American badgers selectively excavate burrows in areas used by black-footed ferrets: implications for predator avoidance

DAVID A. EADS,* DEAN E. BIGGINS, TRAVIS M. LIVIERI, AND JOSHUA J. MILLSPAUGH

Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523-1878, USA (DAE)
United States Geological Survey, Fort Collins Science Center, 2150 Centre Avenue, Building C, Fort Collins, CO 80526, USA (DEB)
Prairie Wildlife Research, P.O. Box 308, Wellington, CO 80549, USA (TML)
Department of Fisheries and Wildlife Sciences, University of Missouri, 302 Natural Resources Building, Columbia, MO 65211, USA (JJM)

* Correspondent: david.eads@colostate.edu

We evaluated how American badgers (*Taxidea taxus*) might exert selective pressure on black-footed ferrets (*Mustela nigripes*) to develop antipredator defenses. In a colony of black-tailed prairie dogs (*Cynomys ludovicianus*) in South Dakota, badgers concentrated their activities where burrow openings and prairie dogs were abundant, a selective behavior that was exhibited by ferrets in the same colony. Badgers excavated burrows more often when in areas recently used by a ferret, suggesting that badgers hunt ferrets or steal prey from ferrets, or both. We also conducted an analysis of survival studies for ferrets and Siberian polecats (*M. eversmanii*) released onto prairie dog colonies. This polecat is the ferret's ecological equivalent but evolved without a digging predator. Badgers accounted for 30.0% of predation on polecats and 5.5% of predation on ferrets. In contrast, both polecats and ferrets have evolutionary experience with canids, providing a plausible explanation for the similar relative impact of coyotes (*Canis latrans*) on them (65.0% and 67.1% of predation, respectively). We hypothesize that ferrets and badgers coexist because ferrets are superior at exploitation competition and are efficient at avoiding badgers, and badgers are superior at interference competition.

Key words: American badger, black-footed ferret, *Cynomys*, digging, evolution, *Mustela eversmanii*, *Mustela nigripes*, predation, *Taxidea taxus*

In western North America, the American badger (*Taxidea taxus*, henceforth "badger") commonly occurs on colonies of prairie dogs (*Cynomys* spp.) and preys on prairie dogs (Koford 1958; Goodrich and Buskirk 1998; Lomolino and Smith 2004). Endangered black-footed ferrets (*Mustela nigripes*, henceforth "ferrets") are obligate predators of prairie dogs that use prairie dog burrows for shelter and rarely stray far from a prairie dog colony. Ferrets are of similar size to prairie dogs, which allows them to hunt prairie dogs within burrow systems, whereas badgers are much larger and commonly excavate burrows to capture prairie dogs. Overlap in habitat use and diet between badgers and ferrets may lead to exploitative and interference competition and such intraguild interactions could have significant ecological consequences for badgers and ferrets alike (Polis et al. 1989; Palomares and Caro 1999).

Badgers are known to kill ferrets (Biggins et al. 2006a) and the risk of badger predation for ferrets may be linked simply to random encounters as both species hunt on prairie dog colonies. Rates of encounter, however, should be elevated if both species select for the same patches of habitat within colonies. Ferrets concentrate their movements in areas of prairie dog colonies with high densities of active openings to burrows, where prairie dogs are relatively abundant (Biggins et al. 1993; Eads et al. 2011a, 2011b). If badgers also select portions of prairie dog colonies with high densities of active burrow openings, the risk of badger predation should be heightened for ferrets.

The encounter rate between ferrets and badgers would be further increased if badgers intentionally use areas occupied by ferrets. Concurrent use of space might suggest that badgers actively seek ferrets, or badgers steal freshly killed prey from ferrets, a form of interference competition observed in many

pairs of carnivores (i.e., kleptoparasitism—Polis et al. 1989). Indeed, although excavation is energetically costly, the reliable presence of carrion in a ferret den might increase the benefits of excavation (Biggins et al. 2012). Alternatively, the badger might actively pursue ferrets whether or not carrion is present because by killing a ferret, a badger can reduce competition with a more specialized predator of prairie dogs (i.e., intraguild predation—Polis et al. 1989; Palomares and Caro 1999) and benefit energetically by consuming the ferret (Biggins 2000; Biggins et al. 2011b).

We used spatial and temporal data for badgers, prairie dogs, and ferrets to evaluate the hypotheses that badgers select areas of prairie dog colonies with high densities of active openings to burrows, where prairie dogs are relatively abundant; and badgers tend to excavate burrows when in areas currently or recently used by ferrets.

