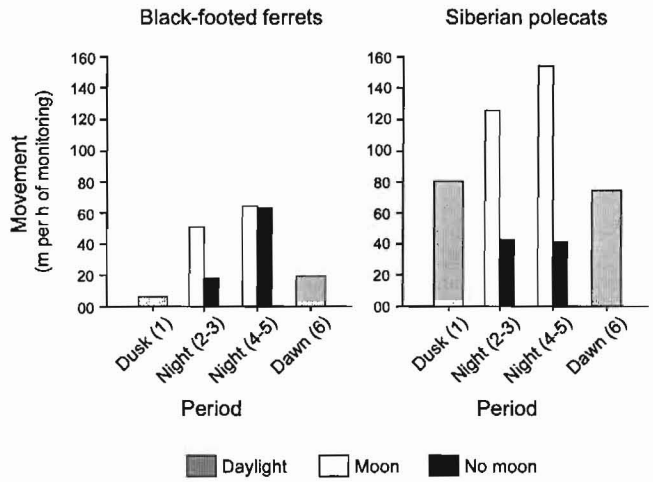

FIG. 3.—Combined effects of moon and time period on movement rates of black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmanii*). Consecutive periods are delimited by 0.5 h before sunset, 1.0 h after sunset, midnight, 1.0 h before sunrise, and 0.5 h after sunrise. Parenthetical numbers refer to periods defined in Table 1.

interaction, separate models were evaluated for each species. Polecats increased their movements significantly with increasing moon illumination ($F_{1,36} = 33.28$, $P < 0.001$), but we did not detect such an effect for ferrets ($F_{1,96} = 0.21$, $P = 0.650$).

DISCUSSION

Siberian polecats and black-footed ferrets are certainly similar in many respects (Clark et al. 1986; Hoffmann and Pattie 1968; Miller and Anderson 1990), yet we detected behavioral differences between the ferrets and polecats released onto prairie dogs towns in North America. Polecats were more active above ground in total than ferrets, travelled farther, were more crepuscular, and were more active on moonlit nights. Polecats in Asia move about twice as far—10–15 km per day (Denisov 1984; Kydyrbaev 1988; Zverev 1931)—as did wild ferrets at Meeteetse (7 km per bout—Biggins et al. 1993). These differences in activity between the species appear correlated with differences in mortality (Biggins et al. 2011). Although ferrets and polecats might be ecological equivalents, they appear not to be perfect ecological surrogates. Behaviors of ferret–polecat hybrids have not been examined closely, but any future attempt at genetic manipulation should proceed cautiously and should involve experimental evaluations of behaviors in the laboratory and during trial releases of reproductively sterile polecats or hybrids. Nevertheless, polecats appear to have been good enough surrogates.

Polecat behaviors resembled ferret behaviors well enough to provide information useful for ferret reintroductions. Use of polecats as ecological surrogates for ferrets highlighted the importance of predation (Miller et al. 1996), and research on captive polecats provided insights into how captive ferrets could be sensitized to predators (Miller et al. 1990a, 1990b).

