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Improving evaluation of nonlethal tools for carnivore management and conservation: evaluating fladry to protect an endangered species from a generalist mesocarnivore

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Abstract

Carnivore conservation and management are global research priorities focused on reversing population declines of imperiled species and identifying more effective and humane management of generalist carnivores with thriving populations. Non-lethal methods to mitigate conflict are increasingly used to advance conservation objectives; however, there is limited knowledge about the effectiveness of many nonlethal methods. We tested a nonlethal tool (fladry), that serves as a barrier to deter wolves *Canis lupus* and coyotes *Canis latrans*, for its efficacy at preventing coyotes from using prairie dog *Cynomys ludovicianus* colonies, the primary prey for critically endangered black-footed ferrets *Mustela nigripes*. We used camera trap data and an occupancy approach to evaluate the tool's efficacy. We measured coyote response to fladry at both a coarse monthly scale (via use, attraction and avoidance probabilities) and a fine scale (via daily activity). Overall, use of areas inside exclosures declined by 60% after 60 days of fladry application and coyotes avoided some previously used areas both within and outside exclosures. Interestingly, coyotes were attracted to previously unused areas surrounding exclosures and increased activity around the periphery of fladry exclosures by 170% immediately after fladry installation, suggesting coyotes actively explored these areas and may have responded to fladry in a way that is counterintuitive to management expectations. Occupancy models provided more robust evaluation of fladry and revealed important behavioral responses relative to other common evaluation techniques (i.e. time until first detected crossing). Our results have implications for future development and evaluation of nonlethal tools for carnivore conservation and management globally.

Introduction

Carnivore conservation is increasingly focused on developing strategies that minimize predation threats of carnivores without negatively impacting their populations (van Eeden *et al.*, 2018). This need is critical for endangered carnivores whose conservation requires they coexist with people on shared landscapes (Ripple *et al.*, 2014), and in situations where the expansion of generalist carnivore populations (Arnold *et al.*, 2012; Hody & Kays, 2018; Drouilly & O'Riain, 2019) is threatening endangered species, livestock and pets and

human health and safety (Allen *et al.*, 2016; Hody *et al.*, 2019; Natrass, Drouilly & O'Riain, 2020). In both contexts, nonlethal tools are needed that prevent and mitigate predation (Gehring *et al.*, 2006; Shivik, 2006). For example livestock guardian dogs, motion-activated floodlights and fladry are nonlethal tools developed to disrupt, frighten and exclude carnivores from designated areas where conflict might otherwise occur.

Fladry is used as a disruptive stimulus to mitigate wolf *Canis lupus* predation on livestock (Okarma & Jedrzejewski, 1997) by taking advantage of wolves' inherent neophobia.

Fladry consists of a continuous strand of rope with strips of flagging sewn or tied to the rope at ~50 cm intervals and strung ~50 cm from the ground. Electrified fladry (i.e. turbo fladry) is a modification that carries an electric charge along the 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 on working ranches (Young *et al.*, 2019b). Fladry is now used in many parts of the world where nonlethal management of wolves is deemed necessary (e.g. Iliopoulos *et al.*, 2019). Although coyotes *Canis latrans* have similar neophobic responses to that of wolves (Mettler & Shivik, 2007), the horizontal spacing of flags on commercial fladry and turbo fladry is likely unsuitable for smaller-sized coyotes (Davidson-Nelson & Gehring, 2010). As a result, a recent captive study used the ratio of wolf body width to the horizontal spacing between fladry flags and narrowed the spacing of flags for use with coyotes (Young, Draper & Breck, 2019a). The study found that modified coyote fladry, when compared with commercial fladry, nearly doubled the duration of effectiveness when used with coyotes (Young *et al.*, 2019a); however, coyote fladry has yet to be tested in a field setting.