For ferrets, the cost of losing carrion to a badger is lower than the cost of death, suggesting ferrets may have evolved effective means to evade badgers (Dawkins and Krebs 1979; Lima and Dill 1990; Caro 2005). Indeed, ferrets select for burrow systems with multiple openings that can provide alternate avenues of escape from an excavating badger (Biggins 2012). In contrast, a purported ecological equivalent of the ferret (Biggins et al. 2011a), the Siberian polecat (*Mustela eversmanii*, henceforth "polecat") of Asia, apparently evolved without a badgerlike digging mesopredator, which might have left it relatively susceptible to predation by such a predator. However, ferrets evolved with terrestrial canids as predators (e.g., the coyote [*Canis latrans*]) and polecats evolved with the red fox (*Vulpes vulpes*—Zhou et al. 1994), suggesting that both ferrets and polecats may have evolved effective defenses against canids. Experimental releases of both ferrets and polecats on ferret habitat provided an opportunity to examine competing risks of predation by badgers and coyotes for the 2 closely related species of *Mustela*. This retrospective analysis of published data (Biggins et al. 1999, 2006a, 2011a, 2011b) has particular relevance to the susceptibility of ferrets to badgers and coyotes (the latter carnivore is considered the most lethal predator to ferrets—Biggins et al. 2006a, 2011a, 2011b). Thus, we also tested the additional hypotheses that badgers kill polecats more commonly than ferrets, due to the polecat's lack of evolved defenses against an excavating mesopredator; and coyotes kill ferrets and polecats at similar rates, given that ferrets and polecats both evolved under predation risk from a canid predator.

MATERIALS AND METHODS

Study period and site.—During 13 June–10 October 2007 and 11 June–27 September 2008, we monitored ferrets and badgers in a 452-ha colony of black-tailed prairie dogs (*C. ludovicianus*) in the Conata Basin, South Dakota (Eads et al. 2011a, 2011b). The colony is called the South Exclosure or SC07 (43°45′N, 102°18′W). Most of the South Exclosure was within Buffalo Gap National Grassland, land administered by the United States Forest Service. The northern tip of the colony

extended into Badlands National Park, a site administered by the National Park Service. Livieri (2006) described characteristics of the Conata Basin and the history of ferret reintroductions there. At the start of our sampling, the South Exclosure had been characterized by relatively high densities of burrow openings and prairie dogs, and consistently inhabited by ferrets since 1997. Consequently, the colony was considered high-quality habitat for ferrets. 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).

We hypothesized that badgers select areas of prairie dog colonies with high densities of active openings to burrows. Between July and mid-September 2007, a team used Trimble CMT MC-V global positioning system receivers (Trimble Navigation Limited, Sunnyvale, California) to map locations of burrow openings in our study colony (Jachowski et al. 2008; Eads et al. 2011a, 2011b). Burrow openings were classified as "active" if the opening was at least 7 cm wide and fresh prairie dog scat was within 0.5 m of the opening (Biggins et al. 1993), allowing us to relate badger observations to active burrow openings.

Spotlight surveys.—Observers conducted spotlight surveys (Biggins et al. 2006b) for ferrets and badgers on nearly consecutive nights during each field season (Eads et al. 2012b). A survey route was established to maximize coverage of the colony and to minimize overlap (Biggins et al. 2006b; Jachowski et al. 2011). We identified ferrets via passive integrated transponder tags (AVID Microchip I.D. Systems, Folsom, Louisiana) or unique dye markings; a passive-integrated-transponder–reader loop antenna circumscribed an occupied burrow opening and acquired a ferret's identification numbers as the tagged ferret emerged from the burrow through the antenna (Biggins et al. 2006b). Badgers were not individually indentified. We denoted each badger observation as "excavation" (badger excavating a burrow) or "nonexcavation." Observers collected locations of ferrets and badgers via handheld global positioning system units (Fig. 1).

