

THESIS

UNDERSTANDING AND MITIGATING COYOTE PREDATION
ON BLACK-FOOTED FERRETS

Submitted by

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In partial fulfillment of the requirements

For the Degree of Masters of Science

Colorado State University

Fort Collins, Colorado

Fall 2019

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ABSTRACT

UNDERSTANDING AND MITIGATING COYOTE PREDATION ON BLACK-FOOTED FERRETS

Coyotes (*Canis latrans*) kill more livestock than any other mammal in the U.S. and can be important predators of vulnerable native fauna. In prairie ecosystems, coyotes are the primary predator of endangered black-footed ferrets (*Mustela nigripes*; hereafter, ferret), where coyote predation can significantly hamper ferret recovery efforts. To better understand coyote predation on ferrets we used remote wildlife cameras, occupancy models, and overlap of circadian activity patterns to investigate multiple abiotic, biotic, and temporal factors hypothesized to influence coyote use of prairie dog colonies, and by proxy coyote-ferret interactions. We first assessed coyote preferences between prairie dog colonies and surrounding available grasslands and found coyotes used prairie dog colonies nearly twice as much as surrounding grasslands. Next, we investigated biotic and abiotic factors that may influence coyote use and frequency of use on prairie dog colonies. We found high coyote use across our study area, but frequency of use varied across prairie dog colonies and was higher in areas of high badger occurrence. Badgers and coyotes are known to form hunting associations and high overlap between coyote and badger activity patterns in our study further supported spatial use patterns revealed by our occupancy analysis. Strong interspecific competition and patterns of resource selection between badgers and ferrets have been documented in previous studies, and as a result, our study suggests that coyote attraction to badgers may be the principal influence on coyote-ferret interactions. To mitigate coyote predation on ferrets we excluded coyotes from ferret occupied areas with a new non-

lethal tool, coyote fladry (hereafter; fladry), and rigorously assessed fladry's effectiveness for future use in both ecological and agricultural scenarios. Using wildlife camera data, we evaluated coyote fladry with multi-season occupancy models, where we estimated probabilities of use (i.e., occupancy), avoidance (i.e., extinction), attraction (i.e., colonization), and activity (i.e., detection) in response to fladry. Our results indicate fladry reduced coyote use and activity within protected areas for at least 60 days; however, coyotes also increased activity around, and were attracted to, the periphery of fladry exclosures, suggesting fladry may function in a way that is counterintuitive to management expectations. Occupancy models permit robust evaluation of nonlethal tools beyond binary terms of success and failure and provide valuable additional information, such as the behavioral responses of carnivores to these tools. Coyote fladry does not deter badger use of protected areas, and given the importance of badgers in predicting coyote use of colonies, future efforts to reduce coyote predation on ferrets should compare the effectiveness of tools that exclude both badgers and coyotes to our study's results.

ACKNOWLEDGEMENTS

Funding for this project was supported by the USDA National Wildlife Research Center, the Christine Stevens Wildlife Award from the Animal Welfare Institute, and the National Resource Defense Council. This thesis would not have been possible without the support and guidance of my advisor, S. Breck, and fantastic committee members L. Angeloni, L. Bailey, and D. Eads. I also thank D. Biggins, E. Gese, T. Livieri, Z. Strong, and J. Young for their invaluable insights that helped shape the objectives of this study. T. Funabashi was instrumental in the success of all field activities and we would not have collected the data we did without his enduring energy and enthusiasm. Although plans for trapping and collaring coyotes encountered unforeseen difficulties, I thank D. Lewis and B. Jolley for trapping tips and assistance. J. Bowser (USGS small mammal trapping crew) and G. Schroeder (Wind Cave National Park) provided excellent information about the study area during project development. T. Tretten provided insight and access to USFWS National Ferret Conservation Center for cameras testing. L. Pejchar (CSU), K. Wilkins (CSU), J. Young (NWRC), and P. Dobesh (United States Forest Service) provided cameras to support camera trap monitoring, The USGS small mammal and plague crew and members of the Colorado State Chapter (CSU) of The Wildlife Society provided invaluable help installing, maintaining, and deconstructing fladry exclosures. M. Jimenez and members of the Bailey Lab (J. Crockett, A. Feuka, E. Hanslowe, B. Hardy, D. Martin, P. Marques) helped immensely with installing fladry exclosures and provided substantial help with early drafts of this thesis.

DEDICATION

It was during my second semester as an undergraduate student at Colorado State University (CSU) when I came across an advertisement for an urban coyote talk hosted by the CSU chapter of The Wildlife Society (TWS). Some sort of scheduling conflict (i.e., probably a strong desire for an evening trail run) regrettably precluded me from attending the talk but I was pleased to see that the speaker, Dr. Stewart Breck, had welcomed students to reach out if they had any further questions. I promptly wrote Dr. Breck, informing him that I was gutted to have missed his talk – would he be willing to meet with me talk about coyotes? Dr. Breck wrote back, letting me know that he'd be happy to meet and that he sincerely hoped my guts were okay. I began working with Dr. Breck (hereafter; Stewart) on an undergraduate research project a short time later – and so began a totally unforeseen pivot in the direction of my life – one that has given me immense joy and the greatest satisfaction I have ever known. I am forever grateful for the opportunities, support, wisdom, and enthusiasm that Stewart imparted on me and look forward to lifelong friendship and collaboration.

I am equally grateful for the distinct privilege of working with Dr. Larissa Bailey. I meet Larissa shortly after my initial conversation with Stewart, where she first introduced me to the broader world of wildlife research as primary advisor to the CSU chapter of TWS. Attending TWS meetings left me awe inspired and allowed me to appreciate the combined complexities and creativity of research. I have grown to deeply admire Larissa's keen passion, interest, intellect, and encouragement and strive to emulate these qualities in my own work. I am enormously grateful to have be adopted as a member of the Bailey Lab and will be forever grateful to have been a part of this team. I am also thankful to have worked alongside the

incredible faculty, staff, and students that comprise CSU's Department of Fish, Wildlife, and Conservation Biology, with an extra special thanks to Ken Wilson.

On a more personal note, I am appreciative of my family for their perpetual support. I received nothing but encouragement and support from parents and siblings when I decided to return to school at 26 years old to get my undergraduate degree. I am especially thankful to my mother, Julia, who has always been my biggest fan – unabashedly yelling words of encouragement from soccer field sidelines of my youth to this very day. I met my husband, Simon, as I was beginning to wrap up my undergraduate studies and it is he who first entertained conversations about the pros and cons of embarking on graduate studies. I cannot express in words (verbal or written) how sincerely grateful I am to have had his support throughout the experience – from carrying t-posts across the prairie to reading through drafts and listening to talks – thank you. On many accounts, Simon should receive a wildlife biology degree alongside me; his thoughtful engagement in discussions about newly learned ecological concepts and the details of my research instilled a newfound confidence in my present ability to conduct research.

Finally, I would like to thank my dogs, Josey and Riley. Josey has been a constant force in my life I would not be where I am today with our her. The early years of Josey's life came with a boundless energy that first introduced me to trail running; Josey and running have thus been faithful companions as I conducted this research. Her wagging tail on a trail in front of me has served as a calming metronome and provided me with the ability to make consistent progress. Riley joined our family after in the first few months of this program and she has helped to both refine patience and provide daily doses of innocent, goofy happiness. My love of dogs are the reason I am here today, and I am thankful for the immense joy these two pups bring me each and every day.

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CHAPTER 1

INTRODUCTION

The black-footed ferret (*Mustela nigripes*; hereafter, ferret), is a highly endangered (Biggins 2012) mustelid that is dependent upon the prairie dog (*Cynomys* spp) ecosystem for food and cover (Campbell et al. 1987, Forrest et al. 1988, Miller et al. 1996, Hoogland 2013). Once thought to be extinct, the discovery of a remnant ferret population in 1981 (Schroeder and Martin 1982) led to the capture of all remaining wild individuals and initiation of an intensive captive breeding recovery effort. Ferrets have since been successfully reintroduced to numerous locations throughout their historic range in the Great Plains, but due primarily to issues with plague (*Yersinia pestis*, an introduced disease) in prairie dogs and associated mammal communities, recovery efforts are ongoing and will likely continue for the foreseeable future (Miller et al. 1996). In addition to plague, one of the principal recovery challenges is predation of ferrets by native carnivores. For example, predation accounted for the greatest mortality in the remnant Meeteetse population (Forrest et al. 1988) and more than 95% of all reintroduced ferret mortalities at South Dakota and Montana reintroduction sites (Biggins 2000, Biggins 2006). Primary predators include badgers (*Taxidea taxus*), great-horned owls (*Bubo virginianus*), and coyotes (*Canis latrans*) but of these predators, coyotes are the most important and have accounted for up to 67% of predation mortalities in radio-tagged ferrets (Eads et al. 2015).

Coyote predation on ferrets is best defined as intraguild predation, a form of interference competition amongst sympatric competitors (Polis et al. 1989, Case and Gilpin 1974). Intraguild predation differs from classic predation as the victim is often left unconsumed (e.g., Biggins et al. 2011a) and the removal benefits the superior competitor through the reduction of future

competition for any shared prey base (Palomares & Caro 1999, Polis & Holt 1992). Coyote predation on ferrets is almost always nocturnal, which raises an interesting question about why coyotes are utilizing prairie dog colonies at night given that the primary biomass (i.e., diurnal prairie dogs) are mostly underground and unavailable to coyotes. It is possible that coyotes are simply hunting or traveling across their territory and are encountering ferrets by chance. It is also possible prairie dog colonies are rich sources of alternative prey and that these other resources are attracting coyotes to prairie dog colonies, resulting in greater incidental predation on ferrets (Eads et al. 2015). Furthermore, little is known about the underlying causes of coyote-ferret interactions or how these interactions may be shaped by other community members. For example, badgers appear to be attracted to areas used by ferrets (Eads et al. 2013) and coyotes have been observed hunting in association with badgers (Minta et al. 1992); therefore, badgers may attract coyotes to areas occupied by ferrets (Eads et al. 2013). As a result, developing a better understanding of coyote use of prairie dog colonies and the community dynamics that might influence this use is one of two objectives in the study.

Translocation of surplus wild born ferret kits is an important recovery tool for ferrets (Biggins et al. 2011b) and the management of predation can help in this recovery effort. For example, electric fencing has been used to exclude coyotes from prairie dog colonies for 30-60 days post release to enhance survival of vulnerable individuals adjusting to new areas (Breck et al. 2006). Matchett et al. (2013) found evidence that electric fencing could effectively exclude coyotes, increasing survival of ferret kits during dispersal periods, and possibly making more kits available for translocation. However, due to highly variable ferret survival estimates (Breck et al. 2006), low sample sizes (Matchett et al. 2013), and the disproportionate effects of “problem individuals” (Linnell et al. 1999), the effectiveness of such efforts is yet to be comprehensively

understood. In addition, though electric fencing is an effective tool for non-lethal coyote management, application involves extensive labor (i.e., set-up, take-down, and maintenance) and a high cost of fence materials (\$3,815/km; Matchett et al. 2013), which may limit widespread use.

Fladry, a non-lethal tool developed as a disruptive stimulus to mitigate wolf predation on livestock, is significantly less expensive (\$1898/km) and is effective for up to 60 days in wild settings (Musiani et al. 2003). Commercial fladry consists of a continuous strand of rope with long strips of red flagging sewn or tied to the rope at 50cm intervals and strung 50cm from the ground (Musiani et al. 2003). This spacing is likely unsuitable for smaller-sized coyotes (Davidson-Nelson and Gehring 2010) and efforts are underway using captive coyotes to test a new fladry design for its effectiveness at deterring coyotes. Electrified fladry, fladry that carries an electric charge along the continuous strand of rope, increases the effectiveness of fladry (Lance et al. 2010) through addition of an adverse stimulus (i.e., electric shock, Shivik 2006) and is also less expensive (\$2882/km) than electrified fencing. Fladry is most commonly used to mitigate conflict with livestock but could be an effective tool to reduced ferret mortality during the critical period of kit dispersal. Testing electrified fladry for its effectiveness at excluding coyotes from areas critical for juvenile ferrets forms the second objective of this study.

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CHAPTER 2

COYOTE USE OF PRAIRIE DOG COLONIES IS MOST FREQUENT IN AREAS USED BY AMERICAN BADGERS

OVERVIEW

Interspecific killing occurs when a dominant predator kills a subordinate predator to reduce competition for shared prey and is an important consideration in the recovery of endangered species. In prairie ecosystems, coyotes (*Canis latrans*) are the primary predator of endangered black-footed ferrets (*Mustela nigripes*; hereafter, ferret) and presumably compete for prairie dog (*Cynomys* spp) prey. Coyote predation on black-footed ferrets is an apparent example of interspecific killing; however, interactions between these two species deviate from classic predictors of interspecific killing in the carnivore guild. In addition, coyote predation on ferrets presumably occurs at night when ferrets are active above ground but primary prey biomass on colonies (i.e., diurnal prairie dogs) are inaccessible to coyotes, presenting a perplexing temporal mismatch between actual and expected times that coyotes and ferrets come into conflict. Our study investigated multiple abiotic and biotic factors hypothesized to influence coyote-ferret interactions using remote wildlife cameras, occupancy models, and overlap of circadian activity patterns. We first evaluated coyote preferences between prairie dog colonies and surrounding available grasslands and found coyotes used prairie dog colonies ($\hat{\Psi} = 0.77$, 95% CI [0.48, 0.93]) nearly twice as much as surrounding grasslands ($\hat{\Psi} = 0.37$, 95% CI [0.21, 0.57]). Next, we investigated biotic and abiotic factors that may influence coyote use and frequency of use on prairie dog colonies. We found high coyote use across all areas on prairie dog colonies; however, frequency of use varied across colonies and was higher in areas of high American badger

occurrence (*Taxidea taxus*; 68.10% cumulative model weight). Badgers and coyotes are known to form hunting associations and high overlap between coyote and badger activity patterns (i.e., 81%) further supports the spatial use patterns revealed by our occupancy analysis. Strong interspecific competition and patterns of resource selection between badgers and ferrets have been documented in previous studies, and as a result, our study suggests that coyote attraction to badgers may be the principal driver of coyote-ferret interactions.

INTRODUCTION

Interspecific killing is an important form of competition where a dominant predator benefits from killing, but not eating, a subordinate predator (*in sensu* Oliveira and Pereira 2013) and results in reduced competition for shared prey (Polis & Holt 1989, Polis & Holt 1992, Palomares & Caro 1999). Mortality resulting from this type of interaction is an important consideration in many systems and is particularly relevant in the recovery of endangered species (Goodrich and Buskirk 1999, Connell and Slatyer 1977). In prairie ecosystems, coyotes (*Canis latrans*) and endangered black-footed ferrets (*Mustela nigripes*; hereafter, ferret) both prey on prairie dogs (Biggins 2000, Chronert 2007) and coyotes are the primary predator of ferrets, accounting for up to 67% of predation-based mortalities (Eads et al. 2015, Breck et al. 2006). However, this apparent example of interspecific killing is perplexing based on two primary observations.

First, interspecific killing is thought to occur most frequently between more taxonomically related species, those with high dietary overlap, and between species with intermediate levels of body size overlap (i.e., when the dominant predator is 2-5.4 times larger than the subordinate predator; Donadio and Buskirk 2006). In contrast, coyotes and ferrets are members of different taxonomic families, only have moderate dietary overlap (i.e., prairie dogs

comprise ~60-90% and ~38% of ferret and coyote diets, respectively; Brickner et al. 2014, Campbell et al. 1987, Chronert 2007), and coyotes are approximately 13 times larger than ferrets (Biggins and Schroeder 1988, Bekoff 1977). Second, ferrets are highly specialized predators of prairie dogs and have evolved nocturnal behaviors and fossorial morphology that allow them to hunt prairie dogs below ground at night, while coyotes lack specialized fossorial adaptations and are most commonly observed employing a “sit-and-wait” hunting strategy at prairie dog burrow entrances during daytime and crepuscular periods of above ground prairie dog activity (e.g., Lehner 1981, Kiriazis et al. 2006, Slobodchikoff 2002). Moreover, coyote predation on ferrets occurs at night (Biggins 2000, Breck et al. 2006) when prairie dogs are presumably inaccessible to coyotes, thus it is unclear what is attracting coyotes to prairie dog colonies at this time and driving coyote-ferret interactions.

Incongruent observations between classic predictors of interspecific killing in the carnivore guild and an apparent temporal mismatch between nocturnal ferret activity patterns and the diurnal activity of prairie dogs argues that direct competition for prairie dogs is not a primary motivation for coyote-ferret interactions. Although coyotes have been observed at higher densities and in greater relative abundance on prairie dog colonies in comparison to un-colonized grasslands (Krueger 1986, Ceballos et al. 1999), if coyotes preferentially use prairie dog colonies in relation to surrounding grasslands is unclear (Chronert 2007). In addition, there is considerable uncertainty about the strength of various abiotic, biotic, and temporal factors (e.g., Eads et al. 2015, Poessel et al. 2011, Biggins 2000) that could predict coyote use of prairie dog colonies. Identifying preferences and predictors may provide insight into primary influences on coyote-ferret interactions. In this study we explore a variety of competing hypothesis that could

influence coyote use of prairie dog colonies including landscape features, prairie dog colony attributes, alternative prey sources, intraguild interactions, and community activity patterns.

Landscape features have been documented as important predictors of predation risk in carnivore systems (Hebblewhite et al. 2005, Kauffman et al. 2007) and preferential use of certain features by coyotes may increase ferret predation risk in proximity to these areas. Poessel et al. (2011) modeled coyote use of prairie dog colonies in relationship to linear features (i.e., roads, drainages, fence lines) in attempt to predict coyote predation risk on ferrets and did not find evidence that these features increased risk; however, other landscape features, such as those that provide vegetative structural variation across otherwise open prairie habitats, have yet to be explored and may be important predictors of coyote use of prairie dog colonies.