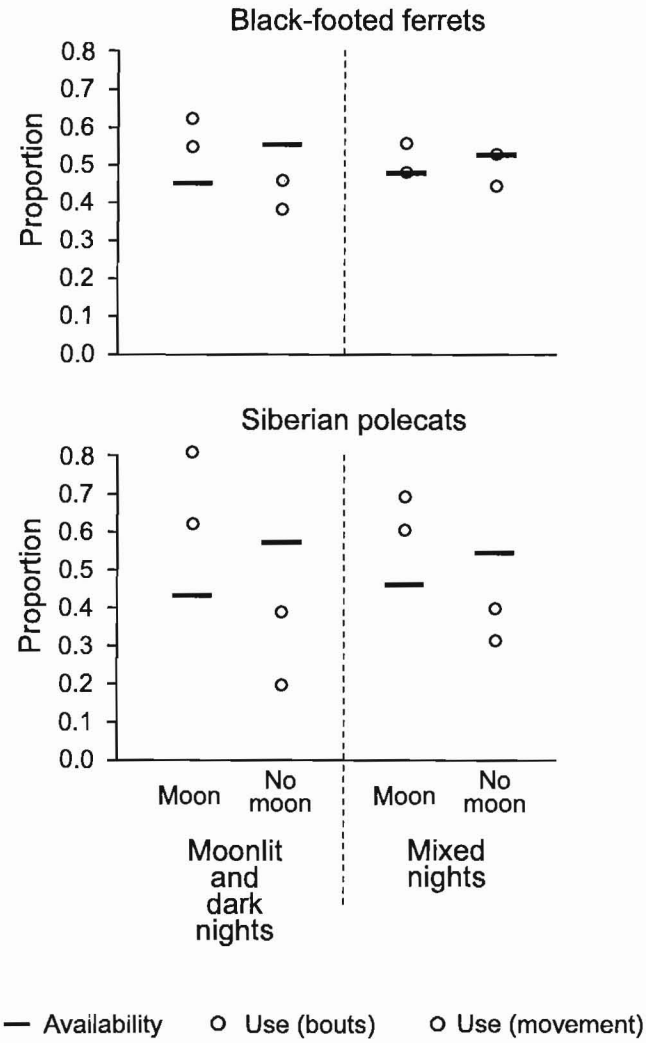

FIG. 4.—Proportionate use (bouts of activity and distances moved) in moonlit and nonmoonlit periods by black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmanii*) compared to proportionate availability (cumulative telemetric monitoring time) within those periods. Dark nights were nights with <1.5 h of moonlight available, moonlit nights had <1.5 h without moonlight, and mixed nights were the remainder.

Releasing polecats onto prairie dog towns gave insights into providing protection and supplemental food for ferrets postrelease (Miller et al. 1994; Biggins 2000). Just as ecological equivalents are seldom truly equivalent but provide important insight nonetheless, ecological surrogates need not be perfect surrogates to provide important information to conservation biologists and wildlife managers.

We predicted that ferrets would avoid being active during periods when coyotes and diurnal predators were active and that polecats would avoid periods when red foxes are active in Asia. As predicted, ferrets were predominantly nocturnal, but polecats did not show a clear pattern. Also as predicted, ferrets were least active during evening periods, the time reported for greatest coyote movement, and ferrets were more active during postmidnight hours when coyotes are least active

(Andelt and Gipson 1979; Gese et al. 1989; Laundré and Keller 1981; Woodruff and Keller 1982). This pattern suggests avoidance of times of coyote activity by ferrets.

In contrast to ferrets, polecats in our study were far more active during day and showed less marked patterns of nocturnal behavior. Their pattern of activity was consistent with potential avoidance of Asian red foxes (Zhou et al. 1994b), with the consequence that polecats were more likely than ferrets to be active when coyotes were active.

We had predicted that both ferrets and polecats would avoid moonlight. Instead, polecats were most active during full moonlight, and ferrets showed a preference for moonlight during early night. Coyotes are primarily visual hunters (Wells and Lehner 1978), making moonlit activity by ferrets difficult to explain, especially because ferrets do not seem to need moonlight to kill prairie dogs. We speculate that ferrets are active during moonlight because they are able to navigate more efficiently during exploration of large areas or to locate areas of dense prey and other ferrets (Eads et al. 2011). This topic requires further research.

We hypothesize that the preference of ferrets for activity in the postmidnight hours and their significant avoidance of evening and morning crepuscular periods is canalized behavior due to selective pressure by coyotes and is not a learned behavior (Lima and Dill 1990). This activity pattern was evident in the wild Meeteetse population of ferrets (Biggins et al. 1986) and was observed in several generations of captive-bred ferrets (Vargas and Anderson 1998). We would expect that captive-reared ferrets, maintained in cages and fed during the day, would have abandoned the postmidnight peak of activity if that behavior were due to risk assessment and choice. If the circadian rhythms of ferrets are canalized, the inability of polecats to match the behavior of ferrets might be innate as well. Alternately, lacking the specialized behavior of ferrets to hunt prairie dogs in the burrows, polecats might have been forced to be active above ground during day.