Data analyses.—Do badgers select areas of prairie dog colonies with high densities of active burrow openings (i.e., areas used by ferrets)? We compared numbers of active burrow openings in areas used by badgers and random areas deemed available to badgers under a use–availability design (Johnson 1980). In this analysis, badger locations included excavations and nonexcavations. All badger observations were collected at a burrow opening. Thus, using the map of burrow openings in ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California), we shifted each badger location to the nearest mapped burrow opening, regardless of activity. Then we used ArcGIS to generate 1 random location per badger location, limiting the random locations to the colony and centering them on the nearest burrow opening. The random locations were apparently available to badgers, but we did not observe badgers using any of the random locations. We buffered all badger locations and random locations by 20-m-
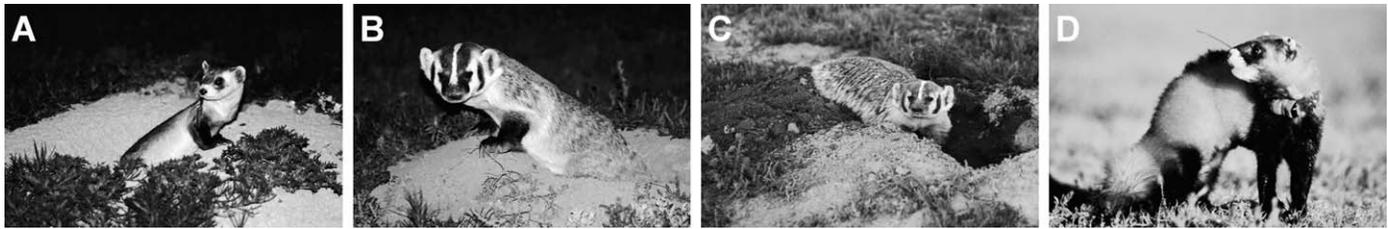
Fig. 1.—We monitored A) black-footed ferrets (*Mustela nigripes*) and B) American badgers (*Taxidea taxus*) inhabiting a 452-ha colony of black-tailed prairie dogs (*Cynomys ludovicianus*) in the Conata Basin, South Dakota. C) During some observations, we located a badger as it actively excavated a burrow. In addition, we conducted an analysis of mortality data for adult ferrets and D) adult Siberian polecats (*M. eversmanii*) released onto prairie dog colonies during 1989–2006. The spotlight data permitted investigation of resource selection by badgers relative to ferrets, and the mortality data permitted investigation of differential rates of badger or coyote (*Canis latrans*) predation on adult ferrets and polecats. (Images A, B, and C by DAE; image D by DEB.)

radius circular plots (0.13 ha) and counted the number of active burrow openings in each plot. These counts were nonnormal (Shapiro–Wilk tests, $P < 0.001$). Thus, in program R (version 2.13.2—R Development Core Team 2011), we used distribution-free Mann–Whitney U-tests to compare numbers of active openings in badger plots and random plots with the 2007 and 2008 data combined ($\alpha = 0.10$).

Do badgers tend to excavate burrows when in areas currently or recently used by ferrets? In this analysis, we investigated temporal associations between fresh badger excavations and ferret observations. In ArcGIS 9.2, we superimposed a grid of square cells (80×80 m) on the study colony, and counted the number of active burrow openings in each cell (ACT). The size of the cells reduced spatial autocorrelation of counts for active burrow openings in cells, which should have increased the probability of badgers selecting resources in a cell to access those resources, not resources in neighboring cells (Eads 2009; Eads et al. 2011b). We created separate grids for the 2007 and 2008 data and excluded cells used by only 1 or neither species, thus restricting the grids to cells used by ferrets and badgers within a field season. We classified each cell as a cell in which a badger was observed as it actively excavated a burrow (1) or a cell in which badgers did not observably excavate (0). We further classified each cell with a temporal variable that related the badger excavations to the timing of ferret activity (TIMING). Specifically, in each cell we counted the number of days between the badger excavation and all ferret observations in that cell, and then classified each cell as encompassing an excavation completed by a badger when a ferret was present in a similar period (i.e., badger excavated 0–10 days after a ferret observation) or a different period (i.e., badger excavated before or > 10 days after a ferret observation). We used the 10-day definition of TIMING because a badger might excavate a den recently abandoned by a ferret to acquire carrion, but as time progresses the carcasses in an abandoned den would presumably decompose, or prairie dogs might reoccupy the burrow and eat the carcasses (Hoogland 1995). We combined the 2007 and 2008 data and then fit binary logistic regression models to relate the occurrence of badger excavations in cells to the timing of excavations relative to ferret occupancy (similar or different period of TIMING). We included ACT as a control variable. In program R, we fit a general model with both main effects and a model with the ACT control variable alone and used a likelihood-ratio test to determine if the TIMING effect increased model fit ($\alpha = 0.10$).

Mortality data analysis.—Are polecats killed by badgers more often than ferrets, and are polecats and ferrets killed by coyotes at similar rates? We used mortality data from published studies of radiotagged polecats and ferrets released on prairie dog colonies—all animals were raised in captivity and released to the wild. Polecats were reproductively sterilized and released on prairie dog colonies in Colorado and Wyoming during 1989–1990 to compare rearing and release methods that would be later used for ferrets, and to examine the hypothesis of ecological equivalency for the 2 *Mustela* species (which was supported—Biggins et al. 2011a, 2011b). Ferrets were released to colonies in Arizona, Colorado, Montana, South Dakota, Utah, and Wyoming during 1991–2006 for repatriation and continued testing of rearing and release strategies (Biggins et al. 1999, 2006a).

We reexamined the cumulative data to compare causes of mortality for ferrets and polecats as described in the supporting material (Biggins et al. 1999, 2006a, 2011a, 2011b). We restricted the data to polecats ($n = 41$) and ferrets ($n = 73$) with identified sources of mortality. We used chi-square tests of independence to contrast numbers of polecats and ferrets killed by badgers or coyotes.

