

Chapter 6

Interactions Among American Badgers, Black-Footed Ferrets, and Prairie Dogs in the Grasslands of Western North America

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Abstract – American badgers (*Taxidea taxus*) and black-footed ferrets (*Mustela nigripes*) sometimes occur sympatrically within colonies of prairie dogs (*Cynomys* spp.) in the grasslands of western North America. From the perspective of a simplified food web, badgers are consumers of ferrets and, to a greater extent, prairie dogs; ferrets are specialized consumers of prairie dogs; and prairie dogs are consumers of vegetation. We review information on the predatory behaviours of badgers, which collectively demonstrate that badgers exhibit complex hunting strategies to improve their probability of capturing prairie dogs and, perhaps, ferrets. We also review studies of interactions between badgers and ferrets, which suggest that there is selective pressure on badgers to compete with ferrets, and pressure on ferrets to compete with and avoid badgers. We then speculate as to how prairie dogs might shape interactions between badgers and ferrets, and how badgers could spread the plague bacterium (*Yersinia*

pestis) among prairie dog colonies. Lastly, we provide recommendations for research on this tractable system of semi-fossorial predators and prey.

INTRODUCTION

American Badgers (*Taxidea taxus*) are short, stout carnivores that inhabit a variety of grassland habitats in North America where they consume a diversity of animals and some plant material (Long 1973). Within the intermountain grasslands and prairies of their range, badgers commonly occupy colonies of prairie dogs (*Cynomys* spp.), burrowing rodents that live in aggregations of harem-polygynous families (Koford 1958). When occupying prairie dog colonies, badgers sometimes interact with, kill, and consume black-footed ferrets (*Mustela nigripes*), federally endangered, obligate predators of prairie dogs (Biggins *et al.* 2006b). Thus, from the perspective of a simplified food web (Elton 1927), badgers are consumers of ferrets and, to a greater extent, prairie dogs; ferrets are specialized consumers of prairie dogs; and prairie dogs are consumers of vegetation (Figure 1).

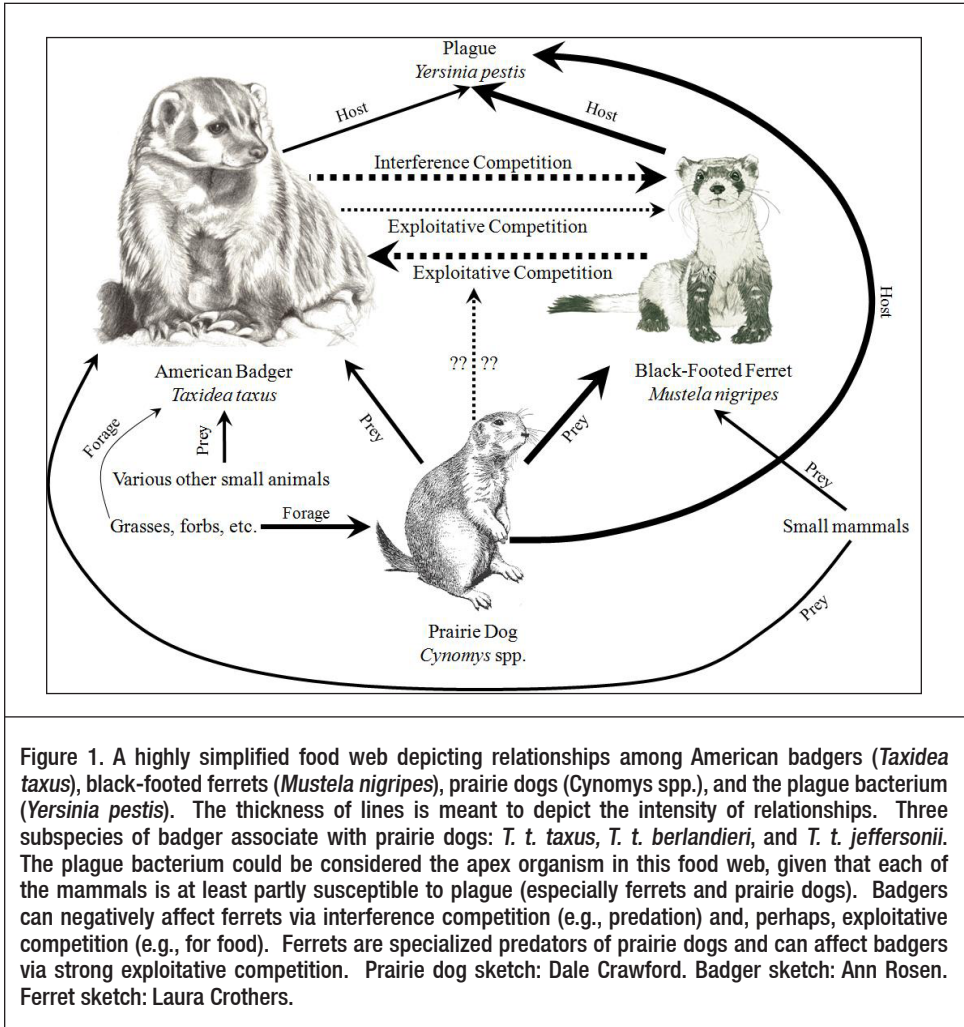
The relationship between American badgers and black-footed ferrets suggests that there is selective pressure on badgers to effectively compete with ferrets, because ferrets are specialized predators of prairie dogs, whereas badgers are not (Polis *et al.* 1989). In addition, there is selective pressure on ferrets to effectively compete with and avoid badgers, and pressure on prairie dogs to avoid badgers and ferrets (Lima and Dill 1990; Caro 2005). These selective pressures would be expected to favour co-evolutionary responses involving hunting efficiency for badgers and ferrets, and antipredator defences for ferrets and prairie dogs (Brodie and Brodie 1999; Abrams 2000). Moreover, this system contains 3 interconnected species, suggesting that 1 of the species may influence and perhaps arbitrate or shape interactions between the others (Morin 1999).

In this chapter, we discuss the ecology, behaviour, and coexistence of American badgers, black-footed ferrets, and prairie dogs in the contexts of (i) predator-prey arms races, (ii) intraguild predation, and (iii) other indirect interactions. We review studies and observations of the hunting behaviours of badgers and competitive interactions between badgers and ferrets, with implications for their coexistence. In addition, we speculate as to how prairie dogs might indirectly shape interactions between badgers and ferrets. We also examine the roles that badgers could play in spreading disease among prairie dog colonies, with special reference to plague, an exceptionally lethal zoonosis that devastates prairie dog and ferret populations. First, however, we review the natural histories of badgers, ferrets, and prairie dogs.