Predation avoidance is an important issue for ferret reintroduction programs. Nonetheless, foraging and energetics could contribute to the behavioral differences between polecats and ferrets. The benefits (prey acquired) to polecats of spending extensive time above ground should outweigh the costs (energy expended and risk of predation). Night temperatures in winter likely produce a substantial thermoregulatory cost for aboveground activity by ferrets and polecats (Harrington et al. 2006). Seasonal changes in pelage seemed more pronounced in our captive polecats than in captive ferrets, with winter hair of polecats becoming longer and lighter colored. Also, the basal metabolic rate of captive polecats is more seasonally variable than that of captive ferrets (Harrington et al. 2003). We hypothesize that polecats are better insulated than ferrets in winter (a topic that needs further investigation) to be active above ground.

Searches for ferrets are often conducted using spotlights at night (Biggins et al. 1998, 2006b), yet ferrets spend >90% of their nonday hours below ground. Searches should be done when ferrets are most active. Efficiency of searches should be greatest in the early morning hours of darkness and with bright moonlight. Initial dispersal following releases and translocations, however, might be reduced by releasing ferrets during the dark phase of the moon.

Acknowledgments

Funding for this project was provided by the United States Geological Survey, Smithsonian Institution, Loudon Area Ferret Fanciers, Friends of the National Zoo, National Fish and Wildlife Foundation, and United States Army. We are especially grateful to Wildlife Trust for long-term support of this conservation effort. We are deeply indebted to the Wyoming Game and Fish Department and the Henry Doorly Zoo (Omaha, Nebraska) for producing the ferrets that were reintroduced in 1991. The National Zoo Conservation and Research Center provided logistical support, housing, food, and husbandry for captive polecats. The United States Army Pueblo Chemical Depot and the National Zoo Conservation and Research Center allowed us to convert buildings into polecat conditioning arenas. Ranchers at Hasty, Colorado, Veteran, Wyoming, and Shirley Basin, Wyoming, graciously allowed us to work on their lands. J. Ma and Z. Zhao, Northeast Forestry University (Ministry of Forestry), Harbin, China, were instrumental in obtaining polecats from Inner Mongolia. The United States Army Corps of Engineers provided housing and office facilities at Hasty, Colorado. L. Phillips of Brookfield Zoo, Chicago, Illinois, and S. Monfort and J. Zoziarski of the National Zoo, Washington, D.C., performed sterilization surgery on ferrets, and R. Opferman provided veterinary assistance on many occasions. Space does not permit individual acknowledgment of the many technicians and volunteers who worked on ferret and polecat releases, but their help is sincerely appreciated. We appreciate the helpful reviews of this paper by B. Wunder, J. Detling, W. Andelt, P. Shafroth, B. Iko, and D. Eads. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the United States government.

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Special Feature Editor was Barbara H. Blake.

APPENDIX I

Comparisons, measures used, and analysis methods for assessing effects of time of day and moonlight on activities of black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmanii*) in Wyoming and Colorado.

Primary comparison	Basis of measure	Data subset	Unit of observation	Attribute	Analysis method
Polecat, ferret	Location	All data	Animal	Movement rate	MGLM[a]
Day, nonday	Pulse rate	All data (by species)	Bout	Count	Availability, use[b]
4 periods	Location	Nonday (by species)	Bout	Count	Availability, use[b]
4 periods	Location	Nonday (by species)	Animal	Total movement	Descriptive
Moon, no moon	Location	Night, dark and moonlit (by species)	Bout	Count	Availability, use[b]
Moon, no moon	Location	Night, dark and moonlit (by species)	Animal	Total movement	Descriptive
Moon, no moon	Location	Night, mixed (by species)	Bout	Count	Availability, use[b]
Moon, no moon	Location	Night, mixed (by species)	Animal	Total movement	Descriptive
Moon illumination	Location	Night, moon illumination $\geq$ 20% (by species)	Bout	Movement	MGLM[a]

[a] MGLM = multivariable general linear modeling.
[b] Neu et al. (1974).