Attributes such prairie dog density, colony size, or location within a colony could also influence how coyotes use areas within prairie dog colonies. If coyotes and ferrets are both attracted to areas on colonies with similar densities of prairie dogs, this could indicate direct competition for prairie dogs between coyotes and ferrets and suggest that coyote predation on ferrets may result from chance encounters in these areas despite an apparent temporal mismatch in activity patterns between the species (e.g., Kiriazis et al. 2006, Slobodchikoff 2002). However, an important consideration in assessing attraction to particular prairie dog densities may depend on the scale at which coyotes select areas to use on colonies. For example, fine scale prairie dog densities likely reflect the coterie structure of prairie dog families, and these higher density pockets on colonies are used preferentially by both badgers and ferrets (Biggins et al. 2006, Eads et al. 2013, Grassel and Rachlow 2018, Biggins et al. 1993, Eads et al. 2011). In contrast, coyotes primarily rely on visual cues and focus their attention over wider areas while hunting (Horn and Lehner 1975, Wells 1978, Minta et al. 1992), and as a result, prairie dog densities

across broad swaths of colony may be a more relevant scale for understanding coyote use of prairie dog colonies.

In addition to prairie dog prey biomass, colonies are also rich sources of alternative prey (Agnew et al. 1986, Kruger 1986) and coyotes may be attracted to areas used by these other prey species. Rabbits (*Sylvilagus* spp) are a ubiquitous component of coyote diets and rabbit densities have been reported as being up to 27 times higher on prairie dog colonies in comparison to surrounding grasslands (Hansen & Gold 1977). Further, the activity patterns of both coyotes and lagomorphs (rabbits and *Lepus* spp) overlap during nocturnal and crepuscular periods (Arias-Del Razo et al. 2001, Mech 1966) and thus nocturnal rabbit activity may facilitate opportunistic coyote interspecific killing of ferrets. For example, Eads et al. (2015) found that coyotes selected for areas of prairie dog colonies used by rabbits, although rabbits did not appear to select high prairie dog density portions of colonies.

Coyote-ferret interactions may also be shaped by other members of the carnivore guild, such as badgers (*Taxidea taxus*). Badgers have strong, specialized thoracic digging limbs, prefer high density portions of prairie dog colonies, and selectively excavate burrows in areas used by ferrets, presumably to unearth prairie dogs that ferrets have cached (Eads et al. 2013, Eads et al. 2016). While badgers exert interspecific killing pressures on ferrets, and will consume ferrets that they kill, badgers only account for approximately 5% of all predation-based ferret mortalities (Biggins 2000). Coyotes, however, can be attracted to badgers actively excavating burrows (Eads et al. 2016), have been observed hunting in association with badgers (Minta et al. 1992), and this attraction to badgers may increase the rate of coyote-ferret encounters (Eads et al. 2013, Eads et al. 2016).

Our primary objective for this study was to address competing hypotheses for coyote use of prairie dog colonies (Table 1), and better understand spatial and temporal influences of coyote use to inform ferret conservation. Using wildlife cameras and an occupancy approach, we first determined if coyotes preferentially use prairie dog colony habitats compared to surrounding available grasslands (Hall et al. 1997). Second, we investigated predictors of coyote use and frequency of use on prairie dog colonies, including landscape features (e.g., travel routes, riparian areas), prairie dog colony attributes (e.g., prairie dog density at two scales, colony size, proximity to colony edge), use by alternative prey (i.e., lagomorphs), and interspecific interactions with other members of the predator community (i.e., badgers). Third, we investigated the circadian patterns of coyotes on prairie dog colonies in comparison to adjacent grasslands and periods in which ferrets are known to be most active (1-3 am, Biggins 2000). Finally, we assessed activity overlap of coyotes with prairie dogs, lagomorphs, and badgers to draw connections between spatial and temporal influences of coyote attraction to prairie dog colonies.

STUDY AREA

Our study was conducted between 24 June-30 August 2018 in the northern unit of Badlands National Park (BNP) and the surrounding Buffalo Gap National Grasslands (BGNG) in southwestern South Dakota. Together, BNP and BGNG contain 5875ha of black-tailed prairie dog habitat and are home to the largest population of wild black-footed ferrets (~115 individuals; T. Livieri, *unpublished data*). BNP and BGNG were dominated by mixed-grass prairie where prairie dog colonies were notable by the presence of close-cropped grasses, burrow mounds, and the prevalence of small forbs and shrubs (Livieri and Anderson 2012, Agnew et al. 1986). Primary BGNG land uses included hunting and the grazing of both domestic cattle (*Bos taurus*)

and bison (*Bison bison*). Primary BNP land uses were recreation, tourism, and sanctuary for species such as bison, bighorn sheep (*Ovis canadensis*), and pronghorn antelope (*Antilocarpa americana*). Topography of the area was primarily flat with interspersed arroyos, bands of layered Badlands rock formations, and riparian areas that contained cottonwood trees (*Populus deltoides*). Two state highways (240 and 44) and two county highways (509 and 590) interconnected BNP and BGNG with an assortment of minimally traveled forest service roads and fence lines throughout the area.

METHODS

Personnel from BNP and BGNG conducted bi-annual black-tailed prairie dog surveys in which colonies were delineated and prairie dog density was roughly estimated as high, medium, or low. Using data from 2017 surveys, we identified the largest, intact prairie dog colonies (greater than 65 ha) with known ferret presence. Where multiple prairie dog colonies greater than 65 ha occurred in close proximity, we clustered colonies into subcomplexes of interconnected habitat (Biggins et al. 2006). Using these criteria, we identified eight prairie dog colony subcomplexes (hereafter referred to as colonies) that were included in our study, six in BGNG and two in BNP (Fig. 1.). To compare coyote use between prairie dog colonies and grasslands we delineated an 850m buffer around each colony, where our buffer distance was determined by the radius of the average coyote core home range in our study area (1.5km²; Schroeder 2007) and comprised grasslands available to coyotes that used prairie dog colonies.

Camera surveys

We placed remote wildlife cameras in our two habitats of interest (i.e., prairie dog colonies and surrounding grasslands) during two 30-day rotations, and collected data from 24 June to 24 July, 2018 and 31 July to 30 Aug, 2018. We randomly placed four cameras at least

400m apart in both habitats at each of the eight colonies, resulting in a total of 32 cameras on colonies and 32 cameras on grasslands during each of our two rotations (total camera locations = 128). An exception to this placement occurred in the first rotation when one of our BGNP colonies was inaccessible by vehicle or foot due to muddy conditions and thus did not receive cameras. We instead redistributed these cameras to the two colonies within BNP, resulting in six cameras on colonies and grasslands at these locations during the first rotation.

Cameras were placed on t-posts approximately 50cm from ground level. To increase the probability of coyote detection on prairie dog colonies, all cameras were placed 7.5m from the center of the nearest active prairie dog burrow entrance. Cameras on colonies were pointed at the active prairie dog burrow entrance at a randomly selected cardinal azimuth. Active burrows were determined by the presence of fresh scat (i.e., greenish, black, or dark brown), visual observation of prairie dogs, and mound scratching activity (Biggins et al. 1993, Livieri *personal communication*). Cameras on grasslands were also placed approximately 50cm from ground level and 7.5m from the nearest feature that would increase coyote detection (i.e., two-track road, game trail, cattle trail, drainage entrance).

Three different brands of camera traps were used in our study. Brands and their respective model included Browning BTC Series (n=30), Bushnell Trophy Series (n=23), and Cuddeback Longrange IR (n=11). Cameras were systematically placed across each colony to ensure interspersed distribution of camera brands. Where possible, we attempted to program all cameras similarly with a medium sensitivity, the smallest delay possible between photographs (≤ 1 s), and in bursts of three photos. All cameras were equipped with infrared flash to reduce the effects of flash on coyote behavior. While we programmed cameras similarly, camera brands are known to have variable detection ranges, fields of view, and sensitivity; thus, we included

camera brand as a covariate in all occupancy models to account for inherent variability in camera performance (see *Nuisance variables* below).

Camera data

Camera data was processed using the Colorado Parks and Wildlife Photo Warehouse software (Ivan et al. 2016), where each photo was identified to species by two independent observers, except in the cases of very large photo sets (i.e., at camera units that had >10,000 photos due to grass blowing in the wind or high bovine activity) where only one observer identified species in the photo set. The lead author verified species for any images that were not congruently identified by two observers, and all species in large photo sets. Camera data was used to construct detection histories for each camera unit for occupancy modeling; specifically, we divided the 30 days of sampling into 10 sampling occasions (i.e., each survey consisted of 3 days). We censored data from any periods in which cameras malfunctioned for the entirety of a survey (e.g., dead batteries, camera knocked down by cattle) and accounted for malfunctions during only a portion of each survey (see *Nuisance variables*).

Occupancy analysis

We used occupancy models to investigate if coyotes used prairie dog colonies preferentially, and if so, the biotic and abiotic predictors of occupancy on colonies. An important assumption of static occupancy models is that the species status at a unit (occupied or not) does not change within a sample season (MacKenzie et al. 2017). In this case of wide ranging carnivores, occupancy (Ψ) estimates are interpreted as the probability that a unit is “used” rather than “occupied” by the species of interest during the specified season (i.e., the 30-day period; MacKenzie et al. 2017). In addition, detection probability or the probability that the species is detected during a survey at a used unit can relate to the relative use of a unit or local species

abundance (Royle and Nichols 2003, Royel et al. 2005, Lewis et al. 2015). When modeled with covariates, detection probability can provide important information about the frequency a unit was used (i.e., fine scale measurement of use during a 3-day survey at used units).

We constructed two occupancy analyses in Program MARK (White and Burnham 1995) and used AICc selection to assess model performance (Burnham and Anderson 2002). In our first analysis, we used all 128 camera units to investigate coyote use preferences between prairie dog colony and grassland habitat (Table 1). We only considered nuisance detection probability variables (see *Nuisance variables*), and the effects of rotation (i.e., Rotation) and habitat (i.e., Habitat; prairie dog colony and grasslands) on coyote use.

Next, we focused our second analysis on prairie dog colony habitat only ($n = 64$ camera units; Table 1) to investigate patterns of coyote use and frequency of use in relationship to landscape features, prairie dog colony attributes, and species interactions. Based on our first analysis, we excluded the effect of Rotation and included an additive effect of Browning cameras (see below: *Nuisance variables*) on all detection probability structures. Prior to modeling, we tested for correlations among measured covariates using Pearson's product-moment correlation and excluded covariates where $|r| > 0.7$ (Dormann et al. 2013). We found site-specific conditional occupancy for badgers was highly correlated with fine scale prairie dog density ($r = 0.85$).

Using a single-species, single-season occupancy approach, we constructed models with all combinations of one variable of interest on coyote use (Ψ ; 8 variables; Table 1), and frequency of use (p) modeled as an additive function of Browning camera and one other variable of interest on (9 variables; Table 1), resulting in 72 models. We included null structures for both probability of use and frequency of use (i.e., $\Psi(\cdot)$ and $p(\cdot)$) in all possible combinations, creating a balanced set of 90 models. We evaluated the importance of each variable by calculation of

cumulative model weights (Doherty et al. 2012). For each of the top three use and frequency of use variables we ran seven additional models with all possible variations on detection to verify the assumed influence of Browning (i.e., $p_{\text{variable}} + p_{\text{Browning}} + p_{\text{Effort}}$; $p_{\text{variable}} + p_{\text{Effort}}$; $p_{\text{Browning}} + p_{\text{Effort}}$; p_{variable} ; p_{Browning} ; p_{Effort} ; p_{null}); however, these models were only used for verification and not included in our final model set.

Nuisance variables

Camera brand was identified a key predictor of variation in detection probability in a concurrent study that used the same three camera brands (Windell et al. 2019 *in prep*). We included camera brand as a covariate in our first set of models (Table 1) and all models of conditional badger occupancy (see *Species Interactions*). Use of Browning cameras increased detection probability in comparison to Bushnell and Cuddeback cameras in both our first set of models and the concurrent study, thus we used Browning cameras as a covariate in each of our second set of occupancy models (Table 1). Cameras were also sometimes ripped from t-posts due to rubbing activities from cattle and bison and thus not operational during the entire rotation. As a result, we developed a covariate that reflected the proportion of each survey for which a camera was functional (Effort) and included this covariate in our first analysis. Given the minimal support for this covariate in our first set of coyote models we only used the Effort covariate to check a subset of the top models in our second set of models.

In addition to camera related nuisance variables, we accounted for the potential influence of rotation (Rotation) on coyote use of units to account for any variation between our two sampling periods and vegetation height (Veg) on detection probability. We used the Robel pole method to determine visual obstruction (i.e., VO; vegetation height) at each camera unit (Robel et al. 1970) in the camera's field of view. Given an approximate average camera field of view of 45

degrees (trailcamerapro.com), we identified two 30m transects at the 15 degree and 30 degree marks within the camera's field of view. Two VO measurements were recorded on opposite sides of each transect line at 2m intervals, for a total of 60 measurements per camera unit. Measurements from the two transects were then averaged to provide a single VO value for each camera unit (Veg).

Landscape features

We identified three variables that could influence coyote use at camera units in our study area: distance to riparian areas (Rip); distance to two-track roads (Two-Track); and distance to streams and gullies (Stream; Table 1). Riparian areas could provide cover, water, and den sites across the otherwise open and relatively unprotected grasslands. Two-Track USFS roads and service roads within BNP could serve as travel corridors for coyotes. Streams and gullies could serve multiple purposes, including areas of cover, water sources, den sites, and travel corridors. We predicted that as distance to each of these three variables decreased, coyote use would increase. Shapefiles of riparian areas (including lakes and ponds), two-track roads, streams and gullies were acquired from the USDA Data Gateway and we used ArcMap (Esri, Redlands, CA) and measured the distance (m) to each of these features from our camera locations.

Prairie dog colony attributes

We considered four attributes to investigate the role of prairie dogs in coyote use on colonies: fine scale prairie dog density at each camera unit (PD Fine); broad scale prairie dog density measured across all colonies (PD Coarse); colony size (Size); and distance from each camera to the colony edge (Edge; Table 1). Because coyote selection for prairie dog density could occur at multiple scales we measured prairie dog densities at fine and coarse scales, in addition to calculating the total amount of prairie dog colony habitat available (i.e., Size). If

coyote use varied in relationship to distance from edge of the colony (i.e., Edge), this metric could provide information about patterns of preference with proximity to adjacent grasslands or preferences related to patterns of succession on prairie dog colonies. For example, colony centers are typically the oldest, most established portions of colonies and feature the most altered vegetative structure in comparison to surrounding grasslands (Krueger 1986).

To measure fine scale prairie dog density (PD Fine), we counted all burrows within a 30m buffer of each camera (0.28ha) and classified each burrow as active or inactive. Burrows were considered active based on the same criteria used to select active burrows for camera placement (Biggins et al. 1993). We used the linear relationship Biggins et al. (1993) reported between black-tailed prairie dog active burrow counts and individual animals to estimate prairie dog abundance as:

$$\text{Prairie dog abundance} = 0.179 \times \text{number of active burrows}$$

Local density per hectare was calculated by dividing estimated prairie dog abundance by the number of hectares sampled. To measure broad scale prairie dog density, we used a modification of the strip transect technique of Biggins et al. (1993). The modified technique consists of counting the number of active and inactive prairie dog burrows along strip transects spaced 200m apart and running the entire length of the colony using an all-terrain vehicle outfitted with a 3m stretch of electrical conduit pipe. We used two GPS devices to maintain bearing and mark locations of active and inactive burrows. Strip transects sampled approximately 1.5% of 4ha plots delineated across the entirety of each focal colony (Biggins et al. 1993). In ArcGIS we extracted colony size and the distance of each camera location to the edge of the prairie dog colonies from BGNG and BNP prairie dog colony surveys.

Species interactions

We were interested in coyote interactions with badgers and lagomorphs (i.e., *Sylvilagus* spp, *Lepus townsendii*), but due to very few lagomorph detections on prairie dog colonies, we were unable to model conditional occupancy probabilities or calculate activity overlap for these species. For badgers, we calculated unit-specific conditional occupancy estimates ($\Psi_{\text{conditional}}$) and included these estimates as unit-specific covariates to assess whether badger use influenced coyote use or frequency of use (Table 1). We estimated the conditional occupancy probability of badgers (i.e., the probability that badgers used the unit, given of survey results; if a species was detected at a unit, $\Psi_{\text{conditional}}=1$) using single-season occupancy models in program PRESENCE (Hines 2006). Badger models included the influence of Bush, Brown, Effort, Veg, and time variation across occasions on detection probability (see *Nuisance variables*). We modeled occupancy with respect to PD Fine, PD Coarse, Size, and Rotation, along with the additive effects of PD Fine and PD Coarse. To evaluate whether the detection of badgers during a given 3-day survey influenced coyote detection during that same survey, we included detections of badgers as survey-specific covariates when modeling coyote detection probability on prairie dog colonies (Massara et al. 2016; Table 1).