In this study, we use coyotes as a model species to demonstrate how nonlethal tools can manage the impacts of expanding mesocarnivore populations on other natural resources, such as endangered species. Coyotes have expanded their range by more than 40% in the past century (Prugh *et al.*, 2009; Hody & Kays, 2018) and their recent success has resulted in management challenges similar to those posed by other mesocarnivores (e.g. Gehrt, Riley & Cypher, 2010; Smith, McDonald & Wilkinson, 2012; Trouwborst, Krofel & Linnell, 2015). Coyotes have been identified as problematic in the recovery of imperiled species, where coyote predation can have significant impacts on small, vulnerable populations (Goodrich & 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). In addition, coyotes are considered the most important predator of the endangered black-footed ferret *Mustela nigripes* in prairie ecosystems, where they can cause substantial challenges in reintroduction efforts (Biggins, 2000; Breck *et al.*, 2006). Black-footed ferrets cannot exist without large populations of their primary prey species, prairie dogs *Cynomys* spp. (Biggins *et al.*, 1993; Biggins, Lockhart & Godbey, 2006), and have been reintroduced to prairie dog colonies throughout the western USA, where coyotes contribute to >65% of predation on reintroduced ferrets (Biggins *et al.*, 2006).

We used an occupancy framework to evaluate the efficacy of a nonlethal tool, turbo coyote fladry (hereafter, fladry), by measuring changes in coyote use, avoidance, attraction and activity of areas sampled by camera traps (Table 1). We tested fladry in a grassland ecosystem where black-tailed prairie dog (*C. ludovicianus*) colonies are a preferred habitat of coyotes (Krueger, 1986; Ceballos, Pacheco & List, 1999; Windell, 2019), and used fladry to protect portions of prairie

dog colonies identified as critical black-footed ferret habitat. Testing fladry in this setting presented both a unique ecological application for fladry and an environment where variation in biotic and abiotic factors that might influence predator use was relatively easy to measure (e.g. local prairie dog density, proximity to riparian areas, streams and roads).

Our overarching goal was to conduct the first field test of coyote fladry in an ecological context and evaluate fladry's efficacy in terms of use and activity. We had three objectives. First, to determine how fladry affected the probability of coyote use of areas within and directly outside of fladry exclosures. We expected to use within exclosures would abruptly decline with fladry application because coyotes would avoid previously used areas within fladry exclosures and then gradually increase to levels observed prior to installation as they became habituated to fladry (Table 1). Second, to determine how coyote activity changed due to the presence of fladry. We expected fladry would be highly disruptive and decrease coyote activity not only within fladry exclosures but also around the periphery of these areas. Alternatively, coyotes could increase activity around the periphery of fladry exclosures as they investigated the flagging, thus providing insight into the development of behaviors leading to greater conflict (Table 1). Finally, we compared our method of evaluation (i.e. occupancy) to a more common method of evaluating nonlethal tools (i.e. measuring the number of days until first detected crossing) to help evaluate the benefits of using an occupancy approach.

Materials and methods

Overview

We conducted our study on black-tailed prairie dog colonies in the northern unit of Badlands National Park (BNP) and the surrounding Buffalo Gap National Grasslands (BGNG) in southwestern South Dakota, USA (Fig. 1; Supporting Information Appendix S1). The study was conducted from August through December 2018 across 5875 ha of black-tailed prairie dog colonies in BNP and BGNG which together comprise the largest population of free-ranging black-footed ferrets (~115 individuals). Our study used fladry to protect critical black-footed ferret habitat (i.e. high-density prairie dog colonies). We used data from 2017 surveys to identify the largest intact colonies (>65 ha) with medium to high prairie dog density and known ferret presence. We identified seven prairie dog subcomplexes of varying sizes (Agate, Conata West, Heck Table, Lower Sage Creek, Prairie Wind, Sage Creek, Steer Pasture; hereafter, colonies) as our study area (Fig. 1; Table 2). All procedures for studying live animals were approved under USDA-NWRC Animal Care and Use Committee protocol QA-2886.