AMERICAN BADGERS, BLACK-FOOTED FERRETS, AND PRAIRIES DOGS

American badgers and black-footed ferrets are semi-fossorial carnivores of the mammalian family Mustelidae. Male badgers can weigh more than 13 kg but, on average, males and females typically weigh about 8.6 and 6.3 kg, respectively (Long 1973; Lindzey 2003). In contrast, male and female black-footed ferrets weigh only about 1 and 0.7 kg, respectively (Hillman and Clark 1980; Anderson *et al.* 1986).

American badgers exhibit specialized thoracic limbs, paws, and claws (Figure 1) that are



used to excavate burrows (Moore *et al.* 2012). In contrast, ferrets are not specialized for digging. However, they are shaped thinly and can easily enter most prairie dog burrows, providing them with opportunities to stalk prairie dogs below ground, ambush prairie dogs at burrow openings, and escape from terrestrial and aerial predators (Miller *et al.* 1996; Biggins 2000).

The genus *Cynomys* is represented by 5 species: black-tailed (*C. ludovicianus*), Mexican (*C. mexicanus*), white-tailed (*C. leucurus*), Gunnison's (*C. gunnisoni*), and Utah (*C. parvidens*) prairie dogs. Badgers hunt all of these species, whereas ferrets occupy colonies of black-tailed, white-tailed, and Gunnison's prairie dogs. In general, prairie dogs are 0.5–1.5 kg sciurid rodents that are efficient at creating burrows, which are often characterized by 2 or more openings above ground (Figure 2; King 1955; Hoogland 1995). These openings

lead underground to subterranean labyrinths of interconnected tunnels and nesting chambers (Hoogland 1995). Prairie dogs sometimes use soil and vegetation to plug burrow openings or tunnels (Wilcomb 1954; Sheets *et al.* 1971). Burrow plugging plays a large role in subsequent discussions in this chapter because the plugs might indirectly affect interactions between badgers, ferrets, and prairie dogs.

Prairie dogs uniquely alter grassland habitats and are considered keystone species and ecosystem engineers due in part to their grazing and burrowing behaviours and their role as prey for a multitude of predators (Kotliar *et al.* 2006). The ecological importance of prairie dogs is exemplified in the case of black-footed ferrets because prairie dogs comprise 60% or more of the ferret's diet (Brickner *et al.* 2014) and a "breeding family" of ferrets (1 adult female, 3.3 kits, and 0.5 adult male; Biggins *et al.* 1993) kills about 800–2,000 prairie dogs in its home range per year (Miller and Reading 2012). Moreover, ferrets use prairie dog burrows as den sites and refuge from predators and inclement weather (Houston *et al.* 1986; Biggins *et al.* 1993, 2006a).

American badgers are less specialized than ferrets on prairie dogs as prey (Azevedo *et al.* 2006) but commonly prey on all 5 species of prairie dogs and excavate and use prairie dog burrows as den sites (Koford 1958; Goodrich and Buskirk 1998). Moreover, badgers prey upon other species that use prairie dog colonies including burrowing owls (*Athene cunicularia*; Desmond *et al.* 2000), *Sylvilagus* rabbits, *Peromyscus* mice, *Crotalus* rattlesnakes (Jackley 1938), and ground-nesting birds (Baker *et al.* 1999). Presumably as a result, badgers are usually more abundant on prairie dog colonies than on uncolonized grassland (Bailey 1905, 1931; Krueger 1986; Ceballos *et al.* 1999; Lomolino and Smith 2004; Shaughnessy and Cifelli 2004; but see Baker *et al.* 1999; Milne-Laux and Sweitzer 2006).

While many prey species inhabit prairie dog colonies and are potentially available to



Figure 2. A section of black-tailed prairie dog (*Cynomys ludovicianus*) habitat in Grassland National Park, Saskatchewan, Canada. Prairie dogs use soils and vegetation to create the dark humps in the foreground; these burrow mounds contain openings that descend below ground into prairie dog burrow systems. Photo © Travis Livieri.

American badgers, the amount of prairie dog biomass in a colony likely far exceeds the biomass of any other vertebrate prey available to badgers, suggesting badgers use prairie dog colonies primarily to prey on prairie dogs. Using a mean weight of 760 g for a black-tailed prairie dog (Biggins *et al.* 1993) and a density of about 40 prairie dogs ha⁻¹, a potential 34 kg of prairie dog biomass ha⁻¹ would be available to badgers (see also Clark 1989, p. 63).

Prairie dog colonies can provide American badgers with an abundance of prey, but prairie dogs are highly efficient at detecting predators (Hoogland 1981) and use body movements and vocalizations to inform each other when a predator is present (Hoogland 1995; Slobodchikoff *et al.* 2009). Consequently, when a badger arrives at a colony or emerges above ground during daylight hours, prairie dogs are often able to respond quickly and retreat to a burrow.

The scenario changes during the winter months for prairie dogs in the white-tail subgenus (*Leucocrossuromys*), given that these *Cynomys* are obligate hibernators (*C. gunnisoni*, *C. leucurus*, *C. parvidens*). Before hibernating, white-tailed prairie dogs, and perhaps other *Leucocrossuromys*, use soil to plug tunnels that lead to their nesting chambers (Biggins *et al.* 2012a). They then enter deep bouts of torpor during which they may expend 80% or more of their winter energy budget (Bakko and Nahorniak 1986). During hibernation, a prairie dog's muscles "lock" (Slobodchikoff *et al.* 2009, p. 22), suggesting that it would be at an increased risk to predation. Telemetry data suggest that black-footed ferrets hunt active prairie dogs until most of these prey have descended below ground to hibernate (Biggins *et al.* 2012a). Thus, for ferrets, it seems that excavation of hibernating prairie dogs "has an energetic cost that exceeds the costs of hunting active prairie dogs", perhaps because ferrets are relatively poor diggers (Biggins *et al.* 2012a, p. 153). The opposite would seemingly apply to American badgers for at least 2 reasons: (i) adult females must acquire considerable fat stores in winter to support the energetic requirements of lactation in spring, which are nearly quadruple the expenditure for most mammals (Harlow *et al.* 1985) and (ii) badgers are highly efficient diggers (Michener 2014), as discussed below.