Circadian activity

To understand if coyotes use different parts of each day more than expected, and to compare this use across prairie dog colonies and grasslands, we divided each day into five distinct periods including: Day, Dawn, Dusk, Early Night, and Late Night. We used the *suncalc* package (Agafonkin and Thieurmel 2019) in R (R Development Core Team 2019) to extract the times of nautical dawn, sunrise end, nautical dusk, sunset start and nadir (i.e., the darkest time of night) to delineate these periods. Day was bound by sunrise end and sunset start, Dusk by sunset

start and nautical dusk, Early Night by nautical dusk and nadir, Late Night by nadir and nautical dawn, and Dawn by nautical dawn and sunrise end. Using these categories, we calculated the expected proportion of activity within each of time period assuming even activity across all categories (Lendrum et al. 2017). We determined categories at the midpoint of each rotation (i.e., 15 days into each sampling period) and averaged proportions across our two rotations, yielding an expected percentage of time in each category as 5.43% for Dawn and Dusk, 60.46% for Day, and 14.33% for Early and Late Night. We considered detection events to be independent if detections were >1hr apart (Lewis et al. 2015, Lendrum et al. 2017) and used a Chi-Square goodness of fit test ($\alpha = 0.05$) to assess whether the observed proportions of time in each category differed from expected proportions on grasslands and prairie dog colonies To provide an ecological interpretation of temporal variation in coyote activity across colonies and between habitat types (i.e., prairie dog colonies and surrounding grasslands), we calculated the differences in proportions of activity in each category and expected values as odds ratios. To do this we first transformed the proportion of photos (p) into odds ($p/(1-p)$) on prairie dog colonies (p_{colonies}) and grasslands ($p_{\text{grasslands}}$) and then calculated the ratio of these ($\text{odds}(p_{\text{colonies}})/\text{odds}(p_{\text{grasslands}})$) (Lendrum et al. 2017).

We used the *overlap* package (Meredith and Ridout 2013) in R to determine diel activity patterns for coyotes on prairie dog colonies and grasslands, and between coyotes, badgers, and prairie dogs. We calculated the overlap of activity between these species following recommendations provided by the authors and calculated 95% confidence intervals for overlap estimates using 10,000 bootstrap simulations (Ridout and Linke 2009, Meredith and Ridout 2013).

RESULTS

Camera data

Cameras recorded a total of 233,875 photos of a variety of prairie species over 7,680 trap nights. Species captured included antelope (n=6,179), badgers (n=260), bighorn sheep (n=89), bison (n=57,693), bobcats (n=5), cattle (n=115,587), coyotes (n=663), ferrets (n=23), mule deer (n=1,777), porcupine (n=30), prairie dogs (n=46,787), rabbits (n=137), raccoons (n=12), white-tailed deer (n=3,247) and white-tailed jackrabbits (n=11). We recorded 66 and 22 independent detections of coyotes on prairie dog colonies and grasslands, respectively. For the other focal species of interest, we recorded 17, 1, and 820 independent detections of badger, lagomorphs, and prairie dogs, respectively, on prairie dog colonies.

Occupancy analysis

Our first analysis suggested that (Table 2) coyote use differed between camera units on prairie dog colonies and grasslands, with higher coyotes use on prairie dog colonies ($\hat{\Psi} = 0.77$, 95% CI [0.48, 0.93]) relative to the surrounding grasslands ($\hat{\Psi} = 0.37$, 95% CI [0.21, 0.57]). When considering only camera units on prairie dog colonies, we found little spatial variation in coyote use among camera units (Table 3). Coarse scale prairie dog density was the best-supported of our 8 potential covariates, but only accounted for 15.62% of the cumulative model weight, with conditional use by badgers (hereafter, badger use) and fine scale prairie dog density holding similarly low cumulative model weights (i.e., 12.04% and 10.47%, respectively; Table 4). Browning camera was an important nuisance detection probability variable for all models. In addition to the effect of Browning cameras, badger use was the most important predictor of the frequency of coyote use and was included in nine of the ten top models (Tables 3 and 4).

Coyotes used camera units more frequently when badgers also used a unit over the course of the season (Fig. 2.)

Circadian activity

Coyote circadian activity patterns varied between prairie dog colonies and surrounding grasslands (Fig. 3). On prairie dog colonies, coyotes were active 2.75 times more than expected during crepuscular periods of dawn ($\chi^2=12.40$, $p = 0.0004$) and dusk ($\chi^2=12.40$, $p = 0.0004$), whereas on surrounding grasslands coyote activity at dawn ($\chi^2=2.47$, $p = 0.1162$) and dusk ($\chi^2=0.14$, $p = 0.7042$) was similar to expectations (Fig. 3). Coyotes used daytime less than expected on both prairie dog colonies ($\chi^2=25.48$, $p = <0.0001$) and grasslands ($\chi^2=51.71$, $p = <0.0001$); however, coyotes were 5.65 times more likely to be active on colonies than grasslands during the day (Fig. 3). On prairie dog colonies, coyotes were active similar to expectations during the Late Night period ($\chi^2=3.30$, $p = 0.0692$) when ferrets are most active, and were active 2.60 times more than expected during the Early Night period ($\chi^2=17.80$, $p = <0.0001$; Fig. 3). On grasslands, coyotes were more active than expected during both Late Night ($\chi^2=33.87$, $p = <0.0001$) and Early Night ($\chi^2=67.58$, $p = <0.0001$) periods (Fig. 3.).

Coyote and badger activity overlap on prairie dog colonies was high (overlap = 0.81, 95% CI [0.67, 0.96]), and both species were most active during nocturnal periods (Fig. 4). Coyotes had low overlap with prairie dog activity patterns (overlap = 0.33, 95% CI [0.24, 0.42]), and primary overlap occurred during crepuscular periods (Fig. 4.)

DISCUSSION

We found that coyotes used prairie dog colonies more than twice as much as surrounding grasslands, supporting the notion that prairie dog colonies are attractive to coyotes and used preferentially. Because coyotes used most camera units on prairie dog colonies, identification of

a single predictor of use at the monthly (i.e., season) scale was difficult to assess and yielded a fair amount of uncertainty surrounding specific predictors of coyote use. However, over a shorter three-day (i.e., survey) period, we found that coyote use was more frequent at units also used by badgers (Fig. 2), indicating that coyotes are attracted to either the presence of badgers or badger sign (e.g., excavated prairie dog burrows). Further, badgers and coyotes both exhibited strong overlap in diel activity patterns, with peak activity occurring during nocturnal periods for both species (Fig. 3). This suggests a high probability of direct coyote-ferret interactions, where the diel activities of badgers may attract coyotes to specific areas on prairie dog colonies. We conclude badgers play an important role in spatial and temporal patterns of coyote use on prairie dog colonies and as a result, may increase the potential for coyote interactions with ferrets.

On prairie dog colonies, coyote use (i.e., monthly scale) was not well supported by any of the predictors we identified (Table 4) due to the prevalence of thresholds (i.e., high estimates of use beyond a low boundary) with a large amount of variability. Of the predictor variables, coarse scale prairie dog density held the greatest amount of cumulative model weight followed closely by badger use and fine scale prairie dog density (Table 4). Here, it is interesting to note that badger use and fine scale prairie dog density were highly correlated ($r= 0.85$). We hypothesize that prairie dog density variables are more likely to influence coyote use on colonies, but we could not confidently support this notion. In addition, fine scale and coarse scale prairie dog density were not correlated and thus our results may reflect a lack of appropriate scale to assess prairie dog density as related to coyote preferences on colonies.

Frequency of coyote use on prairie dog colonies provided us with fine scale information about what attracted coyotes to specific units. Here, we found strong support that the frequency a coyote used a unit increased as badger use increased (Fig. 2; Table 4). Coyotes appear to be

generally attracted to the excavation activities of badgers (Eads et al. 2016), and this may help to explain increased frequency of coyote use in areas used by badgers. Further, badgers and coyotes have been observed hunting in association and it is believed that the association mutually benefits both predators (Minta et al. 1992, Lehner 1981). Badgers and ferrets both select for fine scale, high density areas of prairie dog colonies, where ferrets place strong exploitative competition pressures on badgers and badgers place strong interference competition pressures on ferrets (Eads et al. 2016). In addition, badgers selectively excavate burrows in areas used by ferrets, and ferrets appear to cache dead prairie dogs in multiple locations below ground in part as a strategy to divert the attention of kleptoparasitizing badgers (Eads et al. 2013, Eads et al. 2016, Biggins et al. 2012). Although correlative, badger attraction to units used by ferrets and coyote attraction to units used by badgers may increase ferret predation risk and result in badger mediated interspecific killing of ferrets by coyotes.

In addition to intraguild interactions, the role of lagomorphs in shaping coyote patterns of activity and use on prairie dog colonies has been thought to have a strong influence of coyote-ferret interactions (Biggins 2000, Eads et al. 2015). This is due to the importance of lagomorphs in coyote diets and documented similarities in the crepuscular and nocturnal activity peaks of coyotes and lagomorphs (Arias-Del Razo et al. 2011). Further, the cyclical nature of lagomorph populations has been hypothesized to influence the risk of ferret predation, where hazard to ferrets should decrease in periods of low lagomorph numbers as coyotes become more diurnal and shift their focus to hunting prairie dogs (Biggins 2000). Our study coincided with a low period in the lagomorph population cycle, and we detected only a single lagomorph on prairie dog colonies during our camera trapping efforts. Overall coyote use of colonies was high and occurred predominantly during nocturnal periods, despite low occurrence of lagomorphs, and we

can conclude that coyote use of prairie dog colonies was not a result of attraction to lagomorphs at this time. However, coyotes are highly adaptive and may shift their attention to lagomorphs during high periods in the population cycle when this prey source is abundant. To this end, we observed increased diurnal use of colonies by coyotes as compared to surrounding grasslands which may reflect a shift to focus on prairie dogs during low lagomorph periods (Fig. 3).

We were also interested in investigating patterns of activity between coyotes, prairie dogs, and badgers, as well as variation in diel patterns of coyote activity on colonies in comparison to available grasslands and in relationship to the activity of ferrets. Coyotes have been observed hunting on prairie dog colonies across all circadian periods (T. Livieri, *personal communication*; R. Windell, *personal observation*) and are widely considered to be active primarily during crepuscular and nocturnal periods (e.g., Andelt and Gipson 1979, Holzman et al. 1992, Arias-Del Razo et al. 2001). In contrast, ferrets have strongly canalized activity patterns, resting safely below ground during the daytime and becoming most active between 1-3am. Biggins (2000) hypothesized that ferrets developed this canalized behavior to reduce conflict with coyotes; however, coyote behavior is highly plastic and activity patterns can be readily adapted (Kitchen et al. 2000). For instance, coyotes may increase activity on prairie dog colonies during crepuscular periods, especially at dawn, when prairie dogs are first emerging and encountering ferrets at this time. Alternatively, the activity patterns of other prey or badgers may attract coyotes to colonies and define periods of time when ferrets are at high risk of predation. Coyotes were 2.75 times more active on prairie dog colonies during crepuscular periods of dawn and dusk than would be expected and used prairie dog colonies during daytime periods 5.65 times more than surrounding grasslands. This suggests that coyotes hunt prairie dogs during their active periods and are attracted by prairie dogs to colonies at these times (Fig. 4). Although

overlap between coyote and prairie dog activity patterns was low (i.e., 33% overlap), cessation and onset of peak coyote activity during dawn and dusk, respectively, similarly coincided with a converse pattern of onset and cessation of prairie dog activity. Increased activity during dawn hours when prairie dogs are first emerging may be a particularly fruitful time for coyotes to hunt prairie dogs. However, the bulk of coyote activity on prairie dog colonies still occurred during both nighttime portions of the diel cycle (Fig. 3), where their activity patterns strongly overlapped those of badgers (Fig. 4) and supported the pattern we observed in the occupancy portion of our study. Coyotes were 2.60 times more active than expected during the pre-nadir period and active in alignment with expectations during the post-nadir period. This suggests that, while coyotes are still primarily active throughout the night, the canalized post-nadir activity pattern of ferrets may provide a small benefit by reducing the costs of risk assessment during nocturnal periods.

Coyote use of prairie dog colonies, and the resulting interspecific killing of ferrets by coyotes, appears to be most strongly influenced by biotic interactions. There was marginal support for coyote preference at high coarse scale prairie dog densities across larger swaths on colonies, and we suggest that future research continue to focus on coyote preferences in prairie dog colony use at multiple scales. Coyote use of camera units was far more frequent if they had also been used by badgers and our study suggests that coyote attraction to badgers may be the principal driver of coyote-ferret interactions. As a result, further study of badger-coyote associations and the degree to which these associations influence ferret predation risk is an important area of future research for ferret conservation, especially during reintroduction efforts.

TABLES AND FIGURES

Table 2.1. Variables used in two sets of occupancy models used to evaluate coyote habitat preferences and predictors of coyote use in the context of black-footed ferret conservation. The first set of models (Model Set 1) modeled coyote preferences in use between prairie dog colony and grassland habitats. The second set of models (Model Set 2) investigation the influence of landscape features, prairie dog colony attributes, and species interactions on coyote use of prairie dog colonies. Variables were modeled on both use (i.e., occupancy; Ψ) and frequency of use (i.e., detection probability; p) as either site- or survey-specific variables.

Variable	Model Set	Parameters	Specificity	Description
Habitat	1	Ψ	Site	Variation between prairie dog colony and grassland habitat types
<i>Landscape Features</i>				
Rip	2	Ψ, p	Site	Distance of camera to nearest riparian area
Stream	2	Ψ, p	Site	Distance of camera to nearest stream or gully
Two-Track	2	Ψ, p	Site	Distance of camera from nearest two-track road
<i>Colony Attributes</i>				
Edge	2	Ψ, p	Site	Distance of camera from edge of colony
Size	2	Ψ, p	Site	Size of prairie dog colony for a given camera
PD Coarse	2	Ψ, p	Site	Prairie dog density measured coarsely across a 4ha area encompassing each camera
PD Fine	2	Ψ, p	Site	Prairie dog density measured finely within a 30m buffer of camera
<i>Species Interactions</i>				
Badger	2	Ψ, p	Site	Conditional probability of badger use
Badger Fine	2	p	Survey	Whether or not a badger was detected in a survey at a given camera
<i>Nuisance Variables</i>				
Rotation	1	Ψ	Site	If a camera was included in the first (June) or second (July) rotation of cameras
Veg	1	p	Site	Average vegetative visual obstruction at a camera
Brown	1, 2	p	Site	Use of Browning camera
Bush	1	p	Site	Use of Bushnell camera
Effort	1	p	Survey	The proportion of days within a survey that a given camera was functional

Table 2.2. Model selection results for coyote use (Ψ) and detection (p) between two different habitat types (Habitat), prairie dog colonies and surrounding grasslands, in Badlands National Park and Buffalo Gap National Grasslands, South Dakota in 2018. Models first tested the potential influence of camera type (Browning=Brown; Bushnell=Bush), proportion of surveys for which the camera was operational (Effort), visual obstruction from vegetation (Veg), and a time effect across surveys (Survey) on detection probability, followed by any potential seasonal effects between camera rotations (Rotation) and Habitat.

Model ^a	AICc	Δ AICc	AICc Weights	Parameters	Deviance
Ψ (Habitat), p (Brown)	485.16	0	0.600	4	476.81
Ψ (Rotation*Habitat), p (Brown)	487.75	2.59	0.164	6	475.00
Ψ (Rotation*Habitat), p (Brown+Veg)	489.33	4.17	0.075	7	474.31
Ψ (Rotation*Habitat), p (Brown+Bush)	489.49	4.33	0.069	7	474.47
Ψ (Rotation*Habitat), p (Brown+Bush+Effort)	491.32	6.15	0.028	8	474.00
Ψ (.), p (Brown)	491.49	6.32	0.025	3	485.28
Ψ (Rotation), p (Brown)	491.82	6.66	0.021	4	483.47
Ψ (Rotation*Habitat), p (Bush)	493.48	8.32	0.009	6	480.72
Ψ (Rotation*Habitat), p (Veg)	495.33	10.16	0.004	6	482.57
Ψ (Rotation*Habitat), p (Effort)	495.67	10.50	0.003	6	482.91
Ψ (.), p (.)	496.58	11.42	0.002	2	492.48
Ψ (Rotation*Habitat), p (Survey)	503.51	18.35	0.000	14	471.43
Ψ (Rotation*Habitat), p (Brown+Bush+Effort+Veg+Survey)	504.57	19.41	0.000	18	461.66

^aThe plus sign (+) denotes an additive effect between covariates and the dot (.) denotes no covariate effect on Ψ or p .

Table 2.3. Model selection results for the top 10 models of coyote use (Ψ) and detection (p) on 8 prairie dog colony subcomplexes with known black-footed ferret presence in Badlands National Park and Buffalo Gap National Grasslands, South Dakota in 2018 using a balanced model set. All models included the additive effect of Browning trail cameras (Brown) and survey effort (Effort) on p .

Model ^a	AICc	Δ AICc	AICc weights	Parameters	Deviance
$\Psi(\cdot), p(\text{Brown+Badger})$	315.98	0	0.18	4	307.26
$\Psi(\text{PD Coarse}), p(\text{Brown+Badger})$	316.97	0.99	0.11	5	305.88
$\Psi(\text{Edge}), p(\text{Brown+Badger})$	318.05	2.07	0.06	5	306.96
$\Psi(\text{PD Fine}), p(\text{Brown+Badger})$	318.15	2.17	0.06	5	307.06
$\Psi(\text{Rip}), p(\text{Brown+Badger})$	318.29	2.31	0.06	5	307.20
$\Psi(\text{Stream}), p(\text{Brown+Badger})$	318.30	2.32	0.06	5	307.21
$\Psi(\text{Size}), p(\text{Brown+Badger})$	318.33	2.36	0.05	5	307.24
$\Psi(\text{Two-Track}), p(\text{Brown+Badger})$	318.34	2.37	0.05	5	307.25
$\Psi(\text{Badger}), p(\text{Brown+Badger})$	318.34	2.37	0.05	5	307.25
$\Psi(\cdot), p(\text{Brown+PD Fine})$	319.64	3.66	0.03	4	310.93

^aThe plus sign (+) denotes an additive effect between covariates and the dot (.) denotes no covariate effect on Ψ or p .