Fladry experiment

We modified standard turbo fladry to a narrower flag spacing of 27.9 cm (Young *et al.*, 2019a) and tested its effectiveness

Table 1 We tested the efficacy of modified turbo fladry for excluding coyotes *Canis latrans* from portions of prairie dog *Cynomys ludovicianus* colonies in South Dakota, USA from August to December 2018

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

Occupancy parameters were defined with respect to coyote response to fladry treatments. 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 expected 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).

at excluding coyotes from areas within fladry exclosures on each treatment colony (Fig. 1). To test the effectiveness of this tool, we used a randomized before-after-control-impact design within an occupancy framework. We focused our experiment in autumn because this is a critical period when ferrets, in particular kits emerging for the first time, are very vulnerable to predation and the use of temporary protection from coyotes could greatly enhance the conservation of this species (Breck *et al.*, 2006; Matchett, Breck & Callon, 2013). We randomized the assignment of control ($n = 2$) and treatment ($n = 5$) colonies (Table 2) using an unbalanced design (Shaffer & Johnson, 2008). Resident coyotes are territorial and utilize distinct home ranges, where areas they use more than 50% of the time are defined as core use areas (Schroeder, 2007). To minimize the chance of individual coyotes visiting more than one exclosure, all fladry treatments were separated by ≥ 1.5 km, the diameter of coyote core use areas in BNP and BGNP (Schroeder, 2007). Each of our five treatment colonies (where fladry exclosures were installed) enclosed 8 ha of prairie dog colony habitat (i.e. approximate size of female ferret core use area; Livieri & Anderson, 2012) and control colonies received no fladry for protection. All colonies were monitored using an array wildlife camera traps. Camera arrays and exclosures were placed near the center of each selected colony, where prairie dog density was observed to be highest (Fig. 1).

We used camera traps to collect coyote detection data and divided our prairie dog colonies into two strata. Our first stratum comprised the area inside the fladry exclosure and the second stratum was delineated as a 100-m buffer surrounding the exclosure (Fig. 1). Four cameras were placed in each stratum, yielding a total of 20 cameras per stratum on our five treatment colonies and eight cameras per stratum on our two control colonies (total of 56 cameras; Fig. 1). Although control colonies lacked exclosures, we installed cameras in the same arrangement. Sample units (hereafter, units) were defined as the effective area sampled by each

camera. Based on an average camera detection range of 30 m and a 45-degree field of view (Trailcampro.com, Springfield, MO), the effective area sampled by each camera was ~ 0.28 ha, or about 1/8 of the area within exclosures. As a result, each unit was considered independent; a coyote could easily use an area within or outside the exclosures and never have a chance of being detected by one of our cameras. Not assuming independence of our camera units would violate an important assumption of the occupancy analysis; namely, if a unit is used during a season, there is a nonzero chance of detecting that occurrence in a given survey (MacKenzie *et al.*, 2017).

We used active prairie dog burrows as focal points to increase coyote detection. All cameras were placed on t-posts, approximately 50 cm from ground level and 7.5 m from the center of the nearest active prairie dog burrow opening. To maximize interspersed, cameras inside the exclosure stratum were placed in each corner of the exclosure and pointed towards the center of the protected area. Cameras along the buffer stratum were systematically placed at equal intervals, from a random starting point, along the 100-m stratum buffer line and pointed at the nearest active burrow from a randomly selected cardinal azimuth (i.e. N, S, E, W).

We set up camera stations a minimum of 30 days prior to the trials to allow coyotes to condition to their presence. Following the conditioning period, we set cameras on all seven colonies and collected 30 days of detection data before fladry exclosures were installed. Following pre-fladry data collection, we constructed fladry exclosures on each treatment colony (Fig. 1). Fladry exclosures were established between 8 September 2018 and 2 October 2018, and were timed to be installed with the removal of livestock (i.e. cattle or bison) from United States Forest Service (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 and service cameras. Control sites did not require extensive maintenance and were