HUNTING TECHNIQUES USED BY AMERICAN BADGERS ON PRAIRIE DOG COLONIES

During nighttime spotlight surveys or daytime monitoring of prairie dog colonies, we have observed American badgers most commonly hunting prairie dogs by digging to enlarge the diameter of burrows – the frequency of this hunting technique is further suggested by high proportion of badger-reamed burrows in prairie dog colonies (e.g., 10–62% in Campbell and Clark 1981). In many cases, a badger begins a hunt by emerging above ground and moving among burrow openings, often in a zig-zag pattern (e.g., Proulx and MacKenzie 2012). A badger sometimes stops and inserts its head into a burrow, perhaps to investigate for the scents and sounds of prey, to determine which prey species, if any, is present, and to assess burrow morphology (presence of connected openings). A behavioural sequence can involve alternating between excavation and head insertions, with repetition over variable periods of time (Michener 2004; Licht 2009). These investigatory excavations could stimulate movement by prey inside the burrow, resulting in seismic and auditory cues that a badger could detect (Reichman and Smith 1990; see also Proulx and MacKenzie 2012). For instance, when collecting fleas from burrows, we commonly hear alarm calls from prairie dogs below

ground, vocalizations that badgers would hear.

When excavating a burrow, an American badger alternately brings loose soil to the surface (which often extends away from the burrow openings) and dives below ground to continue digging (Eldridge 2004). Excavations require aggressive digging that can last for >1 h (Eads and Biggins 2008). If successful in capturing prey, the badger either remains below ground at the excavation site or moves its prey to another burrow where it can provision offspring with food (for female badgers) and eat without harassment from terrestrial and aerial scavengers (Michener 2000; Eads and Biggins 2008; Licht 2009).

American badgers can be highly effective at excavating prairie dogs from burrows. For example, 3 badgers in a colony of black-tailed prairie dogs in Kansas excavated and killed at least 9 prairie dogs in a single night (Smith 1958). In a colony of black-tailed prairie dogs in Montana, a female badger excavated 3 separate burrows and successfully killed a prairie dog in each instance (Eads and Biggins 2008). In South Dakota a badger inspected and neglected several burrows before successfully acquiring a black-tailed prairie dog from the 1 burrow it excavated (Licht 2009). A badger in Nebraska partially excavated and abandoned several burrows before successfully capturing a prairie dog (Licht 2009). In another case, D. L. Licht observed a badger at night excavating a black-tailed prairie dog burrow; when he returned in the morning he found the partially consumed remains of at least 3 black-tailed prairie dogs in the freshly excavated dirt at the burrow opening. In a 1-ha colony of Gunnison's prairie dogs in Arizona, C. N. Slobodchikoff (Northern Arizona University, personal communication) noted that a single badger tended to use excavation as a hunting strategy, and estimated that the badger killed about 38 of 50 (75%) of prairie dogs in that colony during a single summer. When prairie dogs are released to artificial burrows, badgers can remove many of the prairie dogs during excavations, thereby inciting biologists to create sturdy burrows that might better protect prairie dogs, such as steel barrels (Long *et al.* 2006).

American badgers sometimes attack prairie dogs that are underground in burrows with only 1 opening to the surface (Eads and Biggins 2008; Licht 2009). In such cases, the prairie dog would be "trapped" below ground and highly susceptible to an excavating badger, unless a soil-plugged tunnel is available and provides the prairie dog with a quick route of escape (as discussed later).

American badgers may also attack prairie dogs (and ferrets) in multiple-opening burrow networks. In doing so, they can use a hole-plugging strategy to reduce escapes. During nighttime in South Dakota, T. M. Livieri watched a badger alternate between (i) excavation of an opening to a black-tailed prairie dog burrow and (ii) use of soil to plug a nearby burrow opening, which presumably connected to the site of excavation via an underground tunnel (see also Koford 1958; Knopf and Ralph 1969; Michener 2004). The repeated checks and manipulation of soil at the plugged opening by the badger might have encouraged prey to stay below ground, thereby facilitating the capture. Badgers also have been observed to plug burrows with human-made objects (e.g., wooden blocks) on colonies of Richardson's ground squirrels (*Urocitellus richardsonii*; Michener 2004).

In addition to using loose soil or human-made objects to plug burrows, American badgers sometimes destroy packed mounds of soil at burrow mounds and use the resulting adobe-like bricks to block the openings. On several occasions within colonies of black-tailed prairie dogs in New Mexico, D. H. Long (Turner Endangered Species Fund, personal communication)

observed fan-shaped piles of loose soil from badger excavations (Eldridge 2004) at burrow openings encircled by hard soil-mounds. In each case, the hard-soil mound was destroyed to the point that chunks of soil enclosed the burrow opening and it seemed badgers had created these obstructions, perhaps to trap prey below ground.

Other intriguing phenomena help American badgers to acquire prairie dogs during excavations. Coyotes (*Canis latrans*) are sometimes attracted to badgers that are excavating a burrow and apparently lie in wait “for the opportunity to quickly scramble and capture” a prairie dog that emerges above ground (Minta *et al.* 1992, p. 815; see also Cahalane 1950). The coyote’s presence is thought to encourage a prairie dog to remain below ground, which could increase the prairie dog’s risk of being killed by the excavating badger (Minta *et al.* 1992). Swift foxes (*Vulpes velox*) also hunt near excavating badgers (Ausband and Ausband 2006), as do raptors (Wauer and Egbert 1977; Devers *et al.* 2004). In South Dakota, T. M. Livieri observed a badger excavating a prairie dog burrow while a swift fox laid prone <2 m away; interestingly, that same burrow had been occupied by a black-footed ferret the previous night.

American badgers can also ambush prairie dogs above ground in daylight. For instance, on 7 occasions in Montana, a female badger rapidly emerged from her den in pursuit of prairie dogs foraging above ground (Eads and Biggins 2008). The badger successfully captured a prairie dog in 2 attacks. In each instance, the badger initiated her pursuit before nearby prairie dogs began to retreat, and her path was directed toward burrow openings selected for escape by the targeted prairie dogs, suggesting the badger predicted the prairie dog’s escape route (Eads and Biggins 2008). For descriptions of similar observations, see Sawyer (1925), Cahalane (1950), Smith (1958, 1967), Schwab (1978), Thompson (1979), and Michener (2004).

American badgers also have been observed to conceal their presence before ambushing prairie dogs (Eads *et al.* 2012a). On 7 occasions in New Mexico, a badger was observed as it ran in a crouched position through tire-ruts along a dirt road lined by patches of fetid marigold (*Dyssodia papposa*) and Russian thistle (*Salsola kali*). In each instance, the badger appeared to be at least partially concealed within the rut. In 1 of those instances, the badger slid over the median of the road, crouched in the right tire-rut, and moved slowly from the rut into a patch of vegetation that seemed to conceal the badger. The badger sprinted from the vegetation and, after a 22-m chase, captured and killed a prairie dog (Eads *et al.* 2012b).