Table 2.4. Cumulative AICc weights for coyote use (Ψ) and frequency of use (p) covariates from a balanced set of models ($n=90$) that include all combinations of one Ψ covariate and one p covariate. No single model held a large portion of the cumulative model weight for use; however, conditional probability of badger use (Badger) held the majority of the cumulative weight for frequency of coyote use.

Covariate	Cumulative AICc weights (%)
Use (Ψ)	
PD Coarse	15.62
Badger	12.04
PD Fine	10.47
Edge	8.25
Rip	7.75
Two-Track	7.59
Size	7.51
Stream	7.35
Frequency of Use (p)	
Badger	68.10
PD Fine	11.56
Rip	9.93
Two-Track	8.18
Edge	0.66
Size	0.22
Badger Fine	0.21
Stream	0.33
PD Coarse	0.23

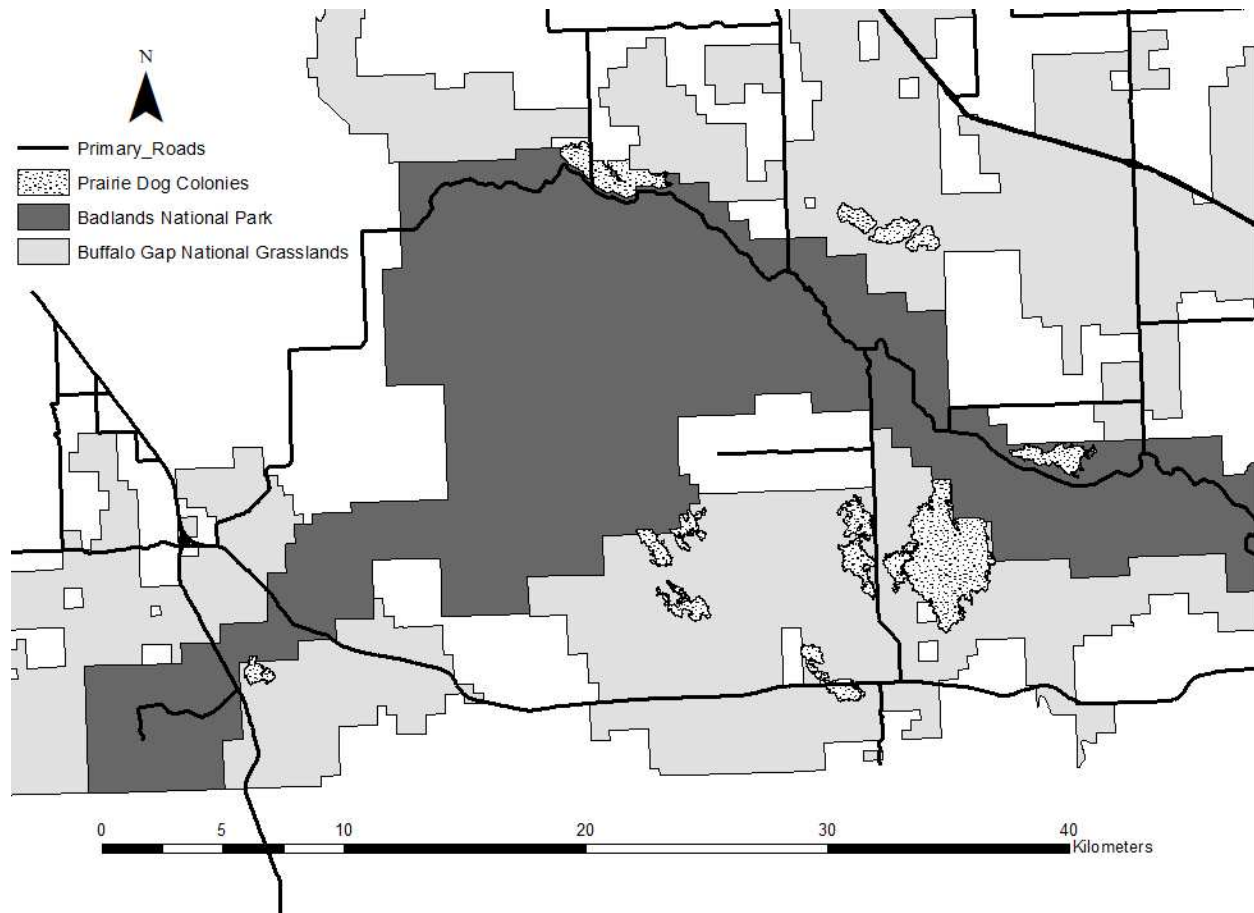


Fig. 2.1. Large (>65ha) prairie dog colonies with known black-footed ferret presence in Badlands National Park and Buffalo Gap National Grasslands, South Dakota were sampled using wildlife camera traps (n=128) in an occupancy framework in 2018. Prairie dog colonies and an 850m buffer of grassland habitat surrounding colonies were sampled to evaluate coyote habitat preferences and assess the strength of predictors of coyote use on prairie dog colonies in the context of black-footed ferret conservation.

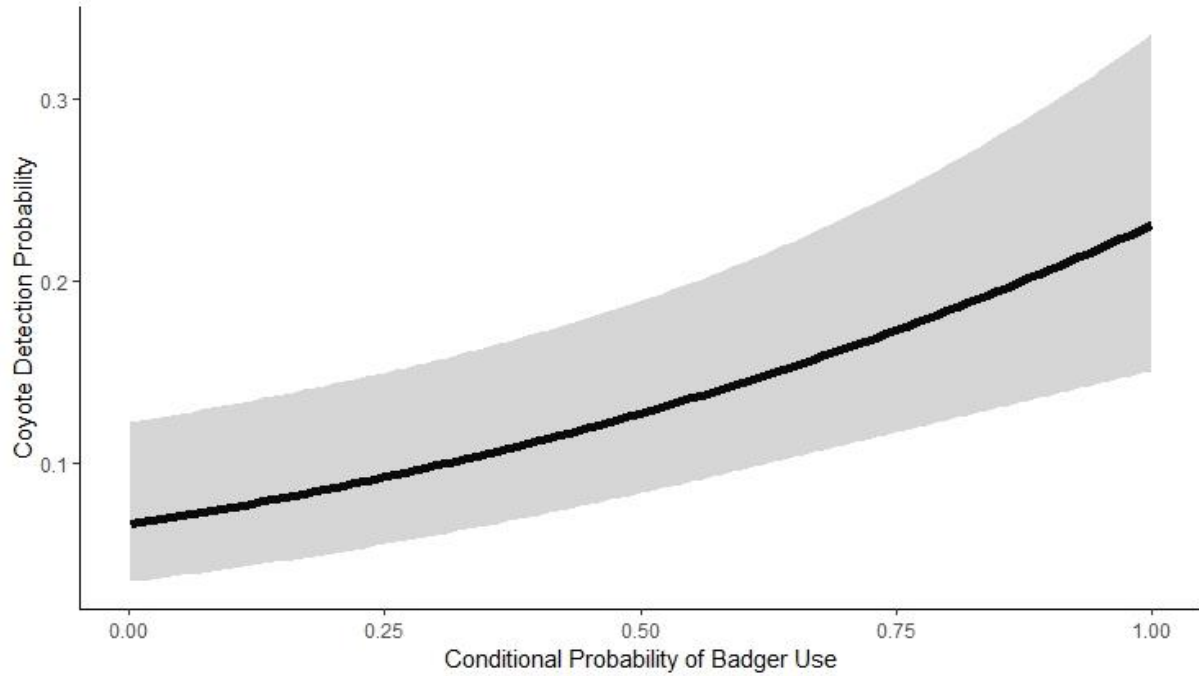


Fig. 2.2. The frequency of coyote use (i.e., detection probability) was positively related to the conditional probability of badger use at camera units on prairie dog colonies in Badlands National Park and Buffalo Gap National Grasslands, South Dakota in 2018. Conditional probability of badger use held the greatest amount of the cumulative model weight (i.e., 68.10%) for predicting the frequency of coyote use at a given unit.

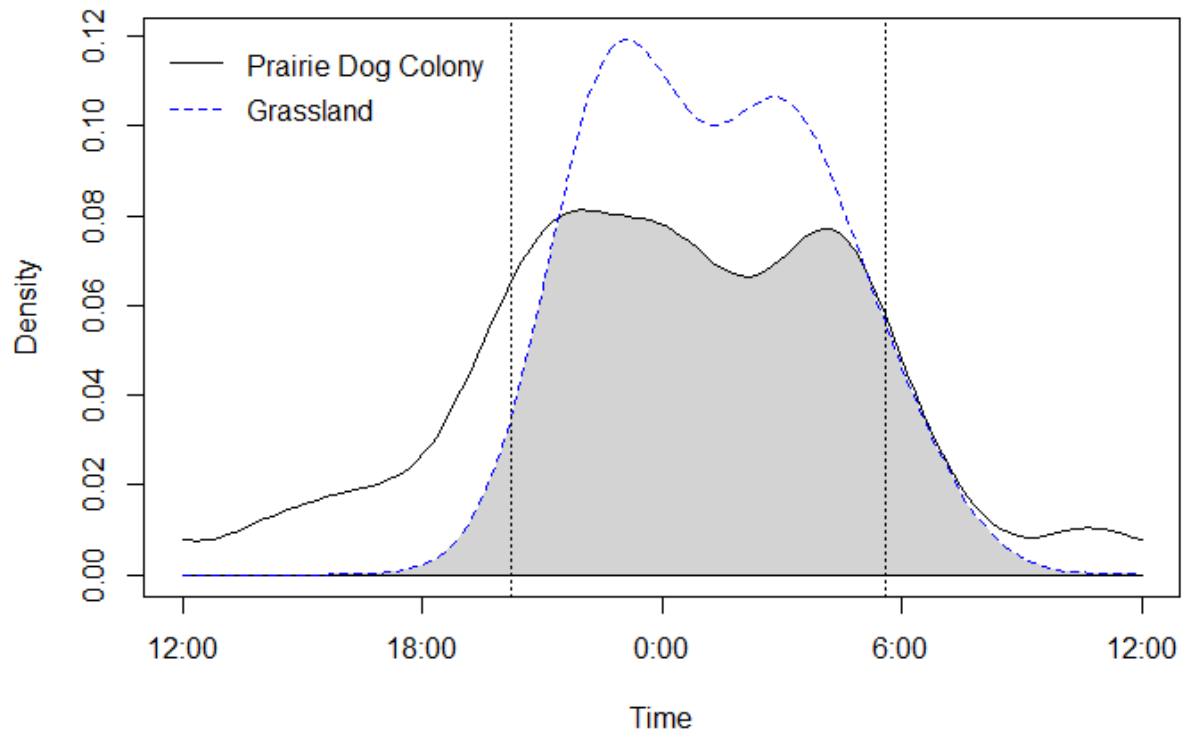


Fig. 2.3. Coyote circadian activity patterns varied between prairie dog colonies (n=66) and surrounding grasslands (n=22) between 24 June-30 August 2018 in Badlands National Park and Buffalo Gap National Grasslands, SD in 2018. Coyotes were 2.75 times more active than expected during crepuscular periods of dawn and dusk and 5.65 times more likely to be active on colonies than grasslands during the day. On colonies, coyotes were active similar to expectations when ferrets are most active (1-3am) and 2.60 times more active than expected during the earlier portions of the night (i.e., pre-nadir). Dashed vertical lines are mean sunrise and sunset times for our sampling period.

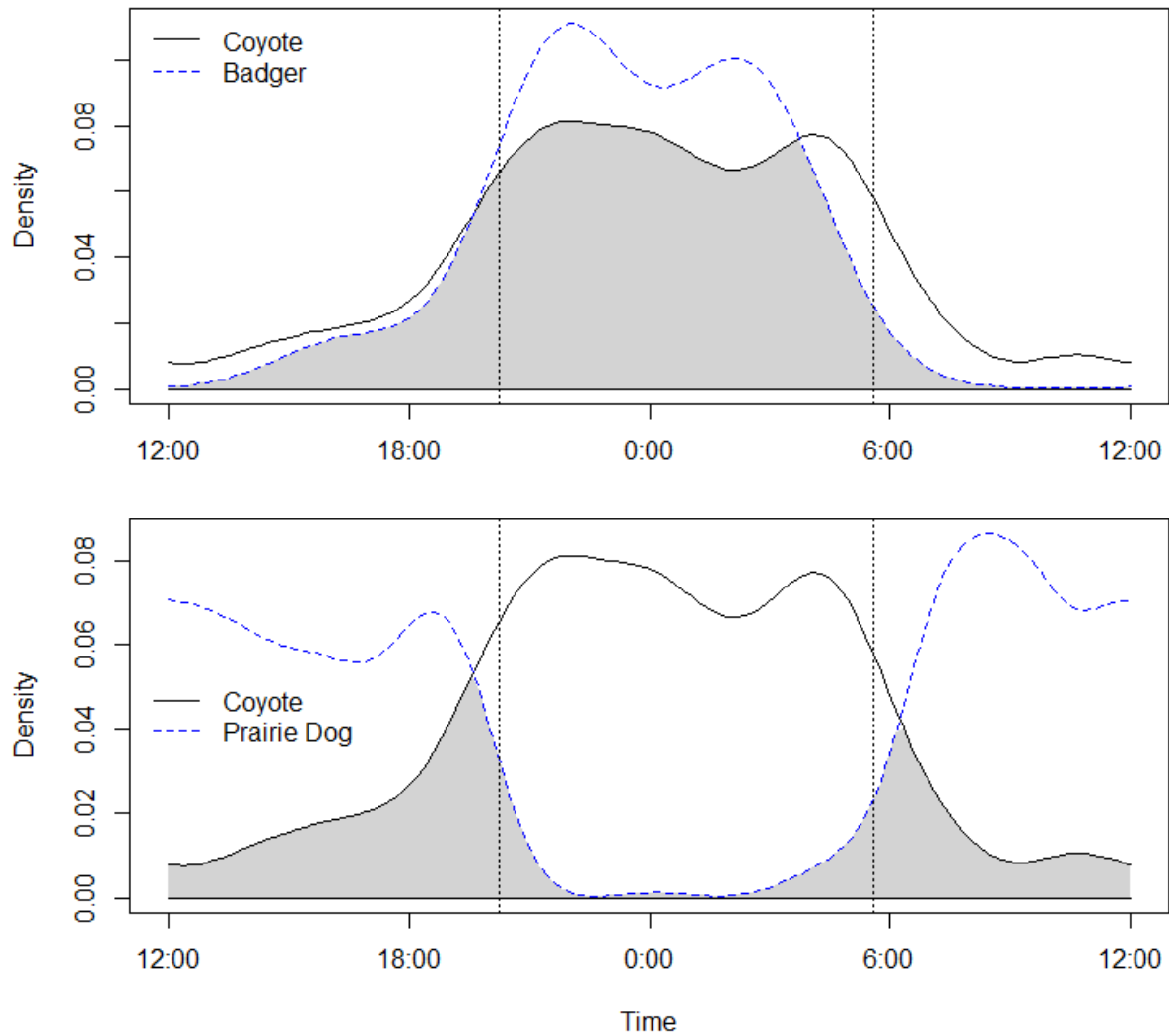


Fig. 2.4. Coyote and badger activity overlap on prairie dog colonies was high (overlap = 0.81, 95% CI [0.67, 0.96]) between 24 June-30 August 2018 in Badlands National Park and Buffalo Gap National Grasslands, SD in 2018. Both coyotes and badgers were most active during the night. Coyotes had low overlap with prairie dog activity patterns (overlap = 0.33, 95% CI [0.24, 0.42]); however, coyotes and prairie dogs exhibited a converse pattern of onset and cessation of activity during crepuscular periods. Dashed vertical lines are mean sunrise and sunset times for our sampling period.

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CHAPTER 3

MODIFIED FLADRY REDUCES COYOTE USE OF PROTECTED AREAS

OVERVIEW

Coyotes (*Canis latrans*) kill more livestock than any other predator in the U.S. and can also be important predators of endangered native fauna. Managing coyote predation is achieved with both lethal and nonlethal tools; however, there is a dearth of knowledge about the effectiveness of these tools. Our objective was to rigorously evaluate coyote fladry, a nonlethal tool developed to repel coyotes, in a field setting. Coyote fladry was tested in a grassland ecosystem, and large prairie dog colonies served as focal areas of study. We used multi-season occupancy models to estimate coyote occurrence (i.e., use) and tested whether use changed in areas protected with fladry relative to control areas. Specifically, we estimated probabilities of extinction (i.e., avoidance), colonization (i.e., attraction), and detection (i.e., activity) to provide additional information about the behavioral response of coyotes to fladry. Coyote behavioral response was measured at a coarse temporal scale (i.e., a month) via attraction and avoidance probabilities and a fine temporal scales via daily activity. We randomly assigned control (n=2) and fladry treatments (n=5) to selected prairie dog colonies and used remote cameras to detect coyotes inside and outside fladry exclosures. We collected data for 30 days before fladry installation on each of our colonies and for 60 days following fladry installation. While number of days until first detection within fladry exclosures was highly variable (range = 9-60 days), we documented a 37% reduction in use by coyotes 30 days after fladry installation and a further decline of 60% during the second 30 days. This decline in use across all 60 days of the fladry treatment was supported by our measure of avoidance ($\epsilon = 0.37$), although the probability of

coyotes avoiding a camera unit was equal both inside and outside exclosures. Patterns underlying attraction varied substantially inside ($\gamma=0.00$) and outside ($\gamma=1.00$) fladry exclosures across all seasons, signifying coyotes only used camera units that had been used prior to fladry installation inside exclosures and that coyotes were attracted to previously unused areas surrounding exclosures. In addition, we documented a 170% increase in coyote activity around the periphery of fladry exclosures immediately after fladry installation, suggesting that coyotes are attracted to fladry immediately after installation. Our results indicate fladry reduces coyote use within protected areas for at least 60 days; however, results related to periphery use suggest it may do so in a way that is counterintuitive to management expectations. Occupancy models permit robust evaluation of nonlethal tools beyond binary terms of success and failure and provide valuable additional information, such as the behavioral responses of carnivores to these tools.