RESULTS

At SC07 in South Dakota, we collected 106 observations of badgers in 2007 (42 excavations and 64 nonexcavations) and 163 observations in 2008 (38 excavations and 125 nonexcavations). Regarding ferrets, we monitored 21 adult ferrets (14 females and 7 males), 5 of which were present in 2007 and 2008 (4 females and 1 male). We collected 979 ferret observations, 90% of which were confirmed as observations of adults ($n = 876$). The remaining 10% of observations included those of ferrets that appeared (visually) to be of adult size, but might include at least some observations of kits (young-of-year). Observations of kits during June to mid-August (before natal dispersal) would seemingly correspond to locations near den sites (i.e., dens used by adult females), given
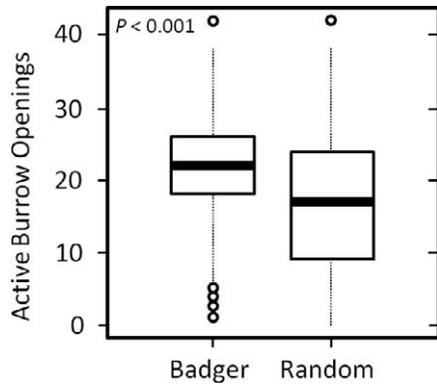
FIG. 2.—Box plot of the number of active black-tailed prairie dog (*Cynomys ludovicianus*) burrow openings in 0.13-ha circle-plots used by American badgers (*Taxidea taxus*) and random plots deemed available to badgers. Data were collected during 13 June–10 October 2007 and 11 June–27 September 2008 on a 452-ha colony of prairie dogs in the Conata Basin, South Dakota. The *P*-value corresponds with a paired Mann–Whitney *U*-test.

kits typically stay near den sites before natal dispersal (Paunovich and Forrest 1987). Observations of kits during the period of natal dispersal (mid-August into early October) could correspond to locations near natal den sites or locations used by an increasingly independent kit that would hunt for itself (Biggins et al. 1985; Miller 1988).

Do badgers select patches with high densities of active openings to prairie dog burrows? Activity of burrow openings was similar between 2007 and 2008 in 192 circular plots distributed throughout the study colony (Eads et al. 2011b), suggesting consistency in burrow activity between field seasons and, therefore, utility in relating badger observations from 2007–2008 to the burrow map from 2007. Badger plots contained 3–42 active burrow openings, whereas random plots

contained 1–38 active openings. Rank values were greater in badger plots than in random plots ($U = 47,353$, $P < 0.001$). Thus, badgers selected areas of the prairie dog colony with high densities of active burrow openings (Fig. 2), a selective behavior exhibited by ferrets in the same study colony during the same study period (Eads et al. 2011a, 2011b).

Do badgers tend to excavate burrows when in patches currently or recently used by ferrets? The temporal main effect of TIMING increased model fit ($\chi^2_1 = 3.70$, $P = 0.054$). While controlling for numbers of active burrow openings (ACT), badgers excavated a burrow more often in cells with recent ferret occurrence (Fig. 3).

With respect to our analysis of released polecats and ferrets, the polecats were relatively heavily impacted by a digging type of mesopredator that was novel in their evolutionary history. Badgers accounted for 30.0% of total predation cases on polecats and 5.5% of predation cases on ferrets ($\chi^2_1 = 13.80$, $P < 0.001$). To underscore this concept, a canid (a shared family of predators for both *Mustela* species) killed similar proportions of each species of *Mustela*; coyotes accounted for 65.0% of total predation cases on polecats and 67.1% of predation cases on ferrets ($\chi^2_1 = 0.05$, $P = 0.820$).

DISCUSSION

Badger and ferret resource selection.—During our study of resource selection, badgers selected areas of the study colony with high densities of active burrow openings where prairie dogs are relatively abundant. This behavior likely reflects selective hunting of prairie dogs by badgers, as documented in an analysis of stomach contents and feces from badgers that occupied colonies of white-tailed prairie dogs (*C. leucurus*) in Wyoming (Goodrich and Buskirk 1998). In using areas of a prairie dog colony with high densities of active burrow openings, badgers concentrated their activities in areas frequently used by ferrets, suggesting spatial associations between the 2 species and, perhaps, a heightened risk of badger predation for ferrets.

In addition to using areas of prairie dog colonies used by ferrets, badgers may be attracted to ferret dens and steal freshly killed prairie dogs or portions of prairie dog carcasses in ferret dens (interference via kleptoparasitism) or actively hunt ferrets. If badgers are attracted to ferret dens, then badgers should excavate burrows more often when in areas currently or recently used by ferrets, before the carrion decays or is consumed by another animal, or before ferrets depart the areas. Temporal data on concurrent occupancy of habitat patches by badgers and ferrets at our site supported this pattern. By targeting excavations in areas with recent ferret occupancy, a badger might acquire easy prey items (dead prairie dogs) but also potentially kill a ferret, thereby reducing competition with a more specialized predator while also acquiring food (badgers often consume the ferrets they kill—Biggins 2000; Biggins et al. 2011b).