American badgers can also ambush prey that are preoccupied with another potential predator. For example, while driving a truck through a colony of Gunnison’s prairie dogs in New Mexico, D. H. Long watched a badger kill a prairie dog that was fleeing the vehicle. D. H. Owings suggested to a teammate (Halpin 1983, p. 52) that California ground squirrels (*Otospermophilus beecheyi*) sometimes “focus so much of their attention on snakes that, during an encounter, other potential predators may be able to approach much closer than would normally be the case”. For example, S. M. Grassel was able to approach within 5 m of a black-tailed prairie dog as it interacted with a prairie rattlesnake (*Crotalus viridis viridis*).

American badgers also attack, kill, and consume black-footed ferrets, although successful predation events may be infrequent. Badgers accounted for only 5.5% of known predation events on radio-collared ferrets (Eads *et al.* 2013), perhaps helping to explain why, to our knowledge, biologists have never observed a badger killing a ferret or carrying a dead ferret

above ground. At first glance, the 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 mustelids has been historically unimportant (Lima and Dill 1990), a topic that we elaborate on later.

To our knowledge, 4 reports have documented observations of badgers interacting with ferrets. Henderson *et al.* (1969) describe an event in which a badger entered a black-tailed prairie dog colony occupied by a female ferret and her kits, all of which were above ground when the badger arrived. The ferret kits descended into a burrow and the badger approached and began to dig into that burrow. The badger noticed the mother ferret above ground and chased her until she descended into a burrow 35 m from her kits. The badger dug into the burrow occupied by the mother ferret, but the event ended when a biologist approached to photograph the badger. Henderson *et al.* (1969) reported that W. E. Garst watched a badger use soil to plug an opening to a burrow occupied by a ferret. Forrest *et al.* (1988) noted 4 occasions in Wyoming when a badger “sniffed and dug” into a burrow occupied by a ferret. On 3 separate occasions in South Dakota, S. M. Grassel located a ferret, set a trap at the focal burrow, and later observed a badger as it excavated into the burrow containing the ferret. The badger excavated parallel to the trap until it bypassed the trap and resumed its excavation underground. Perhaps the badger could smell the ferret or the carcass of a prairie dog killed by the ferret in the burrow, or the ferret-scented trap drew the badger’s attention.

Telemetry studies also indicate that badgers typically attack ferrets by excavating burrows. Namely, the remains of radio-tagged ferrets killed by badgers have been found underground in prairie dog burrows that were excavated by badgers (Biggins *et al.* 1999, 2006b, 2011b; Breck *et al.* 2006; Eads *et al.* 2013).

While excavation appears to be a common form of attack by American badgers pursuing black-footed ferrets, badgers exhibit complex predatory behaviours toward prairie dogs (as noted above) and may also do so when attacking ferrets. Below, we review information which suggests that badgers are attracted to areas recently or currently used by ferrets and we speculate as to how ferrets might avoid badgers.

INTERACTIONS BETWEEN AMERICAN BADGERS AND BLACK-FOOTED FERRETS

Both exploitative and interference competition play a role in mediating interactions between American badgers and black-footed ferrets (Figure 1). Interspecific exploitative competition occurs when one species reduces the amount of a limiting resource available to another (an indirect effect). Alternatively, interference competition occurs when one species directly interferes with its competitor, for instance via aggression, displacement, kleptoparasitism, or intraguild predation (Case and Gilpin 1974; Polis *et al.* 1989; Creel *et al.* 2001).

The probability of intraguild interaction between American badgers and black-footed ferrets would be heightened if the 2 mustelids exhibit similar movements in space and time (Kitchen *et al.* 1999; Palomares and Caro 1999). Prairie dogs and the burrows they actively use are distributed heterogeneously in colonies (Figure 3). Both ferrets and badgers select areas where burrows and prairie dogs are most abundant (Biggins *et al.* 2006b; Eads *et al.* 2011a, 2011b, 2012b; Jachowski *et al.* 2011; Chipault *et al.* 2012; Livieri and Anderson 2012;

Eads *et al.* 2013), suggesting that they “recognize these habitat patches as favourable for the detection of prey” (Proulx and MacKenzie 2012, p. 229). Moreover, in 1 study, badgers selectively excavated burrows in areas recently or currently occupied by ferrets, indicating that badgers are actively attracted to areas used by ferrets (Eads *et al.* 2013). A grid of 80 m $\times$ 80 m grid cells was overlain on a map of badger and ferret locations, and badgers were about 20% more likely to excavate burrows in cells used by a ferret within the past 10 days compared to cells without recent ferret occupancy (Eads *et al.* 2013). Thus, it seems that badgers and ferrets exhibit an intimate relationship in space (i.e., they use similar habitat patches) and time (i.e., they use the patches during similar periods).

Other than the benefits of access to high densities of prairie dogs, are there other advantages for badgers to occupy areas also occupied by ferrets? At least 2 factors might stimulate badgers to select areas near ferrets. First, badgers might steal freshly killed prey from ferrets, a form of kleptoparasitism (Polis *et al.* 1989; Creel *et al.* 2001). Second, badgers may actively pursue ferrets as prey, because a badger would not only reduce competition by killing a ferret but also benefit energetically by consuming it (Polis *et al.* 1989; Palomares and Caro 1999).

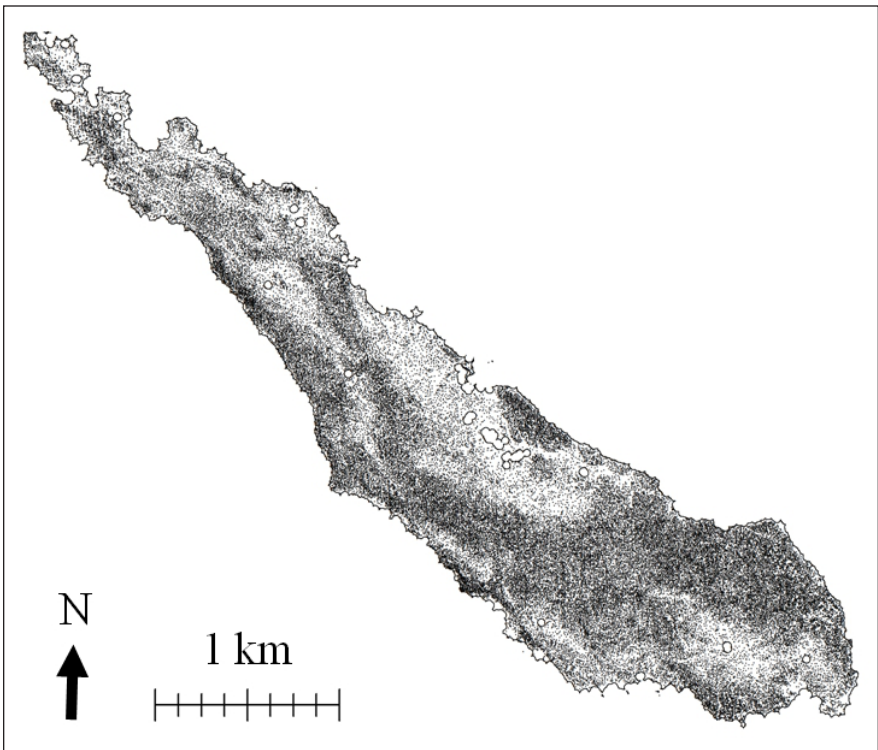


Figure 3. Depiction of active burrow openings (“stippled” background) used by black-tailed prairie dogs during 2007 on a 452-ha colony in Conata Basin, Buffalo Gap National Grasslands, South Dakota, USA. Density of dot-stippling indicates density of burrow openings (Eads *et al.* 2011b).