Figure 1 We tested the efficacy of modified turbo fladry for excluding coyotes *Canis latrans* from portions of prairie dog *Cynomys ludovicianus* colonies in South Dakota, USA from August to December 2018. Four wildlife cameras traps were deployed in the same pattern across each of two stratum on both control and treatment prairie dog colonies (colored polygons) used in our study (see Table 2 for more details about each colony). Square fladry enclosures (red line, panel a) protected approximately 8 ha of prairie dog colony habitat. The light red area within fladry enclosures formed the first stratum (fladry strata) and a 100 m buffer line (black dashed) surrounding the enclosure formed the second stratum (buffer strata; see the Fladry experiment subsection in Methods for details on camera placement). White stars on each prairie dog colony indicate the location of the camera array. White spaces between Badlands National Park (dark grey polygon) and Buffalo Gap National Grasslands (light grey polygon) represent privately held lands.

visited 1–2 times over the course of the study to service cameras.

Camera and covariate data

Three different brands of cameras traps were used in our study: Browning BTC Series ($n = 24$), Bushnell Trophy Series ($n = 21$) and Cuddeback Longrange IR ($n = 11$) and we systematically placed brands to ensure they were interspersed evenly among areas and strata within areas. While we programmed cameras similarly, camera brands are known to have variable detection ranges, fields of view and sensitivity (Meek, Ballard & Fleming, 2015), thus we included camera brand as a covariate on detection probability in all models (see Modeling approach below).

Camera data were processed using the Colorado Parks and Wildlife Photo Warehouse software (Ivan & Newkirk, 2016), where each photo of an animal was identified to species by two independent observers. We used raw camera data to evaluate the date of the first detection within each fladry enclosure and considered coyote detection events at each camera to be independent if detections were >1 h apart

(Lewis *et al.*, 2015; Lendrum, Crooks & Wittemyer, 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 camera trap days per camera site.

We hypothesized four variables could influence coyote use in our study area: distance to nearest riparian area; distance to nearest two-track road; distance to nearest 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 roads are ungraded vehicle paths that have been driven enough to wear distinct tire tracks and 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 expected 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, USA) and measured the nearest distance (m) to each of these features from our camera units.

Table 2 We tested the efficacy of modified turbo fladry for excluding coyotes *Canis latrans* from portions of prairie dog *Cynomys ludovicianus* colonies in South Dakota, USA from August to December 2018

Colony	Treatment	Size (ha)	Pre-fladry start	Fladry start	Fladry breakdown	Days to 1st crossing
Agate	Fladry	1518	8/9/2018	9/8/2018	11/7/2018	9
Heck table	Fladry	131	9/2/2018	10/2/2018	12/1/2018	23
Lower sage creek	Fladry	235	8/16/2018	9/15/2018	11/10/2018	Θ_1
Prairie wind	Fladry	234	8/9/2018	9/8/2018	11/7/2018	UKN
Steer pasture	Fladry	340	8/30/2019	9/29/2018	11/28/2018	Θ_2
Conata west	Control	359	8/11/2018	9/10/2018	11/9/2018	17
Sage creek	Control	325	9/1/2018	10/1/2018	11/30/2018	11

We used seven prairie dog colonies in our study, each of which received a random treatment assignment and varied in size, operational dates and raw number of days until first coyote detection within a fladry enclosure. We installed cameras 30 days prior (Pre-Fladry Start) to installing fladry enclosures (Fladry Start) and removed enclosures after 60 days (Fladry Breakdown). For control colonies no fladry enclosures were installed and the dates listed in the Pre-Fladry Start, Fladry Start and Fladry Breakdown columns represent corresponding time periods for which we monitored change in coyote use in our occupancy analysis. The number listed in the Days to 1st Crossing column for control colonies reflects the first coyote detection within the fladry strata (see Fig. 1). 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 (see the Modeling coyote use dynamics subsection in Methods for details on windstorm). 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.