How might a badger locate and identify a ferret den to steal prey or attack a ferret? Badgers have a highly acute sense of
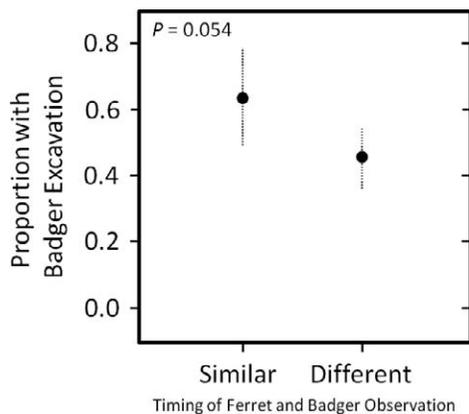

FIG. 3.—Proportion of 80 × 80 m cells (95% confidence intervals) containing an American badger (*Taxidea taxus*) excavation completed 0–10 days after a black-footed ferret (*Mustela nigripes*) was observed in a cell (Similar timing) or > 10 days after a ferret was observed in a cell (Different timing). Data were collected during 13 June–10 October 2007 and 11 June–27 September 2008 on a 452-ha colony of black-tailed prairie dogs (*Cynomys ludovicianus*) in the Conata Basin, South Dakota. The *P*-value corresponds with a likelihood-ratio test.

smell (Minta 1993) and may detect a ferret den via the scent of a ferret or of prairie dog carrion. During a 4-day study in Wyoming, badgers excavated 17 of 18 burrows in which biologists had inserted dead prairie dogs (Biggins et al. 1991), suggesting that badgers can detect carrion in ferret dens via olfaction.

Badger predation on ferrets and polecats.—Badgers were identified as the cause of mortality for ferrets in only 5.5% of cases. When taken alone, this small proportion might leave an impression that badger predation is not a serious problem for ferrets. However, low detection of badger predation on ferrets does not imply that the relationship between the 2 species has been historically unimportant.

The intimate spatial and temporal associations between badgers and ferrets in our study of resource selection and low rates of badger predation on ferrets suggest that ferrets have evolved effective defenses against badgers (Brodie and Brodie 1999) and the defenses might be so effective that badgers are rarely successful in killing a ferret (Lima and Dill 1990:634). For example, ferrets prefer to use multiopening burrow systems, a propensity that might provide ferrets with multiple routes of escape from badgers (Biggins 2012). This hypothesis is supported by observations of prairie dogs that selectively escaped into multiopening burrow systems when attacked by badgers aboveground (Eads and Biggins 2008; Licht 2009), suggesting that the exceptional digging abilities of badgers can indeed favor use of multiopening burrows by prairie dogs and ferrets. Regarding ferrets, perhaps an evolved defense has dampened the potential for badger predation (Lima and Dill 1990; Caro 2005) resulting in low rates of badger predation on ferrets released to prairie dog colonies. This contention is supported by the relatively high rate of badger predation on polecats that evolved in Asia, in the absence of a digging predator. In contrast, polecats and ferrets both have long evolutionary histories with canid predators and might exhibit similar defenses against canids, which could at least partly explain the similar relative proportions of mortality caused by coyotes when polecats and ferrets were released on prairie dog colonies.

Attraction of badgers to areas occupied by ferrets may result in consequences for ferrets beyond direct predation. Kleptoparasitism by badgers would force a ferret to acquire new food, and hunting of live prairie dogs can be dangerous and energetically taxing for ferrets (Vargas and Anderson 1998). In addition, a ferret might increase its rate of movement to avoid areas of its home range used by badgers, or a ferret might increase its digging activities to re-create multiopening burrow systems—both of these behaviors involve energy expenditure (Powell et al. 1985). Lastly, coyotes are sometimes attracted to excavating badgers and can kill prey that emerge aboveground to evade a badger (Minta et al. 1992); if badgers are attracted to areas used by ferrets, badgers might attract coyotes to ferrets.

Although the analysis of mortality data agreed with our hypotheses, those results should be taken as suggestive but not definitive. The mortality data sets were relatively large and collected in multiple localities; however, they were gathered for purposes other than the analysis presented herein. Thus, as is characteristic of many retrospective analyses in ecology, there is potential for confounding factors in our analysis of mortality.