How might a badger locate a ferret’s den? Badgers have a highly acute sense of smell (Minta 1993), so they might be able to detect carrion in a ferret’s den. In Wyoming, badgers quickly found 17 of 18 dead prairie dogs inserted into burrows by biologists (Biggins *et al.* 1991) and a badger was observed excavating a burrow in which a ferret had cached several prey (Richardson *et al.* 1987). Hillman (1968) observed badgers digging into prairie dog burrows previously used, but not currently occupied by ferrets. In Colorado badgers were suspected of digging up carcasses of prairie dogs that died from plague (Fitzgerald and Lechleitner 1974), again suggesting that badgers can detect the scent of carrion in burrows.

It seems likely that badgers are able to detect the odour of a ferret within a burrow, or that a sighting of a ferret might motivate a badger to search for the ferret’s den (Henderson *et al.* 1969). The badger presumably would attack if the ferret entered a single-opening burrow from which there is no escape (Biggins 2012) or if the badger could create such a burrow by plugging all but 1 opening of a multi-opening burrow.

In addition to locating black-footed ferrets by detecting carrion in a ferret’s den, or smelling or observing a ferret, American badgers might take advantage of behavioural cues from prairie dogs. Prairie dogs use soil to plug burrows in areas occupied by ferrets, and they also plug burrows to entomb dead prairie dogs below ground (Biggins *et al.* 2012b; Eads and Biggins 2012). Reichman and Smith (1990) suggest that excavating predators are sometimes attracted to areas with plugged burrows because the plugs provide a cue of the presence of prey and carcasses and might facilitate captures. An abundance of plugged burrow openings in an area also suggests that a ferret is present, and a badger might actively hunt the ferret, as

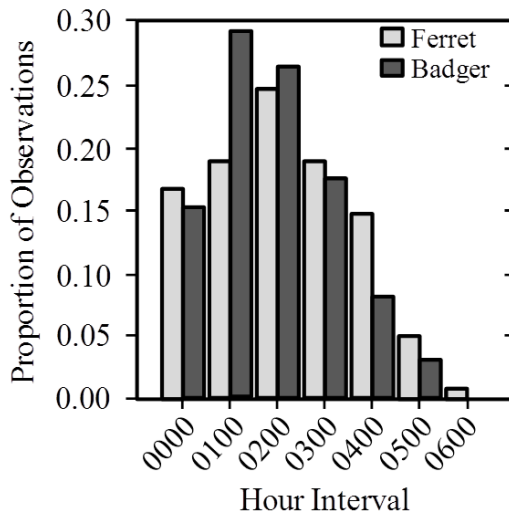


Figure 4. Proportion of black-footed ferret and American badger spotlight observations collected in hourly intervals during our primary sampling period (00h00–06h59) on a 452-ha colony of black-tailed prairies dogs in Conata Basin, South Dakota, June–October 2007 and 2008 ($n = 269$ badger observations, $n = 979$ ferret observations). Eads *et al.* (2012c) described the spotlight surveys.

suggested by Eads and Biggins (2012).

American badgers and black-footed ferrets appear to exhibit similar rates of above-ground movement during similar portions of the night. Within the limits of spotlight surveys by Eads *et al.* (2011b) in a 452-ha colony of black-tailed prairie dogs in South Dakota (midnight until dawn), badgers and ferrets were most active during 01h00–03h00 (Figure 4). Similarities in the timing of above-ground activity and the timing of use of habitat patches (noted above) could increase the rate of contact between badgers and ferrets (Lima and Dill 1990).

While American badgers might be actively attracted to areas used by black-footed ferrets and appear to exhibit increased rates of above-ground activity during periods when ferrets are most active, badgers have accounted for only 5.5% of known predation of radio-tagged ferrets (Eads *et al.* 2013). Thus, it seems that ferrets are either (1) efficient at avoiding badgers or (2) are not highly preferred prey of badgers. Effectiveness of ferret defences against badgers (hypothesis 1) is supported by a comparison of badger predation on ferrets and their ecological equivalents, Siberian polecats (*Mustela eversmannii*), mustelids that evolved in Asia without a digging predator and therefore might lack effective defences against badgers. When polecats and ferrets were released to prairie dog colonies, badgers accounted for 24.4% of known predations on polecats, but only 5.5% for ferrets. In contrast, both ferrets and polecats have similar evolutionary experience with canids, providing a plausible explanation for the similar relative impact of coyotes on them (63.4% and 67.1% of predation, respectively; Eads *et al.* 2013).

Thus, the potential for frequent contact between American badgers and black-footed ferrets due to their mutual affinity to prairie dog habitats should have provided strong selective pressure for ferrets to avoid badgers. Several avoidance behaviours seem plausible. First, ferrets could avoid portions of prairie dog colonies that are most frequently used by badgers. However, badgers appear to be attracted to, and can quickly move into, areas currently occupied by ferrets (Eads *et al.* 2013), thus necessitating other avoidance behaviours.

Second, black-footed ferrets tend to cache prey at more than 1 burrow (Richardson *et al.* 1987), which could provide the ferrets with multiple food-laden sites. Such caching could serve to reduce the need for risky movements above ground (Henderson *et al.* 1969; White *et al.* 1994; Miller *et al.* 1996) and to reduce the probability that a badger will excavate the ferret den when it raids a ferret cache (creating a $1/n$ chance of selecting the ferret's current den; Hamilton 1971). Multiple sites with cached prey might motivate badgers to become preoccupied with pursuing carrion rather than ferrets. Ferrets also may cache prey in burrows near but not connected to their current den site, thereby reducing the risk of encounter with a kleptoparasitizing badger.