We measured local prairie dog density by counting all burrows within a 30-m buffer of each camera, classifying each burrow as active or inactive. 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 density. We used a Welch two-sample *t*-test to explore differences in prairie dog density between control and treatment colonies and between stratum inside and outside fladry enclosures and found no differences (Supporting Information Appendix S2). We tested for correlation between our four habitat covariates using Pearson's product-moment correlation test and retained all covariates in our analysis as none of the correlations exceeded 0.70 ($|r| < 0.70$, Dormann *et al.*, 2013).

Measuring coyote use

Occupancy studies can use models that provide both fine- and coarse-scale measurements of a species' behavioral response (Table 1). We evaluated coyote use within and surrounding fladry enclosures using camera trap detection data and a dynamic (i.e. multi-season) occupancy framework (MacKenzie *et al.*, 2017). We define occupancy (i.e. Ψ) as the probability each unit is used by a coyote during a predefined season. 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) via two dynamic parameters; '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.*, 2017). These parameters are coarse-scale measurements of the species' avoidance (ϵ) or attraction (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; Sollmann *et al.*, 2013; Lewis *et al.*, 2015). 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).

Initial pre-fladry use, avoidance and attraction probabilities (Table 1) were modeled to estimate changes in coyote use in both strata (inside and outside fladry enclosures) over three 30-day seasons, for both treatment and control units. Each season consisted of 30 surveys (i.e. 24 h periods split at noon to capture the more crepuscular and nocturnal activity of coyotes; Andelt & Gipson, 1979; Kitchen, Gese & Schauster, 2000; Windell, 2019), where the first season measured coyote use and activity prior to fladry installation, and the second and third seasons measured coyote use and activity after fladry installation. We censored nine surveys from our detection histories for units on the Prairie Wind colony due to a windstorm with 55 + mph gusts that compromised the enclosure's structure. We also omitted the first crossing data for the Prairie Wind enclosure (Table 2); the first detection inside Prairie Wind occurred the day after the windstorm and likely did not reflect an actual crossing event.

The number of days until first crossing is presented separately from the occupancy framework. First crossing metrics are presented at the colony level and detail how long each fladry enclosure excluded coyotes.

Modeling approach

Given our occupancy models included many parameters (Table 1), we used a hierarchical approach to model a series of interconnected hypotheses (Fig. 2). Our initial model structure included interactions between stratum (str) and treatment (trt) on all model parameters (e.g. Ψ (str $\times$ trt)) including probabilities of use (Ψ), avoidance (ϵ), attraction (γ) and activity (p) probabilities for our three seasons. Additionally, we included seasonal (seas) variation in avoidance (ϵ (str $\times$ trt $\times$ seas)) and attraction probabilities (γ (str $\times$ trt $\times$ seas)) and a linear temporal trend in coyote activity following fladry installation (p_1 (str $\times$ trt), p_2 (str $\times$ trt $\times$ T), p_3 (str $\times$ trt $\times$ T)).

Using this initial model structure, we first investigated the effect of camera brand on detection (i.e. nuisance variation in our ability to detect coyotes; Supporting Information Appendix S3). Next, we modeled the effects of our habitat covariates on coyote use and tested for inherent variation in use between strata and treatments prior to fladry installation at treatment colonies (Ψ , Supporting Information Appendix S4). We then constructed a set of models to address specific hypotheses related to avoidance probability (ϵ) and attraction probability (γ ; Fig. 2, Supporting Information Appendix S5 and S6). Our *a priori* expectation was that coyotes would use camera units in control areas similarly throughout the study and exhibit no avoidance behavior between seasons and avoid previously used camera units inside exclosures immediately after fladry installation (ϵ_1). We tested similar structures for the probability of attraction (Fig. 2, Step 4; Supporting Information Appendix S6). Here, we expected that coyotes would exhibit no attraction to units on control colonies between seasons but, in contrast, would be attracted to units inside fladry exclosures during season 3 (γ_2), after they learned to overcome the fladry barrier.