Implications for coexistence of ferrets and badgers.—Badgers and ferrets exhibit niche overlap in colonies of prairie dogs. Coexistence of ferrets and badgers in prairie dog habitats implies that niche overlap between the 2 species involves trade-offs so one species does not always displace the other (MacArthur and Levins 1967). Ferrets are specialized predators of prairie dogs, are long and thin, and can move with relative ease in prairie dog burrows that are not plugged with soil (Miller et al. 1996). In contrast, badgers are generalist predators that sometimes selectively prey on prairie dogs (Goodrich and Buskirk 1998) and are large mustelids that excavate most burrows if attacking prey belowground (e.g., see Fig. 1B). Ferrets are apparently superior in exploitation competition for prairie dogs, a theoretical prerequisite for a small carnivore to exist with its larger and more powerful counterpart (Holt and Polis 1997; Revilla 2002). In addition, ferrets exhibit behaviors that are highly effective for avoiding badgers (e.g., use of multiopening burrows), which also aids coexistence. In contrast, badgers might coexist with ferrets by stealing prey and exhibiting overt aggression toward ferrets (i.e., interference competition). King and Moors (1979) proposed a similar scenario for sympatric *Mustela nivalis* (a small and efficient predator of small rodents that inhabits burrows with small openings) and *M. erminea* (a larger weasel that can kill *M. nivalis* and steal prey but is too large to enter some rodent burrows without excavation [see also King and Powell 2007:367–377]). The more cosmopolitan diet of badgers also could help them to coexist with ferrets (Schoener 1974).

The above discussion of coexistence suggests that ferrets and badgers can each incur costs from living with the other in colonies of prairie dogs. This assumption seems to apply particularly well to ferrets, given a ferret might suffer a reduction in fitness when a badger steals its prey, a ferret suffers a complete loss of fitness when killed by a badger, and badger predation has apparently exerted a strong selective force upon ferrets for effective antipredator defenses. Costs to the badger may be lower but the badger must compete for prey with a presumably more efficient hunter of prairie dogs. Although somewhat counterintuitive, badgers also might benefit from living with ferrets. Instead of searching and excavating for live prairie dogs that exhibit avoidance behaviors (Hoogland 1995; Eads and Biggins 2008; Eads et al. 2012a), a badger can excavate a ferret den and acquire dead prairie dogs as a reliable source of food. Perhaps if prairie dogs are sufficiently abundant, badgers function less as a predator and more as a kleptoparasite of ferrets, but still as a natural enemy (Raffel et al. 2008). If badgers at least partly benefit from living with ferrets, why do badgers kill ferrets? Assuming that kleptoparasitism by badgers on ferrets is common, badgers could face a trade-off between the costs and benefits of killing or not killing ferrets. By killing ferrets, the badgers are

removing a "tool" that could allow for a steady supply of "free" prey, suggesting a cost to killing ferrets. However, the cost of killing ferrets might not sufficiently counterbalance the benefits of removing a specialized competitor and gaining energy from consuming the ferret.

Evolutionary "arms races" between predators and their prey are fundamental and well-studied biological phenomena that intuitively explain multiple morphological, physiological, and behavioral attributes that are observed in many organisms (Dawkins and Krebs 1979; Brodie and Brodie 1999; Abrams 2000). We provide initial evidence that badgers not only select the same habitat patches as ferrets, but also seek ferrets or dead prey in ferret dens, and that ferrets have evolved defenses against badgers. Results herein raise additional questions regarding the relationship between badgers and ferrets. For example, studies could investigate the cues that badgers might use to locate ferret dens and, conversely, the behavioral defenses that ferrets use against badgers. In addition, we hypothesized above that the use of multiopening burrows by ferrets is an evolved behavior because badgers would seemingly kill a large proportion of ferrets that exhibit maladaptive behaviors during their initial encounters with badgers (suggesting limited opportunities for learning), but studies are needed to evaluate this hypothesis. Monitoring of ferrets and badgers is needed to confirm that badgers steal prey from ferrets and to evaluate how such kleptoparasitism might negatively affect ferrets and positively affect badgers. Presumably, kleptoparasitism or direct contests for carrion, which might occur on occasion, would increase in habitats with low prey density (Palomares and Caro 1999). However, if prairie dogs are scarce, badgers might switch to an alternative prey source (Messick and Hornocker 1981), which would reduce competition between badgers and ferrets for prairie dog prey.

ACKNOWLEDGMENTS

LITERATURE CITED

ABRAMS, P. A. 2000. The evolution of predator–prey interactions: theory and evidence. Annual Review of Ecology and Systematics 31:79–105.

BIGGINS, D. E. 2000. Predation on black-footed ferrets (*Mustela nigripes*) and Siberian polecats (*M. eversmanii*): conservation and evolutionary implications. Ph.D. dissertation, Colorado State University, Fort Collins.