Third, and perhaps most importantly, black-footed ferrets prefer to use burrows with more than 1 opening, thereby providing multiple avenues of escape from an excavating American badger, assuming prairie dogs or badgers have not plugged the burrows (Biggins 2012). Use of burrows with multiple openings as refugia from badgers was first suggested for ferrets by Henderson *et al.* (1969, p. 25) and was discussed during a meeting on the status of ferrets in North Dakota (Grondahl 1973). Later, Biggins (2012) used field data from Wyoming to demonstrate that ferrets selectively use burrows with multiple openings. In that study, the ferrets were captive-born and only 1 individual had experience with burrows. Nonetheless, the ferrets selectively used multi-opening burrows – thus, it is possible that this behaviour

is developmentally fixed (genetically predisposed), perhaps due to selective pressure from badgers over evolutionary time.

Although burrows with multiple openings provide black-footed ferrets with greater safety from American badgers than single-opening burrows, badgers sometimes attract coyotes (Minta *et al.* 1992) and coyotes are problematic predators for ferrets (Breck *et al.* 2006; Biggins *et al.* 2006a, 2011a). Perhaps coyotes kill ferrets that emerge above ground from a multi-opening burrow when escaping from a badger. In such cases, badgers and coyotes could collectively benefit from the death of a ferret because badgers and coyotes both compete with ferrets for prey. Moreover, a badger could benefit from consuming a ferret; in contrast, coyotes commonly do not consume the ferrets they kill (Biggins *et al.* 2011a).

Multi-opening burrows would help adult ferrets escape from American badgers if a coyote is not above ground, but young ferrets might remain below ground as a badger excavates and, therefore, remain vulnerable. The eyes and ears of altricial ferrets are closed until they are about 34–38 days old, at which time they start to crawl (Miller 1988; Vargas and Anderson 1996). Consequently, kits are relatively helpless during the first 4–5 weeks of life. During this period, if a maternal ferret detects a badger excavating into her den, she might sequentially move kits through a tunnel that leads above ground in a direction away from the badger. In the meantime, the badger could access the den and kill some ferret kits. Michener (2004, p. 1025) suggested a similar scenario for Richardson's ground squirrels: "Squirrels are able to carry only 1 offspring at a time in the mouth... and the rarity with which mothers rescued 1 or 2 infants suggests that badgers usually located the nest chamber rapidly and consumed the entire litter, with only the mother eluding capture". Murie's (1992) research with Columbian ground squirrels (*Urocitellus columbianus*) also suggests that badgers commonly ransack young, pre-emergent sciurids. However, at most sites occupied by ferrets, females tend to raise at least 1 kit, suggesting that badgers rarely kill entire ferret litters.

The potential attraction of American badgers to areas occupied by black-footed ferrets could cause a direct increase in predation costs for adult and young ferrets, but also indirect "risk effects" (Creel and Christianson 2008). For example, kleptoparasitism by badgers would force a ferret to seek new prairie dog prey, and hunting of live prairie dogs can be dangerous and energetically taxing for ferrets (Vargas and Anderson 1998; see also Miller *et al.* 1996; Eads *et al.* 2010a). Moreover, a ferret might increase its rate of movement to avoid badgers, a behaviour that would have energetic costs. Also, prairie dogs plug burrows near ferrets and a ferret might increase its digging activities to recreate multi-opening burrows as a defence against badgers. Removal of soil-plugs can involve substantial energy expenditures (Powell *et al.* 1985), as exemplified by a female ferret that completed 319 round-trips in and out of a burrow to remove a soil-plug that was 28-times her body weight uphill and backward over a distance of about 6-times her body length (Biggins *et al.* 2012a).

CO-EXISTENCE OF AMERICAN BADGERS AND BLACK-FOOTED FERRETS

American badgers and black-footed ferrets appear to exhibit an intimate association in colonies of prairie dogs, with overlap in space use and temporal rates of activity, and overlap in diet. How do these competing mustelids coexist?

Black-footed ferrets may coexist with American badgers because adult ferrets are efficient

at avoiding badgers, but also because ferrets are presumably superior in exploitative competition over prairie dogs (Figure 1; Holt and Polis 1997; Revilla 2002). Indeed, ferrets are specialized predators of prairie dogs, whereas badgers have a more cosmopolitan diet over their range (though they can selectively prey on prairie dogs in some cases; Goodrich and Buskirk 1998). For instance, if prairie dogs are scarce in an area, a badger can switch to alternative prey (assuming some are available), whereas a ferret is expected to be less efficient at doing so. Further, badgers can co-exist with ferrets by stealing prey and exhibiting overt aggression toward ferrets (e.g., killing), 2 forms of interference competition (Figure 1; see also King and Powell 2007, pp. 367–377).

In some cases, prairie dog densities might be sufficient to reduce competition between American badgers and black-footed ferrets. Both species select areas with high densities of prairie dogs (Eads *et al.* 2011b, 2013) and intraspecific competition would limit the densities of each predator independently. If prey densities are high and abundance of prey is adequate for both, interspecific competition could be reduced. Moreover, burrows are often abundant in areas where prairie dogs are abundant, thus providing ferrets with more routes of escape from badgers and other predators (Biggins *et al.* 1993, 2006a). Desmond *et al.* (2000) reported higher predation rates on burrowing owl nests by badgers when densities of prairie dog burrows were low and Griebel and Savidge (2007) found low nest predation rates at their site, presumably because burrow densities were high there.

Although counterintuitive at first, American badgers might sometimes benefit from living with black-footed ferrets. For example, badgers often hunt in daylight when prairie dogs are active and exhibit avoidance responses, making excavation of ferret caches an attractive alternative. Nevertheless, the fact that badgers kill ferrets suggests that the benefits of living with ferrets are outweighed by energetic gains of eating ferrets and reducing competition for prairie dogs.

PRAIRIES DOGS AND INTERACTIONS BETWEEN AMERICAN BADGERS AND BLACK-FOOTED FERRETS

Up to this point, we have concentrated on American badgers and black-footed ferrets, with only brief discussion of prairie dogs. Here, we speculate as to how prairie dogs might indirectly affect interactions between badgers and ferrets, perhaps at the expense of ferrets.

As noted previously, prairie dogs plug burrows in areas occupied by black-footed ferrets. In general, prairie dogs create 2 types of soil-plugs: (1) surface plugs that block burrow openings and (2) subsurface plugs below ground (e.g., >1 m; Biggins *et al.* 2012a). Here, we concentrate on subsurface plugs deep below ground. In particular, the following discussion focuses on the “digging speed hypothesis” (Biggins *et al.* 2012b) which posits that prairie dogs create subsurface plugs to reduce their own risk of ferret predation, while also increasing the risk of badger predation for ferrets.