INTRODUCTION

In North America, coyotes (*Canis latrans*) have expanded their range by more than 40% in the past century and now inhabit the majority of the continent (Hody and Kays 2018, Prugh et al. 2009). Coyote expansion is attributed to a variety of factors, including release from apex predator pressures, expanding agricultural landscapes, and their highly plastic diet (Hody and Kays 2018, Prugh et al. 2009, Levy 2012, Fener et al. 2005). In tandem with range expansion, coyotes have become the primary predator of livestock in the U.S. (USDA APHIS 2015a, USDA APHIS 2015b), accounting for nearly 90% of all livestock damage reports in 2017 (USDA APHIS 2017) and the highest percentage of cattle (*Bos taurus*; 40.5%), calf (53.1%), sheep (*Ovis aries*; 54.3%), and lamb deaths (63.7%) in 2014. Coyotes have also been identified as a problematic species in the recovery of imperiled species, where their predation activities can have significant impacts on small, vulnerable populations (Goodrich and Buskirk 1995). For

example, coyotes have contributed to the decline of the endangered San Joaquin kit fox (*Vulpes macrotis mutica*), California least tern (*Sterna antillarum browni*), and desert tortoise (*Xerobates agassizii*) in California (Butchko 1990). They are the most important predator of the endangered black-footed ferret (*Mustela nigripes*) in prairie ecosystems, where they cause substantial challenges in reintroduction efforts (Breck et al. 2006, Biggins 2000).

In both endangered species recovery and livestock management scenarios, lethal and nonlethal strategies are employed to manage coyotes. Nonlethal tools are increasingly used to prevent and mitigate predation (USDA APHIS 2015a, USDA APHIS 2015b) by either physically excluding or behaviorally repelling carnivores (Shivik 2006; Gehring et al. 2006). For example, fladry is a nonlethal tool developed as a disruptive stimulus to mitigate wolf predation on livestock (Musiani et al. 2001, Musiani et al. 2003, Davidson-Nelson and Gehring 2010). Fladry takes advantage of wolves' inherent neophobia and consists of a continuous strand of rope with long strips of red flagging sewn or tied to the rope at ~50cm intervals and strung ~50cm from the ground. Electrified fladry is a modification of fladry that carries an electric charge along the continuous strand of rope. The addition of an electric charge increases fladry effectiveness (Lance et al. 2010) through the addition of an adverse stimulus (i.e., electric shock, Shivik 2006) and has been used successfully in field settings on working ranches (Young et al. 2018).

Although coyotes have similar neophobic responses to that of wolves (Mettler and Shivik 2007), the spacing of flags on commercial fladry and electrified fladry is likely unsuitable for smaller-sized coyotes (Davidson-Nelson and Gehring 2010). As a result, a recent captive study used the ratio of wolf body width to fladry flag width and narrowed the spacing of flags for use with coyotes to test new coyote fladry (Young et al. 2019b). When compared with commercial fladry,

the study found that modified coyote fladry nearly doubled the length of effectiveness when used with coyotes (Young et al 2019); however, coyote fladry has yet to be tested in a field setting.

In general, a great deal of uncertainty remains about the effectiveness of most nonlethal tools (Miller et al. 2014, van Eeden et al. 2018), and this uncertainty can be largely attributed to the small proportion of tools that have been rigorously evaluated. Most field evaluations of nonlethal tools are performed in a management context where evaluation typically consists of before-after comparisons and often with limited resources for monitoring (Breck 2004). Further, how effectiveness is measured is inconsistent, and tools are often categorized as having failed or succeeded based on a variety of qualifying metrics, such as the number of days that a tool can survive permeation (e.g., Musiani et al 2003) or number of livestock attacks (e.g., Ohrens et al. 2019). Tools that have been assessed in this binary framework lose substantial information about their efficacy (e.g., how the tool influenced a carnivore's behavior and overall use of a protected area), do not account for the possibility of individual variation across the targeted carnivore population (Blackwell et al. 2016, Darrow and Shivik 2009), and largely ignore imperfect detection or extraneous variables that may influence success or failure.

Occupancy models account for imperfect detection to estimate dynamics in species occurrence (MacKenzie et al. 2017) and have been used to understand animal behavior (Lewis et al. 2015, Sollmann et al. 2013), human-wildlife conflict (Goswami et al. 2016), and the effectiveness of management actions (Moore et al. 2018). Further, occupancy studies can be relatively cost-effective (MacKenzie et al. 2017) and models include a variety of parameters that provide both fine- and coarse-scale measurements of a species' behavioral response (Table 1). In this study we use an occupancy framework to evaluate the efficacy of a nonlethal tool, electrified coyote fladry (hereafter, fladry), by measuring changes in coyote use, avoidance, attraction and

activity (Table 1). We tested fladry in a grassland ecosystem where prairie dog (*Cynomys spp*) colonies are a preferred habitat of coyotes (Krueger 1986, Ceballos et al. 1999) where variation in biotic and abiotic factors that might influence coyote use are relatively easy to measure (e.g., local prairie dog density, proximity to riparian areas, streams, and roads).

Our primary objectives were to quantify the number of days until coyotes first crossed fladry and measure how fladry impacted coyote use of protected areas. We predicted use within protected areas would abruptly decline with fladry application and then gradually increase to levels observed prior to installation. Accordingly, we expected fladry to influence coyote behavior through measures of avoidance and attraction. We predicted coyotes would avoid areas within fladry exclosures during the first 30 days of fladry application, but may be attracted to (i.e., recolonize) these same areas during the second 30 days of fladry application as they begin to cross the fladry barrier (Table 1). Our second objective was to understand how coyote activity responded to the presence of nonlethal tools, and we considered two alternative hypotheses regarding the fine-scale behavioral response of coyotes to fladry. First, we hypothesized that fladry would be highly disruptive and decrease coyote activity not only within fladry exclosures but also around the periphery of these areas. Alternatively, we hypothesized that although fladry is novel and thus inherently disruptive, coyotes would increase activity around the periphery of fladry exclosures as they investigated the tool, thus providing insight into the development of conflict behaviors (Table 1). Finally, because understanding the costs of installation and maintenance for nonlethal tools is an additional important factor in tool evaluation (Lance et al. 2010), our final objective was to calculate the costs of fladry materials, installation, maintenance, and removal for cost-benefit analysis purposes.

STUDY AREA

We conducted our study in the northern unit of Badlands National Park (BNP) and the surrounding Buffalo Gap National Grasslands (BGNG) in southwestern South Dakota. BNP and BGNG are dominated by mixed-grass prairie with primary vegetation including western wheatgrass (*Agropyron smithii*), buffalograss (*Buchloe dactyloides*), blue grama (*Bouteloua gracilis*), and prickly pear cactus (*Opuntia polyacantha*) (Livieri and Anderson 2012). Black-tailed prairie dog (*Cynomys ludovicianus*) subcomplexes can be distinctly identified by active burrows interspersed across close-cropped grassland. Primary land uses in BGNG include recreation, hunting, and grazing of both domestic cattle (*Bos taurus*) and bison (*Bison bison*). The primary land use of BNP is recreation, tourism, and sanctuary for species such as bison, bighorn sheep (*Ovis canadensis*), and pronghorn antelope (*Antilocarpa americana*). Topography of the area is primarily flat, interspersed with arroyos and bands of layered Badlands rock formations. Riparian areas that contain sparse patches of cottonwood trees (*Populus deltoides*) can be found along the edges of ephemeral drainages and man-made watering holes. Two state highways (240 and 44) and two county highway (509 and 590) interconnect BNP and BGNG with an assortment of minimally traveled forest service roads and fence lines throughout the area (Fig. 1). Together, BNP and BGNG are home to the largest population of wild black-footed ferrets (~115 individuals) and coyotes are common throughout this area.

METHODS

Overview

We conducted our study from August through December 2018. BNP and BGNG biologists conduct bi-annual surveys where black-tailed prairie dog colonies are delineated and density is categorized as high, medium, or low across 5875ha of prairie dog colony habitat.

Using data from 2017 surveys, we identified the largest intact colonies (greater than 65 ha) with medium to high prairie dog density and known ferret presence. Where multiple prairie dog colonies greater than 65 ha occurred in close proximity, we clustered colonies into subcomplexes (Biggins et al. 2006) and selected one colony from this group at random to be included in our fladry experiment. We identified eight prairie dog subcomplexes (Agate, Conata West, Heck Table, Lower Sage Creel, Prairie Wind, Roberts, Sage Creek, Steer Pasture; hereafter, colonies) in our study area (Fig. 1; Table 2) and used all colonies apart from one (Roberts), due to logistical reasons.

Fladry experiment

We modified standard electrified fladry to a narrower flag spacing of 27.9 cm (Young et al. 2019) and tested its effectiveness at excluding coyotes from areas within fladry exclosures on each treatment colony (Fig. 1). Using our seven previously identified colonies we assigned five colonies as treatments (i.e., fladry exclosures installed and monitored with wildlife cameras) and two colonies as control (i.e., no fladry exclosures installed and monitored with wildlife cameras). We separated fladry treatments by ≥ 1.5 km, the average coyote core-use size in our study area (Schroeder 2007), to ensure independence of treatments. Two colonies, Conata West and Agate, were ~300m apart at their closest point and we randomly assigned one of these two colonies to our fladry treatment (Agate) and retained the other as a control (Conata West). Thereafter, we randomly selected four additional colonies for fladry treatment (Lower Sage Creek, Heck Table, Prairie Wind, and Steer Pasture) and used the remaining colony (Sage Creek) as an additional control (Table 2). Each of our five fladry exclosures protected 8ha of prairie dog colony habitat. Exclosures were placed near the center of the selected colony, where prairie dog density was observed to be highest (Fig. 1).

We used wildlife camera traps to collect coyote detection data and divided our prairie dog colonies into two strata to measure differences in coyote use inside and outside fladry enclosures. Our first strata comprised the area inside the fladry enclosure (hereafter, Inside Fladry) and the second strata comprised a 100m buffer surrounding the Inside Fladry strata (hereafter, Outside Fladry; Fig. 1). Across our 5 treatments, we placed four cameras in each strata, yielding a total of 20 cameras in each strata on treatment colonies (i.e., 20 Inside Fladry, 20 Outside Fladry), and 8 cameras in each strata on control colonies (i.e., 8 Inside Fladry, 8 Outside Fladry). Inside Fladry cameras were placed within the enclosures, approximately 5m from each corner to maximize the interspersion of cameras. To place Outside Fladry cameras, we randomly chose a starting point along the 100m buffer and then systematically placed cameras along the buffer at 100m intervals. We defined cameras as our sample units (hereafter, units), where the effective area sampled by each camera was 0.28ha based on an average camera detection range of 30m and a 45-degree field of view (Trailcampro.com, Springfield, MO). Given the lack of landscape features on prairie dog colonies that are typically used to maximize carnivore detection probability in occupancy surveys (e.g., roads, trails), we used active prairie dog burrows as a focal point to increase coyote detection. All cameras were placed on t-posts, approximately 50cm from ground level and 7.5m from the center of the nearest active prairie dog burrow entrance. Inside Fladry cameras pointed towards the center of the enclosure, while Outside Fladry cameras were pointed at the burrow from a randomly selected cardinal azimuth (i.e., N, S, E, W). Active burrows were determined by the presence of fresh scat (i.e., greenish, black, or dark brown), visual observation of prairie dogs, and mound scratching activity (Biggins et al. 1993, Livieri *personal communication*).

Each prairie dog colony had cameras on the landscape starting in early June 2018 as part of a separate study that served as a camera conditioning period. Following the conditioning period, we set cameras on all seven colonies and collected 30 days of detection data before fladry was erected. Following 30 days of pre-fladry data collection, we constructed fladry exclosures around our Inside Fladry strata on each treatment colony to protect the enclosed area from coyote use (Fig. 1). Fladry exclosures were established between 8 September 2018 and 2 October 2018, timed with the removal of livestock (i.e., cattle or bison) from USFS grazing allotments (Table 2). Fladry exclosures were established for 56-60 days (Table 2) and checked every 7-10 days to fix damaged lines due to weather or other disturbance.

Camera and covariate data

Camera data was processed using the Colorado Parks and Wildlife Photo Warehouse software (Ivan et al. 2016), where each photo was identified to species by two independent observers except for units that had very large numbers of photos (i.e., >10,000) due to grass blowing in the wind or high cattle/bison activity. The lead author verified species for any images that were not congruently identified by the two observers and units with large numbers of photos. We first used raw camera data to evaluate the date of first detection within each fladry exclosure and considered coyote detection events to be independent if detections were >1hr apart (Lewis et al. 2015, Lendrum et al. 2017). We censored data from any periods in which cameras malfunctioned (e.g., dead batteries, camera knocked down by cattle) and calculated the number of functional days for each camera.

Three different brands of camera traps were used in our study: Browning BTC Series (n=24), Bushnell Trophy Series (n=21), and Cuddeback Longrange IR (n=11). Cameras were

systematically placed within each strata to ensure the most interspersed distribution of camera brands. Where possible, we attempted to program all cameras similarly with a medium sensitivity, the smallest delay possible between photographs (≤ 1 s), and in bursts of three photos. All cameras were equipped with infrared flash to reduce the effects on coyote behavior. While we programmed cameras similarly, camera brands are known to have variable detection ranges, field of views, and sensitivity (Meek et al. 2015), thus we included camera brand as a covariate in all models to account for inherent variability in camera performance.

We hypothesized four primary variables could influence coyote use in our study area: distance to nearest riparian area; distance to nearest two-track road; distance nearest to stream or gully; and local prairie dog density. Riparian areas could provide cover, water, and den sites across the otherwise open and relatively unprotected grasslands. Two-track USFS roads and service roads within BNP could serve as travel corridors for coyotes. Streams and gullies could serve multiple purposes, including areas of cover, water sources, den sites, and travel corridors. We predicted that as distance to each of these three variables decreased, coyote use would increase. We acquired shapefiles of riparian areas (including lakes and ponds), two-track roads, streams and gullies from the USDA Data Gateway and used ArcMap (Esri, Redlands, CA) and measured the nearest distance (m) to each of these features from our camera units.

We measured local prairie dog density by counting all burrows within a 30m buffer of each camera, classifying each burrow as active, inactive or plugged. Burrows were considered active based on the same criteria used to select active burrows for cameras placement (Biggins et al. 1993). We used the linear relationship Biggins et al. (1993) reported between black-tailed prairie dog active burrow counts and individual animals to estimate prairie dog counts, where the relationship was best described by the regression line through the origin,

Prairie dog count = 0.179 x number of active burrows

and local density per hectare was calculated by dividing estimated prairie dog counts by the number of hectares sampled. To ensure prairie dog density was similar across colonies and strata, we used a Welch Two-Sample t-test to explore differences between control and treatment colonies and between Inside Fladry and Outside Fladry strata. We tested for correlation between our four habitat covariates using Pearson's product-moment correlation test and dropped correlated covariates from our analysis if $|r| > 0.7$ (Dormann et al. 2013).

Modeling coyote use dynamics

We evaluated coyote use within fladry exclosures using camera trap data in a robust design, multi-season occupancy framework (MacKenzie et al. 2017). We define occupancy (i.e., Ψ) as the probability an area (i.e., unit) is used by a coyote during a predefined season. Occupancy estimates correspond to the probability that camera units are “used” rather than “occupied” by the species of interest because wide-ranging movements are typical in carnivore species (MacKenzie et al. 2017). Dynamic occupancy models provide a means to assess changes in coyote use over multiple seasons (e.g., before and after the application of a nonlethal tool) through the two dynamic parameters; namely, ‘extinction’ probability (i.e., ϵ ; the probability that a unit used in the previous season is not used in the current season) and ‘colonization’ probability (i.e., γ ; the probability that a previously unused unit in one season is used in the subsequent season; MacKenzie et al 2003, 2017). These parameters are coarse-scale measurements of the species’ avoidance (i.e., extinction probability, ϵ) or attraction (i.e., colonization probability, γ) to areas in response to the presence of a disruptive stimuli, such as fladry (Table 1). Finally, detection probability (p), accounts for the likely possibility that a species may use an area during

a season, but not be detected on a given survey. Detection probability can also be interpreted as the frequency of use, and differentiates areas that are used often relative to those that may only be used occasionally during a season (i.e., fine temporal-scale use). When modeled with covariates, detection probability can reflect differences in relative use, local abundance, and/or the behavioral response of animals (Royle & Nichols 2003, Royle et al. 2005, Lewis et al. 2015, Sollmann et al. 2013). Because fladry aims to both physically exclude (i.e., decrease abundance) and disrupt coyote behavior, changes in detection probability likely represent combination of changes in local abundance and behavioral responses. These behavioral mechanisms may include varying levels of risk-assessment, exploration, and activity (Sih et al. 2004, Réale et al. 2007, Lima and Dill 1999, Frid and Dill 2002). While measures of abundance and behavioral variation are combined in our estimates of detection probability, for the purposes of this study, we consider detection probability a relative measure of coyote activity (Table 1).

We estimated changes in coyote use in both strata (Inside Fladry and Outside Fladry) over three 30-day seasons, in addition to avoidance, attraction, and activity parameters (Table 1). Our first season (i.e., Pre-Fladry) consisted of the 30 days of sampling prior to installation of fladry exclosures. Our second (i.e., Fladry 30) and third (i.e., Fladry 60) seasons consisted of the first 30 days and second 30 days of sampling post-fladry installation, respectively. On our control colonies, the continuous 90 days of sampling was broken into the same 30-day seasons for comparison. We estimated changes in coyote use and activity for both strata (Inside Fladry and Outside Fladry) and compared these estimates to Pre-Fladry data from all sample units and data from all seasons at control units (i.e., reference level of coyote use and activity). Each season consisted of 30 surveys containing 24hr periods centered around noon to capture the more crepuscular and nocturnal activity of coyotes (e.g., Kitchen et al. 2000, Andelt and Gipson 1979).