BIGGINS, D. E. 2012. Use of multi-opening burrow systems by black-footed ferrets. Western North American Naturalist 72:134–139.

BIGGINS, D. E., J. L. GODBEY, T. M. LIVIERI, M. R. MATCHETT, AND B. D. BIBLES. 2006a. Postrelease movements and survival of adult and young black-footed ferrets. Pp. 191–200 in Recovery of the black-footed ferret: progress and continuing challenges (J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, eds.). United States Geological Survey Scientific Investigations Report 2005–5293:1–288.

BIGGINS, D. E., J. L. GODBEY, M. R. MATCHETT, L. R. HANEBURY, T. M. LIVIERI, AND P. E. MARINARI. 2006b. Monitoring black-footed ferrets during reestablishment of free-ranging populations: Discussion of alternative methods and recommended minimum standards. Pp. 155–174 in Recovery of the black-footed ferret: progress and continuing challenges (J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, eds.). United States Geological Survey Scientific Investigations Report 2005–5293:1–288.

BIGGINS, D. E., L. R. HANEBURY, AND K. A. FAGERSTONE. 2012. Digging behaviors of radio-tagged black-footed ferrets near Meeteetse, Wyoming, 1982–1984. Western North American Naturalist 72:148–157.

BIGGINS, D. E., L. R. HANEBURY, AND B. J. MILLER. 1991. Trial release of Siberian polecats (*Mustela eversmanii*). United States Fish and Wildlife Service, National Ecology Research Center, Progress Report:1–22.

BIGGINS, D. E., L. R. HANEBURY, B. J. MILLER, AND R. A. POWELL. 2011a. Black-footed ferrets and Siberian polecats as ecological surrogates and ecological equivalents. Journal of Mammalogy 92:710–720.

BIGGINS, D. E., ET AL. 1993. A technique for evaluating black-footed ferret habitat. Pp. 73–78 in Management of prairie dog complexes for reintroduction of the black-footed ferret (J. Oldemyer, B. Miller, and R. Crete, eds.). United States Fish and Wildlife Service Biological Report 13:1–96.

BIGGINS, D. E., B. MILLER, L. HANEBURY, AND R. A. POWELL. 2011b. Mortality of Siberian polecats and black-footed ferrets released onto prairie dog colonies. Journal of Mammalogy 92:721–731.

BIGGINS, D. E., M. SCHROEDER, S. FORREST, AND L. RICHARDSON. 1985. Movements and habitat relationships of radio-tagged black-footed ferrets. Pp. 11.1–11.17 in Black-footed ferret workshop proceedings, Laramie, Wyoming, September 18–19, 1984 (S. Anderson and D. Inkley, eds.). Wyoming Game and Fish, Cheyenne.

BIGGINS, D. E., A. VARGAS, J. L. GODBEY, AND S. H. ANDERSON. 1999. Influence of prerelease experience on reintroduced black-footed ferrets (*Mustela nigripes*). Biological Conservation 89:121–129.

BRODIE, E. D., III, AND E. D. BRODIE, JR. 1999. Predator–prey arms races. BioScience 49:557–568.

CARO, T. 2005. Antipredator defenses in birds and mammals. University of Chicago Press, Chicago, Illinois.

DAWKINS, R., AND J. R. KREBS. 1979. Arms races between and within species. Proceedings of the Royal Society of London, B. Biological Sciences 202:489–511.

EADS, D. A. 2009. Evaluation and development of black-footed ferret resource selection models. M.S. thesis, University of Missouri, Columbia.

EADS, D. A., AND D. E. BIGGINS. 2008. Aboveground predation by an American badger (*Taxidea taxus*) on black-tailed prairie dogs

(*Cynomys ludovicianus*). Western North American Naturalist 68:396–401.

EADS, D. A., M. T. J. HAGUE, AND C. G. ZOUBEK. 2012a. American badger (*Taxidea taxus*) uses covert reconnaissance to ambush a black-tailed prairie dog (*Cynomys ludovicianus*). Southwestern Naturalist 57:465–467.

EADS, D. A., D. S. JACHOWSKI, J. J. MILLSPAUGH, AND D. E. BIGGINS. 2012b. Importance of lunar and temporal conditions for spotlight surveys of adult black-footed ferrets. Western North American Naturalist 72:179–190.

EADS, D. A., J. J. MILLSPAUGH, D. E. BIGGINS, D. S. JACHOWSKI, AND T. M. LIVIERI. 2011a. Evaluation of a black-footed ferret resource utilization function model. Journal of Wildlife Management 75:1155–1163.

EADS, D. A., J. J. MILLSPAUGH, D. E. BIGGINS, T. M. LIVIERI, AND D. S. JACHOWSKI. 2011b. Postbreeding resource selection by adult black-footed ferrets in the Conata Basin, South Dakota. Journal of Mammalogy 92:760–770.