Prairie dogs are efficient at digging and they commonly create burrows, whereas black-footed ferrets modify burrows but do not seem to create them (Clark 1989). Thus, it seems that prairie dogs would be faster at digging through subsurface soil-plugs. In New Mexico, 25 adult black-tailed prairie dogs were released from traps to soil-plugged burrow openings and the rodents were able to escape below ground and out-of-sight in approximately 2.5 s

(D. A. Eads, unpublished data). In contrast, ferrets require much more time to excavate soils (Biggins *et al.* 2012a).

In addition to digging faster through subsurface plugs than black-footed ferrets, prairie dogs might excavate plugs in a manner that would impede pursuit by a ferret. For instance, during observations of the 25 prairie dogs mentioned above, each animal deposited soil behind its body, creating a phenomenon that might be envisioned as “swimming” underground with soils re-accumulated as a soil-plug. In this way, soil-plugs might be viewed as “doorways” that are open for movement by prairie dogs, but mostly closed to pursuing ferrets (see also White 2009).

Prairie dogs are thought to sometimes plug all burrow passages when they descend below ground for the night (Henderson *et al.* 1969, p. 17). It seems probable that if a prairie dog inhabits a burrow with 2 or more tunnels leading to the surface and a ferret digs into one of the tunnels to attack, the prairie dog could detect the ferret (e.g., via auditory cues), “swim” into the soil-plugged “doorway,” and deposit soil behind its body, thereby recreating a plug that would serve as a barrier between itself and the ferret. The pursuing ferret would dig slower than the prairie dog, thus allowing the prairie dog to emerge above ground and escape to a nearby burrow (Eads *et al.* 2010b).

The same sort of scenario could apply to prairie dogs that are attacked by American badgers. A badger (of large size) would need to dig through undisturbed soils that might have been tightly compacted for millennia, whereas the prairie dog could dig through its “doorway.” The badger would presumably dig slower than the prairie dog that is “swimming” through loose soils. To escape effectively, the prairie dog would need to emerge and escape when the badger is still underground.

The “digging speed hypothesis” assumes that prairie dogs can “swim” through soil, allowing soil to close behind them. The type of digging we have observed for ferrets involves removal of soil from the burrow (Biggins *et al.* 2012a), so we are hesitant to suggest that “swim-digging” can be used by ferrets as a potential tactic of escape from badgers. Badgers are more efficient diggers than ferrets, and might be able to trap ferrets in a burrow that has plugged tunnels. Thus, from the “swimming” prairie dog’s perspective, the benefits of plugging to reduce their own risk to ferrets could result in an attendant increase in the risk of badger predation for ferrets, thus increasing the potential benefit (for prairie dogs) of creating soil-plugs (Biggins *et al.* 2012b).

The interplay between predator and prey in the “digging speed hypothesis” could be complex and involve “predator stages that progressively bring the predator closer to its quarry” and counterplays by prey that help them to avoid the predator (Caro 2005, p. 4). For instance, when excavating, an American badger can repeatedly check and pile soil on numerous burrow openings, encouraging prey to remain below ground. However, when a badger descends below ground to excavate, a ferret or prairie dog could initiate bouts of digging to escape. The badger may sense seismic cues from its prey, and then return above ground and pile additional soil over the plugged opening, thereby re-encouraging its prey to remain below ground. These ploys and counterplays may continue until the predation event terminates, when either the prey escapes or the badger acquires its prey (or a coyote intercepts the prey).

These hypothetical scenarios serve to increase the potential complexities of predator–prey

interactions. Some of the behaviours have not been documented within the context described and could be rare, but their frequency does not necessarily correlate to importance (Lima and Dill 1990). We posit that both American badgers and black-footed ferrets can sense when prey have increased opportunities for escape and, consequently, might avoid the costs of pursuit when an attack is unlikely to be successful. Nonetheless, a “race” of digging may sometimes occur in this system of predators and prey, and additional research is needed to evaluate the “digging speed hypothesis”.

PLAGUE IN THE FOOD WEB WITH AMERICAN BADGERS, BLACK-FOOTED FERRETS, AND PRAIRIES DOGS

In addition to behavioural interactions like those discussed above, diseases can play a significant role in the food web involving American badgers, black-footed ferrets, and prairie dogs. In particular, the web could be extended to include *Yersinia pestis*, an exceptionally virulent, primarily flea-borne bacterium that causes plague (Figure 1). *Yersinia pestis* was introduced to North America ca. 1900 and was first detected in prairie dogs during the 1930s (Eskey and Haas 1940). North American fleas are able to transmit the bacterium, and some fleas are generalists that parasitize badgers, ferrets, and prairie dogs alike (e.g., *Pulex* spp.; Hopla 1980; Harris *et al.* 2014).

The plague bacterium is highly lethal for ferrets and prairie dogs (Biggins *et al.* 2010; Matchett *et al.* 2010) and behaves much like a predator for these mammals (Biggins 2000). In contrast, badgers exhibit some resistance and might temporarily benefit from plague in some cases because plague-killed prairie dogs and ferrets would provide badgers with easy meals.

If plague erupts in epizootic form, badgers could experience an ephemeral event of resource superabundance. Badgers would seemingly benefit from the “resource pulse” (Yang 2004) more than other predators, because prairie dogs and ferrets typically succumb to plague in burrows and are therefore inaccessible to most terrestrial or aerial predators. The benefits of plague to badgers are likely to be temporary, however, because the number of surviving prairie dogs is typically low (95–100% of prairie dogs die during plague epizootics; Slobodchikoff *et al.* 2009) and insects can consume squirrel carcasses within about 10 days or less (Sullivan 1988). While excavating black-tailed prairie dog burrows in Oklahoma, Wilcomb (1954) found an abundance of larval insects that consume organic matter, including animal carcasses.

During periods when prairie dogs and carcasses are scarce, badgers might switch to alternative prey, but other mammalian prey can also suffer declines when plague erupts in prairie dogs. For instance, following a plague epizootic in colonies of black-tailed prairie dogs in South Dakota (D. E. Biggins, unpublished data), only a single *Peromyscus* mouse was captured during 1,500 trap-nights of effort at off-colony sites, and overall capture rate for small mammals at on- and off-colony sites was 21.6 individuals per 1,000 trap-nights, considerably below capture rates for 2 studies that were done before the plague invasion (41.0–106.3 individuals/1,000 trap-nights on colonies; 28.0–38.3/1,000 trap-nights off colonies; Agnew *et al.* 1986; Cully *et al.* 2010). Thus, badgers may suffer increase rates of mortality or reduced rates of offspring production because of plague-induced declines in the

overall biomass of mammalian prey (Biggins and Kosoy 2001).