Occupancy models

We used Program MARK (White and Burnham 1999) to conduct all occupancy analyses and AICc model selection (Burnham and Anderson 2002). Given the large number of parameters in our models, we used a stepwise approach to model a series of interconnected hypotheses (Fig. 2). Our global model included the interactions of: 1) strata and treatment on initial probability of use during the Pre-Fladry period/season (Ψ); strata, treatment, and season on avoidance (ϵ) and attraction (γ); 2) strata and treatment on activity during Pre-Fladry season (p_1); and 3) strata, treatment, and a time trend on activity during Fladry 30 and Fladry 60 seasons (p_2 and p_3). Using this global model, we first investigated the effect of camera brand on detection (i.e., nuisance variation in our ability to detect coyotes; Appendix 2). Next, we modeled the effects of our habitat covariates and tested for inherent variation in coyote use between strata and treatments prior to fladry installation in treatment areas (ψ_1 , Appendix 3). Retaining the best-supported structure for coyote use in season 1, we constructed a set of models to address specific hypotheses related to avoidance probability (ϵ) and then attraction probability (γ ; Fig 2, Appendices 4-5). Specifically, we explored spatial (strata) and seasonal variation in avoidance probability among camera units in the control areas first, and then tested the same avoidance probability structures for units in/on treated areas (Fig 2, Step 3; Appendix 4). *A priori* we expected no coyote avoidance among camera units in control areas as fladry was not installed, but we expected coyotes to avoid previously used units inside the enclosure after fladry installation. Retaining the best-supported avoidance structure we tested similar spatial (strata) and season structures for the probability of attraction; first for camera units in/on controls areas and then for those units in/on treatment areas (Fig 3, Step 4; Appendix 5). We retained the most

supported model structure in each of these steps before modeling our final parameter, activity (p). Here, we first tested for variation in activity across all cameras in our Pre-Fladry season and across control cameras during Fladry 30 and Fladry 60 seasons to develop a reference level of activity. We retained the resulting reference level of activity and used this as our comparison point for our hypothesized responses Inside Fladry and Outside Fladry across our Fladry 30 and Fladry 60 seasons. These responses included 1) a linear trend across both Fladry 30 and Fladry 60 season, 2) a linear trend during Fladry 30 followed by a plateau during our Fladry 60 season, and 3) a constant change in activity probability during Fladry 30 and 60 (Fig. 2).

Fladry Costs

To determine the cost of fladry we calculated the average cost per kilometer for fladry materials and the average cost of labor per person for fladry set up, maintenance, and breakdown (Lance et al. 2010, Davidson-Nelson and Gehring 2010). Calculation of electrified fladry material costs included fladry, fiberglass posts, fiberglass post attachment clips (i.e., harp clips), t-posts, t-post insulators, electric fence energizer units (including ground rods), and wooden storage reels that were critical for efficient setup, breakdown, and storage. The first kilometer of fladry included the cost of the energizer unit, and all additional kilometers excluded the energizer cost. We calculated labor costs in person hours per kilometer based on a Colorado State University minimum wage of \$10.20 per hour and excluded camera set up and removal time from labor calculations.

RESULTS

Camera and covariate data

Cameras were functional for 4,444 trap nights across 56 camera units, where the average number of functional days was 26.2 days, 26.6 days, and 25.0 days for Pre-Fladry, Fladry 30,

and Fladry 60 seasons/periods, respectively. We recorded a total of 107 independent coyote detection events and detected coyotes on each of our experimental colonies. During the Pre-Fladry season we detected coyotes on each colony in both Inside Fladry and Outside Fladry, except on our Steer Pasture colony where we only detected coyotes in our Outside Fladry enclosure. As expected, the number of days until first coyote detection within a fladry enclosure was highly variable ($\mu = 37$ days, SE 12 days, range = 9-60 days, $n=4$; Table 2).

Prairie dog density was positively correlated with distance to streams ($r = 0.29$) and negatively correlated with distance to two track roads ($r = -0.30$). In addition, distance to riparian areas and streams were positively correlated ($r=0.3932$, $df=54$, $p=0.0027$). Because none of our correlation coefficients exceeded $|r| > 0.7$ we retained all covariates in our analysis. Local prairie dog density did not differ between control and treatment colonies ($\mu_{\text{control}} = 22.29$ pd/ha, $\mu_{\text{fladry}} = 20.28$ pd/ha, $df=28.28$, $p=0.46$), or between the two strata ($\mu_{\text{inside}} = 19.59$ pd/ha, $\mu_{\text{outside}} = 22.12$ pd/ha, $df=48.083$, $p=0.3039$).

We censored 9 surveys from detection histories both inside and outside fladry for our Prairie Wind camera locations due to a windstorm with 55+ mph gusts that occurred on Oct 3, 2018 and caused significant damage to our enclosure on this colony. The Prairie Wind enclosure was completely compromised, where one entire section of the enclosure came untied, creating a large ~250m opening. Due to logistical reasons, fladry could only be checked every 7-10 days and in this case the storm occurred one day after a check on 2 October 2018 and the next check occurred 9 days later on 12 October 2018. In addition, we did not include first crossing data for this enclosure (Table 2); the first detection inside Prairie Wind occurred the day after the wind storm and given the large gap, likely did not include an actual crossing event.

Modeling coyote use dynamics

Our stepwise approach to model selection resulted in a final set of seven candidate models that evaluated hypotheses of fladry influence on activity both Inside and Outside Fladry (Table 3). All models in this final set had similar support (i.e., within $\sim\Delta 2\text{AIC}$ and holding 9-26% of the model weight). However, each model was also greater than $\Delta 3.25\text{AIC}$ from the global base model that included a reference level of activity and signified strong support for activity variation in response to fladry (Table 3). All activity estimates from fladry response candidate models showed congruent directions in their response (i.e., all described a decreased level of activity Inside Fladry and increased level of activity Outside Fladry). All parameter estimates described below come from our top model.

Camera brand strongly influenced detection probability, with Browning cameras having a higher detection probability than our other two camera brands, Bushnell and Cuddeback ($\beta = 1.44$, 95% CI [0.92, 1.96]; Appendix 1). We retained this camera covariate in all future models and report estimated detection probabilities for those units sampled with Browning cameras. We found minimal influence for the effect of distance to road on coyote use ($\Delta\text{AICc} = 1.39$) and found no support for the influence of other habitat covariates (riparian areas and local prairie dog density) on coyote use (Appendix 2). We found no evidence of avoidance across control cameras in either strata and found evidence for equal avoidance across all fladry cameras in both strata and between both seasons ($\epsilon = 0.3702$, 95% CI [0.1717, 0.6250]; Appendix 3). We found no evidence of attraction across control cameras in either strata nor within fladry exclosures ($\gamma = 0.00$, Appendix 4) and very high attraction outside of fladry exclosures ($\gamma = 1.00$, Appendix 4). Activity was constant and equal across both control cameras and fladry cameras during the Pre-Fladry period ($p = 0.0520$, 95% CI [0.0381, 0.0706]; Appendix 5) and we used this combined

model as our reference level to compare to changes inside and outside fladry (Fig. 4). Inside fladry, we found that coyote activity declined after fladry installation and remained at this lower level for the duration of the fladry experiment ($p = 0.03$, 95%CI [0.01,0.062]; Fig. 4). Outside fladry, we found that coyote activity initially increased ($p=0.14$, 95%CI [0.08, 0.24]) before decreasing over the course of the 60 days of fladry treatment to activity levels similar to the reference level after ~50 days (Table 3, Fig. 4).

The initial, pre-fladry use of prairie dog colonies by coyotes was high ($\hat{\psi}_1=0.80$, 95% CI[0.56, 0.93]) across our entire study area but declined Inside Fladry during our Fladry 30 season ($\hat{\psi}_2=0.50$, 95% CI [0.29, 0.72]) and further declined during our Fladry 60 season ($\hat{\psi}_3=0.32$, 95% CI [0.07, 0.57]; Fig. 3). When compared with use at reference units, coyotes used units Inside Fladry 37.02% and 60.34% less during Fladry 30 and Fladry 60 seasons, respectively. Coyote use also declined slightly Outside Fladry, where coyotes used units 12.21% and 7.69% less during Fladry 30 and Fladry 60, respectively.

Fladry Costs

Fladry materials cost \$2,313 for the first kilometer and \$2,130 for each additional kilometer. Five to seven people worked to set up each fladry enclosure, where an average of 13.1 person hours was required to set up one kilometer of fladry, or \$133 per km. Fladry enclosures were maintained every 7-10 days; i.e., checked 5-6 times over the course of our 60-day fladry experiment. Maintenance required was variable based on the amount of damage from weather events such as high winds and heavy snow, but approximately 1.4 person hours per kilometer, or \$14.28 per km per check, was required to walk the perimeter of fladry enclosures to repair the fladry line, untangle flags, check charge at random intervals, and stomp-down/cut vegetation. We had 2-7 people work to breakdown fladry enclosures where an average of 9.3 person hours was

required per kilometer of fladry, or \$95 per km. Labor cost estimates exclude the time required to set, check, and remove camera traps.

DISCUSSION

We tested the efficacy of coyote fladry in an ecological scenario, where the prairie provided us a relatively controlled setting for the first field test of this new nonlethal tool. Fladry excluded coyotes for an average of 37 days (SE = 12 days); however, this number was highly variable among exclosures. Fladry excluded coyotes for the entire 60-day duration of our study at one exclosure but was crossed after only 9 days at another exclosure (Table 2). The variability we observed was mirrored in captive trials of coyote fladry (Young et al. 2019) and has also been observed in other studies (e.g., Musiani and Visalberghi 2001). In addition to variability within trials, the traditional metric of average number of days fladry is effective is problematic for cross-study comparison. For example, Davidson-Nelson and Gehrig (2010) compared visitation inside and outside wolf fladry exclosures on control and treatment farms and reported findings on its effect on coyotes. In their study, coyotes first crossed fladry an average of 47 days (SE=4 days) after fladry establishment, ten days later than the average crossing date in our study. This variation can be attributed to two factors. First, Davidson-Nelson and Gehring (2010) tested fladry by stringing it around the perimeter of a pre-existing fence line, where the fence likely reinforced coyote exclusion. This can make comparisons difficult because fence characteristics (e.g., height, number and type of strands) can vary between farms or be non-existent in scenarios such as the one presented here. Second, in both our study and that of Davidson-Nelson and Gehring (2010), the sample of protected colonies from which to gauge mean crossing date was limited (n=4 and n=7, respectively) and the studies ran for different lengths of time (n=60 days and n=75 days, respectively). This later point is particularly important as protected areas that are

not permeated during the course of a study are recorded as effective for the maximum number of days in the study, which is then used to calculate average days to first crossing. As a result, the length of a study greatly influences the average number of days a tool is effective and highlights the problem of determining efficacy from crossing date alone.

Using a dynamic occupancy approach we were able to assess fladry efficacy beyond simply the number of days the tool was effective. Several model parameters (use, avoidance, and attraction) provided information about how coyotes spatially use units and how this use changed in response to fladry, both inside and outside fladry exclosures at a coarse temporal scale (i.e., over a 30-day season; Table 1). Coyote use of protected areas within fladry exclosures was reduced across all 60 days of our trials. Use inside fladry exclosures decreased by 37.02% during the first 30 days of our experiment, and surprisingly, further decreased by 60.34% (i.e., another 23.32%) during the final 30 days (Fig. 3). In addition, coyotes appeared to marginally decrease their use of units directly surrounding fladry exclosures by 12.2% and 7.7% after the first 30 days of fladry and second 30 days of fladry, respectively (Fig. 3). Estimates of avoidance further supported declined use of protected areas, although the probability of coyotes avoiding a unit was equal across strata and seasons on treatment colonies (i.e., $\varepsilon = 0.37$). More interestingly, the patterns underlying attraction varied substantially inside and outside of fladry exclosures. Inside fladry exclosures coyote attraction was zero (i.e., $\gamma = 0.00$), suggesting that when coyotes did enter fladry exclosures, they only used those areas used prior to fladry installation. Conversely, we observed a very different pattern outside fladry exclosures in which attraction was very high (i.e., $\gamma = 1.00$). This implies that even though we found coyotes avoid a subset of previously used units outside fladry exclosures (i.e., as described by our avoidance estimate), the far stronger response signified coyotes were attracted to previously unused areas surrounding the exclosure.

Our estimates of coyote activity, yielded information about how coyotes interacted with fladry at a finer temporal scale (i.e., daily detection probabilities/rates; Table 1). In the first 30 days after fladry installation, coyote activity within exclosures declined by 47% and remained lower than reference levels for the duration of our fladry experiment (Fig. 4). Outside fladry exclosures we observed a very different pattern, where activity increased by more than 170% after fladry installation before gradually declining to reference level after 49 days. In terms of local abundance and behavioral response, this change in activity provides evidence that coyotes, either at the individual or species level, were attracted to fladry. This attraction to nonlethal tools is counterintuitive to the generally assumed notion of how nonlethal tools influence carnivore behavior and warrants further investigation. For example, a recent study by Ohrens and colleagues (2019) suggested a similar pattern of attraction by Andean foxes (*Lycalopex culpaeus*: hereafter, foxes) to Foxlights (Bexley North, Australia) predator deterrents. Although not statistically significant, Ohrens et al. (2019) found that foxes attacked a total of 25 livestock herds with Foxlights deployed and 15 livestock herds with no Foxlights deployed.

While changes in activity describe variation in the daily use of units in relationship to local coyote abundance, these changes can also be attributed to the behavioral response of coyotes. For example, canids employ investigative behaviors as they learn to overcome nonlethal prevention measures (Much et al. 2018) and investigation of fladry may inherently increase an individual's activity (Sih et al. 2004, Réale et al. 2007). As use and activity is typically randomly distributed across the landscape, the novelty of fladry may alter this pattern by attracting coyotes to the vicinity of exclosures as they investigate and assess fladry risk (i.e., risk-assessment, predator inspection; Lima and Dill 1999, Frid and Dill 2002). As a result, increased activity may reflect the behavior of an individual or individuals that are learning to overcome fladry (e.g.,

Young et al. 2015). In addition, coarse scale measures of attraction and avoidance can similarly provide information about risk-assessment (Table 1). For example, our very high measure of attraction may reflect coyotes exploring the periphery of fladry exclosures, demonstrating the prevalence of risk-assessment behaviors post fladry installation. Given the emerging importance in understanding how behavior influences conflict (Breck et al 2019, Blackwell et al. 2016), future studies could target intraspecific variation and development of these behaviors by supplementing occupancy data with movement data from marked or telemetered individuals. While nonlethal tool efficacy is critical for gauging usefulness in conflict mitigation, effectiveness must be considered in tandem with cost to fully understand and realize its value. Many factors influence these costs (design requirements, labor costs, material choice). For this study, the cost of fladry materials was \$2,313 for the first kilometer and \$2,130 for each additional kilometer. Labor costs for installation, maintenance, and breakdown over a 60-day period cost an additional \$314 per km of fladry. While the number of person hours required for fladry set up reported in other studies has been highly variable (8.5- 31.8 person-hours per km; Davidson-Nelson and Gehring 2010, Lance et al. 2010), our estimate falls within this range (13.1 person-hours per km). Our fladry exclosures were unique in that we did not follow a fence line and thus our installation labor hours may be higher as additional time was required to create a straight “fladry line”. Cost will also vary between electrified vs non-electrified fladry, where additional time is required for the setup of electrified fladry. The fence energizer system (Premier 1) we used was quite simple to install and operate (~5min of additional work per exclosure to install ground rods and connect energizer per exclosure), lowering the cost of actual set up; however, vegetation clipping is a required activity to avoid short circuiting and may further increase setup and maintenance costs. It should also be noted that costs for fladry

installation have increased due to higher minimum wage (i.e., \$10.20/hr minimum wage in our study vs \$8/hr in 2004; Davidson-Nelson and Gehring 2010); however, the cost of materials for electrified fladry has remained consistent over the last 10 years (i.e., \$2,303 for first kilometer and \$2,032 for each additional kilometer in 2007; Lance et al. 2010).

In addition to cost considerations, it is important to consider how fladry efficacy might change if coyotes were excluded from larger areas. Our study excluded coyotes from small portions of prairie dog colonies and it is unclear whether excluding coyotes from larger areas or entire prairie dog colonies would increase coyote motivation to enter exclosures. Related to these questions is the need for increased understanding about how coyote motivation to access wild prey (e.g., prairie dogs) translates to domestic livestock scenarios. Prairie dogs constitute the most frequent mammalian component of coyote diet in our study region (i.e., 38.2% of scat composition; Chronert 2007), but it is unknown if motivation to access prairie dogs differs from motivation to access livestock. Testing the efficacy of coyote fladry for protecting livestock is an important next step for robust evaluation of this nonlethal tool.

We encourage future nonlethal tool evaluation studies to employ an occupancy framework to understand the behavioral response of carnivores to a given tool and evaluate tool efficacy beyond binary terms of success and failure. Management tools have historically been evaluated as being effective (and thus worth using) or ineffective (and thus unworthy for use) based on the duration of a tool's effectiveness at excluding predators or the ability to reduce the number of depredations using before-after measurements (e.g., Davidson-Nelson and Gehring 2010, Lance et al. 2011, Mussiani et al. 2003). These measurements of effectiveness are often collected in management contexts where predators can be challenging to monitor due to their elusive nature, wide-ranging behavior, and limited resources for monitoring. Occupancy studies

provide a simple structure to rigorously estimate multiple dynamic parameters such as use, avoidance, attraction, and activity. This, coupled with their ability to be used with relatively cost-effective technologies, such as camera traps, make occupancy approaches ideal for monitoring wildlife across large areas.