GOODRICH, J. M., AND S. W. BUSKIRK. 1998. Spacing and ecology of North American badgers (*Taxidea taxus*) in a prairie-dog (*Cynomys leucurus*) complex. Journal of Mammalogy 79:171–179.

HOLT, R. D., AND G. POLIS. 1997. A theoretical framework for intraguild predation. American Naturalist 149:745–764.

HOOGLAND, J. L. 1995. The black-tailed prairie dog: social life of a burrowing mammal. University of Chicago Press, Chicago, Illinois.

JACHOWSKI, D. S., J. J. MILLSPAUGH, D. E. BIGGINS, T. M. LIVIERI, AND M. R. MATCHETT. 2008. Implications of black-tailed prairie dog spatial dynamics to black-footed ferrets. Natural Areas Journal 28:14–25.

JACHOWSKI, D. S., J. J. MILLSPAUGH, D. E. BIGGINS, T. M. LIVIERI, M. R. MATCHETT, AND C. D. RITTENHOUSE. 2011. Resource selection by black-footed ferrets in South Dakota and Montana. Natural Areas Journal 31:218–225.

JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

KING, C. M., AND P. J. MOORS. 1979. On co-existence, foraging strategy and biogeography of weasels and stoats (*Mustela nivalis* and *M. erminea*) in Britain. Oecologia 39:129–150.

KING, C. M., AND R. A. POWELL. 2007. The natural history of weasels and stoats: ecology, behavior, and management. 2nd ed. Oxford University Press, Oxford, United Kingdom.

KOFORD, C. B. 1958. Prairie dogs, white faces and blue grama. Wildlife Monographs 3:3–78.

LICHT, D. S. 2009. Observations of badgers preying on black-tailed prairie dogs. Prairie Naturalist 41:134–136.

LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

LIVIERI, T. M. 2006. Ten-year history of the Conata Basin black-footed ferret population: 1996–2005. Prairie Wildlife Research, Wall, South Dakota.

LOMOLINO, M. V., AND G. A. SMITH. 2004. Terrestrial vertebrate communities at black-tailed prairie dog (*Cynomys ludovicianus*) towns. Biological Conservation 115:89–100.

MACARTHUR, R., AND R. LEVINS. 1967. The limiting similarity, convergence, and divergence of coexisting species. American Naturalist 101:377–385.

MESSICK, J. P., AND M. G. HORNOCKER. 1981. Ecology of the badger in southwestern Idaho. Wildlife Monographs 76:1–53.

MILLER, B. J. 1988. Conservation and behavior of the endangered black-footed ferret (*Mustela nigripes*) with a comparative analysis of reproductive behavior between the black-footed ferret and the congeneric domestic ferret (*Mustela putorius furo*). Ph.D. dissertation, University of Wyoming, Laramie.

MILLER, B. J., R. P. READING, AND S. FORREST. 1996. Prairie night: black-footed ferrets and the recovery of endangered species. Smithsonian Institution Press, Washington, D.C.

MINTA, S. C. 1993. Sexual differences in spatio-temporal interaction among badgers. Oecologia 96:402–409.

MINTA, S. C., K. A. MINTA, AND D. F. LOTT. 1992. Hunting associations between badgers (*Taxidea taxus*) and coyotes (*Canis latrans*). Journal of Mammalogy 73:814–820.

PALOMARES, F., AND T. M. CARO. 1999. Interspecific killing among mammalian carnivores. American Naturalist 153:492–508.

PAUNOVICH, R., AND S. C. FORREST. 1987. Activity of a black-footed ferret litter. Prairie Naturalist 19:159–162.

POLIS, G. A., C. A. MEYERS, AND R. D. HOLT. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics 20:297–330.

POWELL, R. A., T. W. CLARK, L. RICHARDSON, AND S. C. FORREST. 1985. Black-footed ferret *Mustela nigripes* energy expenditure and prey requirements. Biological Conservation 34:1–15.

RAFFEL, T. R., L. B. MARTIN, AND J. R. ROHR. 2008. Parasites as predators: unifying natural enemy ecology. Trends in Ecology & Evolution 23:610–618.

R DEVELOPMENT CORE TEAM. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/. Accessed January 2012.

REVILLA, T. 2002. Effects of intraguild predation on resource competition. Journal of Theoretical Biology 214:49–62.

SCHOENER, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

VARGAS, A., AND S. H. ANDERSON. 1998. Ontogeny of black-footed ferret predatory behavior towards prairie dogs. Canadian Journal of Zoology 76:1696–1704.

ZHOU, W., W. WANHONG, AND D. E. BIGGINS. 1994. Activity rhythm of polecat in Qing-zang Plateau. Acta Biologica Plateau Sinica 12:173–187.