American badgers might help to spread *Y. pestis* among prairie dog colonies, thereby negatively affecting ferrets and prairie dogs without directly killing or consuming these animals. The large home ranges of badgers (3–12 km²; Goodrich and Buskirk 1998) might increase their probability of encountering plague-infected rodents and transporting infected fleas within and between prairie dog colonies (Lechleitner *et al.* 1968; Collinge *et al.* 2005). This might explain the high rate of plague prevalence in badgers under natural conditions (Gage *et al.* 1994; Salkeld and Stapp 2006). Nonetheless, the role of badgers in plague transmission and persistence is not well understood and requires investigation.

CONCLUSION: SOME TOPICS FOR FUTURE RESEARCH

The above review highlights several gaps in knowledge, including the following:

1. How abundant are badgers in the prairie dog ecosystem and how often do they use prairie dog colonies? How does their use of prairie dog colonies vary seasonally? Do badgers exhibit increased rates of survival and offspring production when inhabiting prairie dog colonies, relative to off-colony sites? Radio-tracking of badgers and monitoring of mothers with kits may help to answer these questions.
2. Do American badgers sometimes benefit from living with black-footed ferrets, for instance due to increased access to carrion? Studies of badgers in areas with and without ferrets could be revealing.
3. Do American badgers destroy litters of black-footed ferret kits and, if so, at what rate? Intensive observation of maternal ferrets and their dens via real-time observation (Paunovich and Forrest 1987) or video camera (Jachowski 2007) might be useful.
4. How plausible is the “digging speed hypothesis”? Do digging black-footed ferrets allow soil to close behind them as they move forward (i.e., are ferrets capable of “swimming” through soils, like prairie dogs)? Digging speeds could be evaluated for American badgers, ferrets, and prairie dogs living in semi-natural pens, like those used to pre-condition captive-born ferrets before they are released to the wild (Biggins *et al.* 2012b).
5. If the “digging speed hypothesis” is correct, has badger predation selected not only for surface burrow plugging by prairie dogs, but also the creation of long and deep soil-plugs (similar to the ferret influence suggested by Biggins *et al.* 2012b)? Studies of prairie dog burrows in areas with and without badgers might provide an answer to this question.
6. When an American badger is hunting prairie dogs or black-footed ferrets, what variety of objects might it use to plug burrows? Future observations and experiments, with wild badgers and prairie dogs, might answer this question. Or, experiments could be conducted in captivity, with study arenas designed to allow for simulated attacks, while also protecting badgers and prairie dogs, alike, from injury and mortality.
7. Are American badgers and coyotes (or swift foxes) partners when hunting in the same proximity, or do the canids simply parasitize badgers? Concurrent hunting by badgers and coyotes might suggest a “hunting association” or “partnership”, because rodents appear to experience higher rates of mortality if hunted by both of these carnivores in unison (Cahalane 1950; Minta *et al.* 1992). However, badgers tend to remain below ground when a coyote is present, presumably because coyotes are sometimes aggressive toward badgers

(e.g., biting and harassing). Moreover, badgers are rarely observed with more than 1 coyote, presumably because groups of coyotes can cooperatively kill badgers (Rathbun *et al.* 1980; Minta *et al.* 1992; Lindzey 2003, but see Young and Jackson 1951). Also, when coyotes and badgers are observed together, rodents sometimes emerge above ground and are killed by coyotes (Minta *et al.* 1992), suggesting a cost for badgers when hunting near coyotes. Perhaps coyotes sometimes parasitize badgers, which would suggest there is no strict partnership (T. Schoener, as cited by Minta *et al.* 1992, p. 819; see also Wauer and Egbert 1977; Lehner 1981).

8. Do American badgers increase the risk of predation for black-footed ferrets by attracting coyotes to excavation sites and, perhaps, forcing ferrets above ground where they are susceptible to coyotes? Perhaps this scenario would partly help to explain why coyotes are the most problematic predator for ferrets (Breck *et al.* 2006; Biggins *et al.* 2006b, 2011b). Concurrent and intensive monitoring of badgers, coyotes, and ferrets is needed to investigate this question.
9. What are the “risk effects” of American badgers for black-footed ferrets (Creel and Christian 2008)? Further, what effects do soil-plugs have on energy expenditures by ferrets? Studies of ferrets in areas with and without badgers might provide answers to these questions.
10. What are the relative and collective effects of predation from American badgers and ferrets on prairie dog populations? Metabolic studies suggest that an adult badger must consume 2 *Otospermophilus* ground squirrels per day to maintain body weight, and prey requirements would be heightened for adult females that are lactating or providing prey to kits (Harlow *et al.* 1985). Similarly, metabolic studies suggest a ferret family consumes just over 2 prairie dogs per day, with prey requirements heightened for females raising kits (Biggins *et al.* 1993). Badgers and ferrets can both kill numbers of prey beyond their current energetic requirements, and cache the prey as a source of food (Richardson *et al.* 1987; Michener 2000), suggesting impacts beyond those related to current energetic requirements. In addition, badgers and ferrets can selectively prey on young-of-year rodents (Michener 2000; D. E. Biggins and D. A. Eads, unpublished data). From a demographic standpoint, selective predation on young-of-year rodents is important because (1) more prey items are needed for predators to meet their energetic requirements and (2) prairie dogs reproduce only once per year (Hoogland 1995), suggesting litter loss to badgers and ferrets could have important demographic consequences. This collection of information suggests that badgers and ferrets could collectively, and in some cases independently, limit the size of prairie dog populations and rates of colony expansion by these rodents at local scales (Yannone 1973). Badgers have been implicated in reducing natural populations of prairie dogs, and slowing growth of colonies at local scales (Milne-Laux and Sweitzer 2006; Morrison and Peitz 2011).

Conversely, during experiments in which badgers were removed from sites, badger reduction allowed increased colony growth for prairie dogs, again suggesting that badgers can have a significant effect on prairie dog populations (Bailey 1905, 1931). Badgers and ferrets would further limit prairie dog populations if they exert both direct and indirect effects on prairie dogs (i.e., predation and risk effects; Creel and Christian 2008). Additional studies of prairie dogs in areas with and without ferrets/badgers would be useful.

11. What is the role of plague in the food web involving American badgers, black-footed

ferrets, and prairie dogs? Do badgers move plague within and between prairie dog colonies? Do they harbour plague between epizootics and play a role as a reservoir of plague? In general, it is disturbing that *Y. pestis* might be considered as the apex organism in this food web (Figure 1) because it was introduced to North America and the bacterium distorts trophic relationships and ecosystem structure and functioning (Biggins and Kosoy 2001). Conservation of the grasslands of western North America and future studies of badgers, ferrets, and prairie dogs are consequently reliant on additional study and effective management of plague. Further investigations of the ecology of plague should emphasize maintenance of *Y. pestis* during inter-epizootic periods and identify other species of hosts that are involved in the disease cycle, perhaps including badgers.

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