Finally, we wish to highlight the importance of behavior in predator management. Fladry decreased coyote spatial and temporal use within protected areas in our study, and we provide evidence for the “behavioral mechanisms” hypothesis. This hypothesis states that conflict behaviors primarily arise from a limited number of problem individuals that disproportionately exhibit undesirable behaviors (Clua and Linnell 2018, Linnell et al. 1999). Targeted management of problem individuals (e.g., removal) may exert strong artificial selection against conflict behaviors (e.g., increased activity, boldness, and exploration; Breck et al. 2019, Swan et al. 2017, Mettler and Shivik 2007) and increase nonlethal tool efficacy. As a result, nonlethal tool evaluation methods that increase understanding of how conflict behaviors develop and document individual variation in their development are critical to optimize management, increase nonlethal tool efficacy, and promote human-carnivore coexistence.

To maximize fladry effectiveness, we offer several management considerations. First, our study found fladry to be an effective short-term coyote management tool. Fladry decreased coyote use of protected areas up to 60% and entirely excluded coyotes for an average of at least 37 days. However, it is important to note that coyote response to fladry was highly variable (range of effectiveness = 9-60 days), and as such fladry will help to exclude a select number of individuals. Counterintuitive to management expectations, coyotes also exhibited increased activity and attraction around the periphery of fladry exclosures. Our results, and those of others (e.g., Breck et al. 2019, Young et al. 2019, Darrow and Shivik 2009, Mettler and Shivik 2007,

Young et al. 2015), suggest that individual variation in the risk-appetite of coyotes may contribute to this pattern of attraction, with bolder, more exploratory individuals likely approaching (and entering) exclosures first. The length of time nonlethal tools are effective may be increased with targeted lethal removal of individuals that show immediate attraction to tools. For example, capture devices like leghold traps could be set inside the protected area at previously used locations. Finally, fladry is likely to be most effective when applied as an added form of protection against coyotes around fenced or otherwise monitored areas, and during short, critical periods of development for vulnerable animals (e.g., small fenced pastures during lambing, tortoise nest sites, first emergence of black-footed ferret kits).

TABLES AND FIGURES

Table 3.1. Occupancy parameters defined with respect to coyote response to fladry treatments/exclosures. For each response term, we provide the associated occupancy parameter, its temporal scale, the definition of the parameter as it applies to our study, and our predicted response. Coarse temporal scale estimates provide information during or between seasons (i.e., predefined 30-day periods) and fine temporal scale estimates provide information at a daily scale (i.e., the length of each survey).

Response	Parameter	Scale	Definition	Prediction of Treatment Responses
Use	Occupancy (Ψ)	Coarse	the probability a unit is used by coyotes	Decreased use during fladry application
Avoidance	Extinction (ε)	Coarse	the probability that a unit used in the previous season becomes unused	Evidence of avoidance inside fladry exclosures during first 30 days of application as barrier repels coyotes
Attraction	Colonization (γ)	Coarse	the probability that a unit unused in the previous season becomes used	Evidence of attraction inside fladry exclosures during second 30 days of application as coyotes learn to overcome barrier
Activity	Detection (p)	Fine	the probability coyotes were detected during a survey at a used unit	1) Decreased activity both inside and outside fladry exclosures during first 30 days of application; high avoidance 2) Decreased activity inside fladry and increased activity outside fladry during first 30 days of application; attraction to barrier

Table 3.2. Prairie dog colonies included in our study, their random treatment assignment, operational dates, and raw number of days until first coyote detection within a fladry enclosure. The average day of first crossing was 37 days after installation (n=4, SE=12 days). Date to first crossing was not available (UKN) for our enclosure on the Prairie Wind colony due to a windstorm that compromised our fladry barrier 26 days after fladry installation. Prior to this windstorm, no coyotes had been detected within the Prairie Wind enclosure. For Lower Sage Creek (Θ_1 ; total trial days = 56) and Steer Pasture (Θ_2 ; total trial days = 60) colonies, coyotes were never detected within enclosures.

Colony	Treatment	Pre-Fladry Start	Fladry Start	Fladry Breakdown	Days to 1st Crossing
Agate	Fladry	8/9/2018	9/8/2018	11/7/2018	9
Heck Table	Fladry	9/2/2018	10/2/2018	12/1/2018	23
Lower Sage Creek	Fladry	8/16/2018	9/15/2018	11/10/2018	Θ_1
Prairie Wind	Fladry	8/9/2018	9/8/2018	11/7/2018	UKN
Steer Pasture	Fladry	8/30/2019	9/29/2018	11/28/2018	Θ_2
Conata West	Control	8/11/2018	9/10/2018	11/9/2018	—
Sage Creek	Control	9/1/2018	10/1/2018	11/30/2018	—

Table 3.3. The final set of candidate models used a stepwise approach to test activity across the first (p_{30}) and second (p_{60}) 30 days of our fladry experiment both inside ($Flad_I$) and outside ($Flad_O$) fladry enclosures. The best supported base model [BASE: ψ (.), ε (Flad), ε (Cont=0), Y (Flad,str), Y (Cont=0), $p_{Pre}(\cdot)=p_{30}\&p_{60}Cont(\cdot)$, $p_{30}\&p_{60}Flad_I(grp*T)$, $p_{30}\&p_{60}Flad_O(grp*T)$] formed a reference level of detection prior to fladry installation and across control cameras that was used to test three hypothesized activity responses first on $Flad_I$ and then on $Flad_O$. These structures included a constant (.) change in activity, a time trend (T) on activity across all 60 days of our experiment, and a time trend in the first 30 days of fladry application, followed a plateau (P) in activity in the second 30 days. AIC_c = Akaike's Information Criterion adjusted for small sample bias; w_i = AIC_c model weights; L = model likelihood; K = number of parameters in model.

Model	AIC_c	ΔAIC_c	w_i	L	K
BASE - $p_{30}\&p_{60}Flad_I(\cdot), p_{30}\&p_{60}Flad_O(T)$	879.70	0	0.27	1	9
BASE - $p_{30}\&p_{60}Flad_I(\cdot), p_{30}\&p_{60}Flad_O(grp*T)$	880.30	0.60	0.20	0.74	11
BASE - $p_{30}Flad_I(T), p_{30}Flad_I(P), p_{30}\&p_{60}Flad_O(grp*T)$	880.72	1.01	0.16	0.60	12
BASE - $p_{30}\&p_{60}Flad_I(\cdot), p_{30}Flad_O(T) p_{30}Flad_O(P)$	881.04	1.33	0.14	0.51	9
BASE - $p_{30}\&p_{60}Flad_I(\cdot), p_{30}\&p_{60}Flad_O(\cdot)$	881.59	1.88	0.10	0.39	8
BASE - $p_{30}\&p_{60}Flad_I(T), p_{30}\&p_{60}Flad_O(grp*T)$	881.84	2.13	0.09	0.34	12
BASE	885.09	5.38	0.02	0.07	14

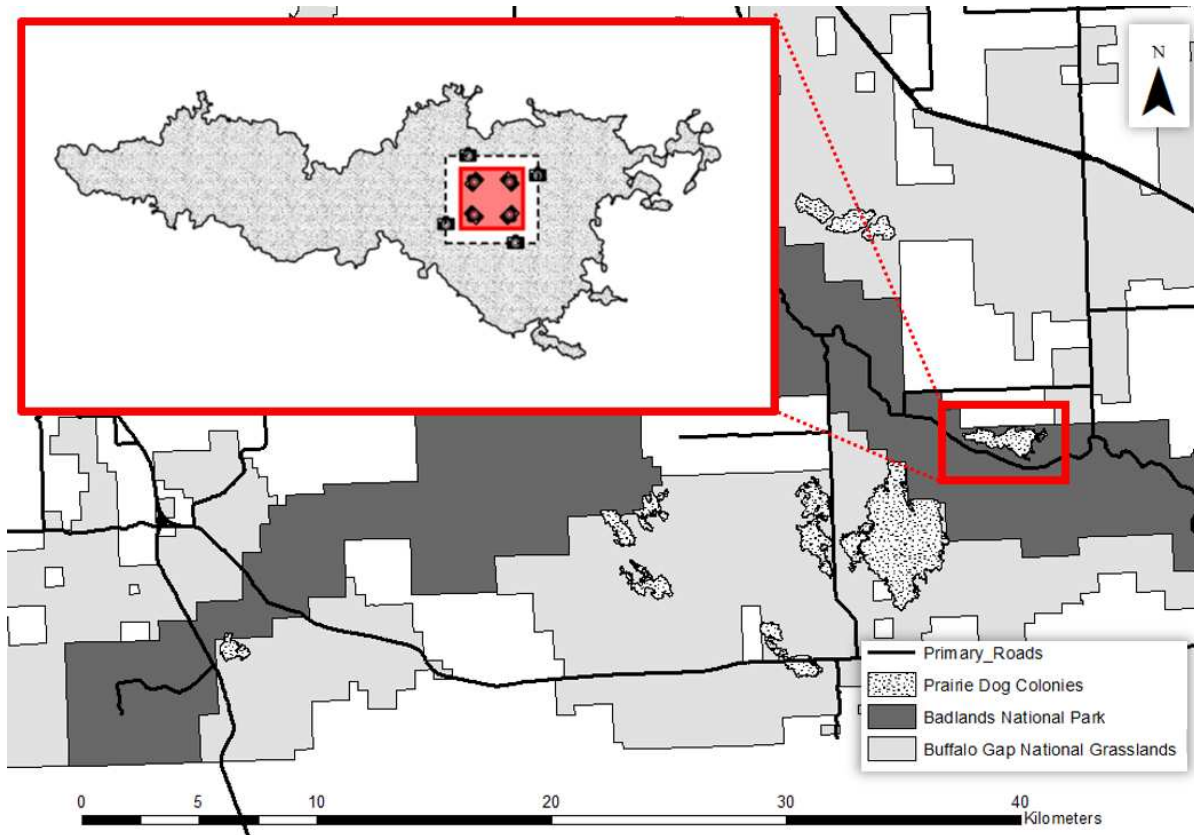


Fig. 3.1. Prairie dog colonies (grey stippled polygon) selected for our fladry experiment were at least 65ha in size. Square fladry enclosures (red line) protected approximately 8ha of prairie dog colony habitat. We deployed four wildlife cameras traps across two strata on each treatment (n = 5) and control (n = 2) colony. The light red area within fladry enclosures formed the Inside Fladry strata and a 100m buffer (dashed line) surrounding the enclosure formed the Outside Fladry strata. Cameras within the Inside Fladry strata all pointed inwards, toward the center of the enclosure and were placed approximately 5m to the inside of each enclosure camera post. Cameras within the Outside Fladry strata pointed in random cardinal azimuths and were systematically placed at 100m intervals along the 100m buffer line.

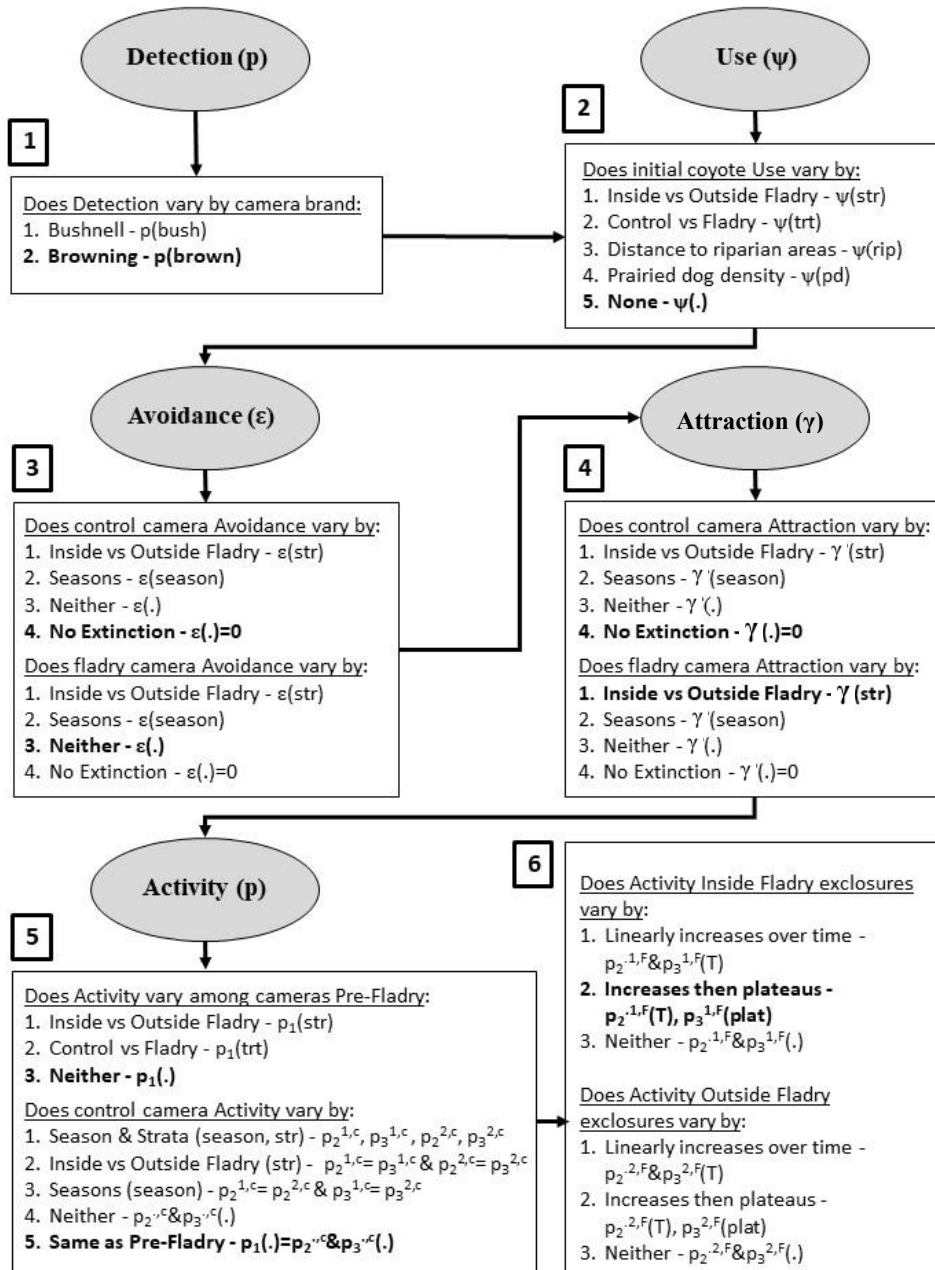


Fig. 3.2. To evaluate changes in coyote use, avoidance, attraction and activity in response to fladry, we used an occupancy framework and stepwise approach to model selection. We began with a global model and then in each step asked a specific question (underlined text), carrying the best supported structure (in **bold**) forward to the next step. We first modeled nuisance detection variation due to camera brand (1), then followed with coyote use (2), avoidance (3), and attraction (4). In our final two steps, we first developed a reference level of activity from data prior to fladry installation (Pre-Fladry) across all cameras and control camera data in all seasons (5) before asking specific questions in regard to coyote activity inside (Inside Fladry) and outside (Outside Fladry) enclosures.

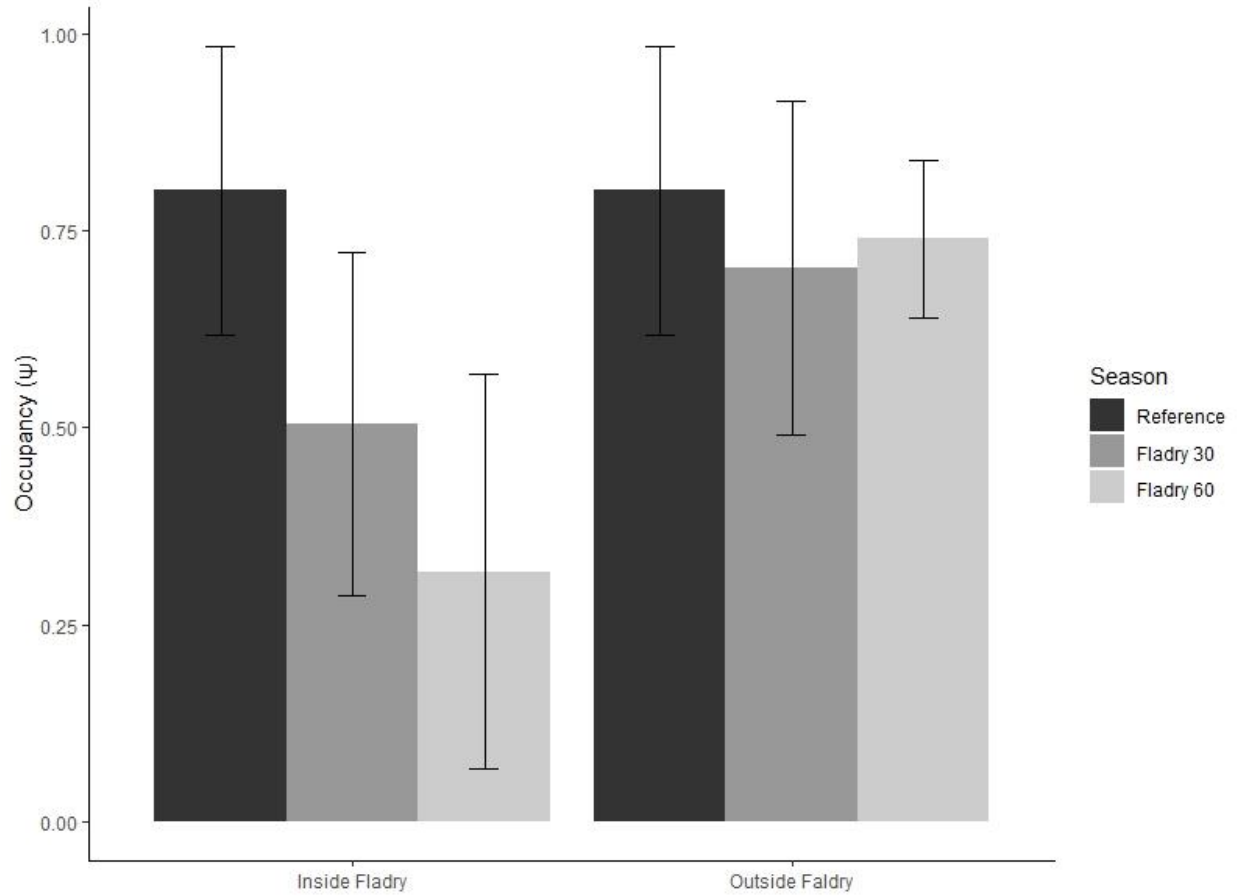


Fig. 3.3. Derived coyote use (Ψ) probabilities and associated 95% confidence intervals for units inside fladry enclosures (Inside Fladry) and outside fladry enclosures (Outside Fladry) during each season: pre-fladry (Reference) and two post-installation seasons (Fladry 30, Fladry 60) at camera units in fladry treatment colonies.

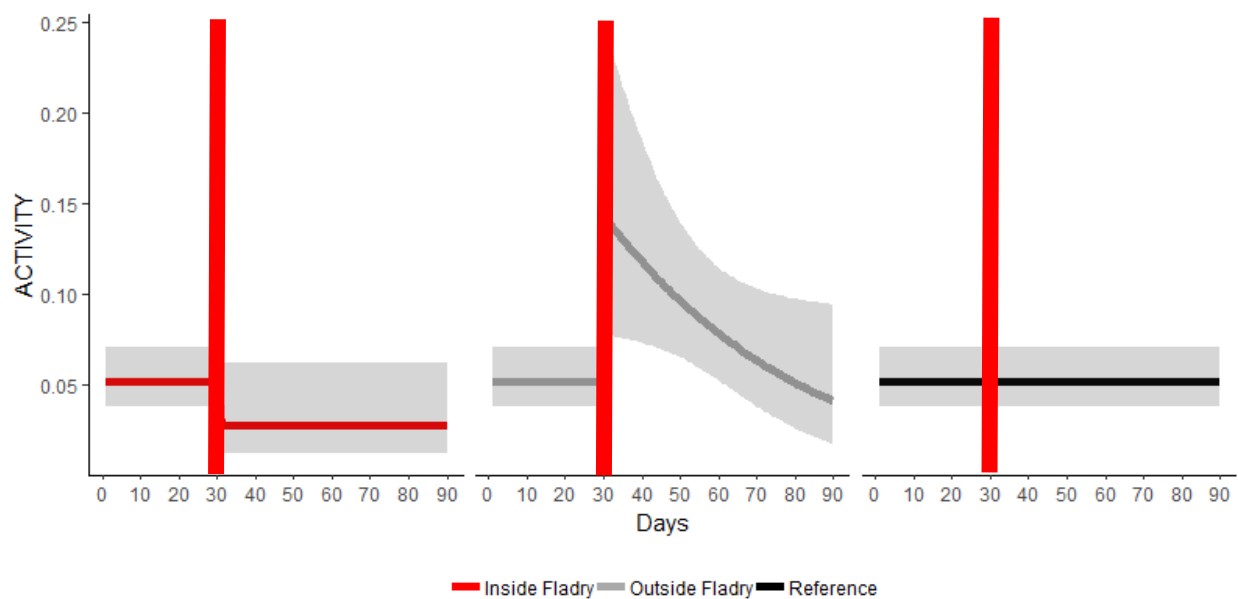


Fig. 3.4. Daily coyote activity, inside fladry exclosures (Inside Fladry; red), outside fladry exclosures (Outside Fladry; grey), and for a reference level of activity (Reference; black) with associated 95% confidence intervals. The first 30 days (Days 1-30; before red vertical bar) reflect detection probability prior to fladry installation across all units. The following 60 days (Days 31-90; after red vertical bar) reflect changes in activity in response to fladry.

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APPENDICIES

Appendix 1. The best supported model for badger occupancy included the effect of fine scale prairie dog density on use and the Bushnell cameras on detection probability ($\Delta AICc = 1.98$; $\Psi_{\text{conditional}} = 0.2295$, range: 0.002-1.000).

Model	AICc	$\Delta AICc$	AIC wgt	no.Par.	Deviance
$\Psi(\text{PD Fine}), p(\text{Bush})$	131.33	0	0.5074	4	123.33
$\Psi(\text{PD Fine}+\text{PD Coarse}), p(\text{Bush})$	133.31	1.98	0.1885	5	123.31
$\Psi(\text{PD Fine}+\text{PD Coarse}+\text{Size}), p(\text{Bush})$	134.07	2.74	0.1289	6	122.07
$\Psi(\text{Rotation}+\text{PD Fine}+\text{PD Coarse}+\text{Size}), p(\text{Bush})$	135.77	4.44	0.0551	7	121.77
$\Psi(\text{Rotation}+\text{PD Fine}+\text{PD Coarse}+\text{Size}), p(\text{Brown}+\text{Bush}+\text{Effort})$	136.58	5.25	0.0368	9	118.58
$\Psi(\text{Rotation}+\text{PD Fine}+\text{PD Coarse}+\text{Size}), p(\text{Brown}+\text{Bush})$	136.96	5.63	0.0304	8	120.96
$\Psi(\text{Rotation}+\text{PD Fine}+\text{PD Coarse}+\text{Size}), p(\text{Effort})$	138.18	6.85	0.0165	7	124.18
$\Psi(\text{Rotation}+\text{PD Fine}+\text{PD Coarse}+\text{Size}), p(\text{Brown}+\text{Bush}+\text{Effort}+\text{Veg})$	138.56	7.23	0.0137	10	118.56
$\Psi(\text{Rotation}), p(\text{Bush})$	138.7	7.37	0.0127	4	130.7
$\Psi(\text{Rotation}+\text{PD Fine}+\text{PD Coarse}+\text{Size}), p(\text{Brown})$	140.6	9.27	0.0049	7	126.6
$\Psi(\text{Rotation}+\text{PD Fine}+\text{PD Coarse}+\text{Size}), p(\text{Veg})$	140.63	9.3	0.0049	7	126.63
$\Psi(\text{PD Coarse}), p(\text{Bush})$	147.59	16.26	0.0001	4	139.59
$\Psi(\text{Size}), p(\text{Bush})$	150.56	19.23	0	4	142.56
$\Psi(\cdot), p(\cdot)$	155.52	24.19	0	2	151.52

Appendix 2. We used a stepwise approach (Fig. 2) to model fladry efficacy. Step one tested the effect of camera brand on detection probability, starting with a global model (GLOBAL) that considered the differences between all treatments and strata (i.e., grp; inside fladry strata on treatment colonies, outside fladry strata on treatment colonies, inside fladry strata on control colonies, outside fladry strata on control colonies) for all parameters. Avoidance (ϵ) and attraction (γ) models included an interaction with a time varying survey effect (t), and activity across the first (p_{30}) and second (p_{60}) 30 days of our fladry experiment included an interaction with a time trend (T). Using this global model, we tested the effects of Browning (brown), Bushnell (bush), and Cuddeback (intercept) cameras including additive effects of brown and bush on detection. Browning cameras greatly increased detection probability and we retained this parameter as part of our global model (CAMERA GLOBAL) in step two (see Appendix 3). AICc = Akaike’s Information Criterion adjusted for small sample bias; w_i = AICc model weights; L = model likelihood; K = number of parameters in model.

GLOBAL: ψ (grp), ϵ (grp*t), γ (grp*t), [p_{pre} (grp), p_{30} (grp*T), p_{60} (grp*T)]

Model	AIC_c	Δ AIC_c	w_i	L	K
GLOBAL + brown	949.91	0	0.81	1	41
GLOBAL + bush+brown	953.28	3.37	0.15	0.19	42
GLOBAL + bush	955.77	5.86	0.04	0.05	41
GLOBAL	963.05	13.13	0.00	0.00	40

Appendix 3. We used a stepwise approach (Fig. 2) to model fladry efficacy. Step two tested for the influence of distance of a unit to nearest riparian area (rip), local prairie dog density at a unit (pd), and the effects of strata (str; inside and outside fladry strata) and treatment (trt; control and fladry treatment) on coyote use using the CAMERA GLOBAL model as the foundation for remaining parameter structures (see Appendix 2). We did not find any of these variables to influence coyote use and retained the null model of use as part of our global model (ψ GLOBAL) in step three (see Appendix 4). AICc = Akaike’s Information Criterion adjusted for small sample bias; w_i = AICc model weights; L = model likelihood; K = number of parameters in model.

CAMERA GLOBAL: ψ (grp), ϵ (grp*t), γ (grp*t), [p_{pre}(grp), p₃₀(grp*T), p₆₀(grp*T)] + brown

Model	AIC_c	Δ AIC_c	w_i	L	K
CAMERA GLOBAL - ψ (.)	940.21	0	0.37	1	38
CAMERA GLOBAL - ψ (road)	941.61	1.39	0.18	0.50	39
CAMERA GLOBAL - ψ (rip)	942.23	2.02	0.13	0.36	39
CAMERA GLOBAL - ψ (pd)	943.24	3.03	0.08	0.22	39
CAMERA GLOBAL - ψ (str)	943.37	3.16	0.08	0.21	39
CAMERA GLOBAL - ψ (trt)	943.43	3.22	0.07	0.20	39
CAMERA GLOBAL - ψ (stream)	943.55	3.34	0.07	0.19	39
CAMERA GLOBAL	949.92	9.70	0.00	0.01	41

Appendix 4. We used a stepwise approach (Fig. 2) to model fladry efficacy. Step three tested for coyote avoidance of fladry exclosures by first testing for avoidance of control units (Cont; last four models) and then testing for avoidance at treatment units (Flad; top four models) using the ψ GLOBAL model as the foundation for remaining parameter structures (see Appendix 3). We maintained a global structure on fladry units including the effects of strata (str; inside and outside fladry strata) and season (sea; first 30 days of fladry and second 30 days of fladry) and tested for control unit variation by str, sea, no avoidance (Cont=0), and avoidance varied by str and sea (Cont). We then retained the best control structure (Cont=0) and next tested for effects of str, sea, no avoidance (Flad=0), and avoidance varied by str and sea (Flad) on fladry units. Our best supported model found coyote avoidance at units to vary both by str and sea (Flad), we and retained this model for use as part of our global model (ϵ GLOBAL) in step four (see Appendix 5). AICc = Akaike’s Information Criterion adjusted for small sample bias; w_i = AICc model weights; L = model likelihood; K = number of parameters in model.

ψ GLOBAL: ψ (.), ϵ (grp*t), γ (grp*t), [$p_{pre}(grp)$, $p_{30}(grp*T)$, $p_{60}(grp*T)$] + brown

Model	AIC _c	Δ AIC _c	w_i	L	K
ψ GLOBAL- ϵ (Flad), ϵ (Cont=0)	921.13	0	0.63	1	31
ψ GLOBAL- ϵ (Flad-sea), ϵ (Cont=0)	924.02	2.89	0.15	0.24	32
ψ GLOBAL- ϵ (Flad-str), ϵ (Cont=0)	924.19	3.06	0.14	0.22	32
ψ GLOBAL- ϵ (Flad=0), ϵ (Cont=0)	925.51	4.38	0.07	0.11	30
ψ GLOBAL- ϵ (Flad-str,sea), ϵ (Cont=0)	929.78	8.65	0.01	0.01	34
ψ GLOBAL- ϵ (Flad-str,sea), ϵ (Cont)	932.44	11.31	0.00	0.00	35
ψ GLOBAL- ϵ (Flad-str,sea), ϵ (Cont-str)	934.17	13.04	0.00	0.00	36
ψ GLOBAL- ϵ (Flad-str,sea), ϵ (Cont-sea)	935.63	14.50	0.00	0.00	36
ψ GLOBAL	940.21	19.08	0.00	0.00	38

Appendix 5. We used a stepwise approach (Fig. 2) to model fladry efficacy. Step four tested for coyote attraction to fladry exclosures by first testing for attraction of control units (Cont; last four models) and then testing for attraction at treatment units (Flad; top four models) using the ϵ GLOBAL model as the foundation for remaining parameter structures (see Appendix 4). We maintained a global structure on fladry units including the effects of strata (str; inside and outside fladry strata) and season (sea; first 30 days of fladry and second 30 days of fladry) and tested for control unit variation by str, sea, no attraction (Cont=0), and attraction varied by str and sea (Cont). We then retained the best control structure (Cont=0) and next tested for effects of str, sea, no attraction (Flad=0), and attraction varied by str and sea (Flad) on fladry units. Our best supported model found coyote attraction at units to vary by str (Flad-str) and we retained this model for use as part of our global model (γ GLOBAL) in step four (see Appendix 6). AICc = Akaike's Information Criterion adjusted for small sample bias; w_i = AICc model weights; L = model likelihood; K = number of parameters in model.

ϵ GLOBAL: ψ (.), ϵ (Flad), ϵ (Cont=0), γ (grp*t), [p_{pre}(grp), p₃₀(grp*T), p₆₀(grp*T)] + brown

Model	AIC_c	Δ AIC_c	w_i	L	K
ϵ GLOBAL - Υ (Flad-str), Υ (Cont=0)	903.75	0	0.42	1	25
ϵ GLOBAL - Υ (Flad), Υ (Cont=0)	904.18	0.44	0.34	0.80	24
ϵ GLOBAL - Υ (Flad=0), Υ (Cont=0)	906.14	2.40	0.13	0.30	23
ϵ GLOBAL - Υ (Flad-sea), Υ (Cont=0)	906.93	3.19	0.09	0.20	25
ϵ GLOBAL - Υ (Flad-str,sea), Υ (Cont=0)	909.40	5.66	0.02	0.06	27
ϵ GLOBAL - Υ (Flad-str,sea), Υ (Cont)	912.30	8.56	0.01	0.01	28
ϵ GLOBAL - Υ (Flad-str,sea), Υ (Cont,str)	915.19	11.44	0.00	0.00	29
ϵ GLOBAL - Υ (Flad-str,sea), Υ (Cont,sea)	915.24	11.50	0.00	0.00	29
ϵ GLOBAL	921.13	17.39	0.00	0.00	31

Appendix 6. We used a stepwise approach (Fig. 2) to model fladry efficacy. In step five we tested for variation in coyote activity among pre-fladry (p_{pre}) and post-fladry ($p_{30\&p60}$) units (last three models) and control camera units (Cont; first five models) using the γ GLOBAL model as the foundation for remaining parameter structures (see Appendix 5). We started by keeping a global structure on $p_{30\&p60}$ (see Appendix 2) and testing for effects of strata (str) and treatment (trt; control and treatment units) in p_{pre} . We found no effect of str or trt on p_{pre} and retained this structure for all pre-fladry cameras in the next set of models ($p_{pre}(\cdot)$). Next we maintained a global structure on post-fladry fladry treatment units ($p_{30\&p60}Flad$) including the effects of str, season (sea; first 30 days of fladry and second 30 days of fladry), and time trend (T) and tested for control unit ($p_{30\&p60}Cont$) variation in activity by str, sea, str and sea, variation only on control units (\cdot), and no variation from pre-fladry data ($p_{pre}(\cdot)=p_{30\&p60}Cont(\cdot)$). We found no variation in pre-fladry or control unit activity and retained this model as BASE GLOBAL for our primary modeling efforts (see Table 3). AICc = Akaike’s Information Criterion adjusted for small sample bias; w_i = AICc model weights; L = model likelihood; K = number of parameters in model.

γ GLOBAL: $\psi(\cdot)$, $\varepsilon(Flad)$, $\varepsilon(Cont=0)$, $\gamma(Flad, str)$, $\gamma(Cont=0)$, [p1(grp), p2(grp*T), p3(grp*T)] + brown

Model	AICc	Δ AICc	w_i	L	K
γ GLOBAL - $p_{pre}(\cdot)=p_{30\&p60}Cont(\cdot)$, $p_{30\&p60}Flad(str, sea, T)$	885.09	0	0.45	1	14
γ GLOBAL - $p_{pre}(\cdot), p_{30\&p60}Cont(\cdot)$, $p_{30\&p60}Flad(str, sea, T)$	885.94	0.86	0.29	0.65	15
γ GLOBAL - $p_{pre}(\cdot), p_{30\&p60}Cont(str)$, $p_{30\&p60}Flad(str, sea, T)$	887.42	2.34	0.14	0.31	16
γ GLOBAL - $p_{pre}(\cdot), p_{30\&p60}Cont(sea)$, $p_{30\&p60}Flad(str, sea, T)$	888.30	3.21	0.09	0.20	16
γ GLOBAL - $p_{pre}(\cdot), p_{30\&p60}Cont(str, sea)$, $p_{30\&p60}Flad(str, sea, T)$	890.68	5.59	0.03	0.06	18
γ GLOBAL - $p_{pre}(\cdot)$, $p_{30\&p60}(grp*T)$	900.38	15.29	0.00	0.00	22
γ GLOBAL - $p_{pre}(str)$, $p_{30\&p60}(grp*T)$	902.07	16.98	0.00	0.00	23
γ GLOBAL - $p_{pre}(trt)$, $p_{30\&p60}(grp*T)$	902.64	17.55	0.00	0.00	23
γ GLOBAL	903.75	18.66	0.00	0.00	25