Finally, we tested for variation in coyote activity associated or not associated with our fladry treatment (Fig 2, Step 5; Supporting Information Appendix S7). We expected similar activity at used camera units not influenced by fladry (i.e. coyote activity during the pre-fladry season and at control sites). We refer to this as our 'reference' activity level which serves as a comparison for our hypothesized responses at treatment units in the two stratum and across the second (p_2) and third (p_3) seasons when fladry had been deployed. We hypothesized that coyote activity at treatment units could: (1) decline linearly (trend, T) across surveys in both the second and third seasons, (2) decline linearly during second season followed by a plateau (P) during our third season and (3) remain constant (.), representing no change in coyote activity at used camera units during both the second and third seasons (Fig. 2).

We used Program MARK (White & Burnham, 1999) to conduct all occupancy analyses. We used AIC_c model selection (Burnham & Anderson, 2002) to identify the top model in each step from a limited set of *a priori* hypotheses (Fig. 2). The best supported model structures were those with the lowest AIC_c values and no uninformative parameters (Arnold, 2010; Leroux, 2019).

Results

Camera and covariate data

Cameras were functional for 4444 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 first, second and third seasons, respectively. Coyotes were detected at 30 of our 56 units over the course of our study: 22 units in season 1; 18 units in season 2; and 15 units in season 3. Detections at the units ranged from 1 to 4 days (i.e. surveys) in seasons 1 and 3 and 1–7 days in season 2. As expected, the number of days until first coyote detection within a fladry exclosure was highly variable ($\bar{x}$ = 37 + days, SE = 12 days, range = 9–60 days, n = 4; Table 2).

Dynamic occupancy analysis

Camera brand strongly influenced detection probability, with Browning cameras having a higher detection probability than our other two camera brands, Bushnell and Cuddeback (effect size on the logit scale: $\hat{\beta}$ = 1.44, 95% CI [0.92, 1.96]; Supporting Information Appendix S3). We retained this camera covariate in all models and report estimated detection probabilities for those units sampled with Browning cameras. We found little or no effect of habitat covariates on initial coyote use (Supporting Information Appendix S4).

The initial, pre-fladry use of prairie dog colonies by coyotes during the first of our 30-day seasons (season one) was high ($\hat{\Psi}_1$ = 0.80, 95% CI [0.56, 0.93]) across our entire study area but declined within exclosures after fladry application during season 2 ($\hat{\Psi}_2$ = 0.50, 95% CI [0.29, 0.72]) and further declined during season 3 ($\hat{\Psi}_3$ = 0.32, 95% CI [0.07, 0.57]; Fig. 3). When compared to control units, coyotes used units inside fladry exclosures 37% and 60% less during the second and third seasons, respectively. Coyote use also declined slightly outside fladry exclosures, where coyotes used units 12% and 8% less during the second and third seasons, respectively. As expected, coyote use and activity did not change over the three seasons at our control units (Supporting Information Appendix S5–S7). In contrast, we found evidence that coyotes avoided previously used units after fladry installation ($\hat{\epsilon}$ = 0.37, 95% CI [0.17, 0.63]; Supporting Information Appendix S5) but were attracted to previously unused units outside the fladry exclosure ($\hat{\gamma}$ = 1.00, Supporting Information Appendix S6).

Coyote activity was similar across all control and treatment units during the first season and remained at this same level at control units throughout the study (Supporting Information Appendix S7). We used this 'reference' activity level to compare to changes in activity at treatment units using our final set of seven candidate models (Table 3; Fig. 4). Several models in this final set had similar support (i.e. within $\sim 2\Delta AIC$ and held 9%–26% of the model weight); however, each model representing a hypothesized response to fladry was better supported than the model with no

Figure 2 We tested the efficacy of modified turbo fladry for excluding coyotes *Canis latrans* from portions of prairie dog *Cynomys ludovicianus* colonies in South Dakota, USA from August to December 2018. We used an occupancy framework and hierarchical approach to model selection to evaluate changes in coyote use, avoidance, attraction and activity at camera units in response to fladry. In each step, we asked a specific question (underlined text) and carried the best supported structure (in bold) forward to the next step. We first modeled nuisance detection variation due to camera brand (1), followed by coyote use (2) and then avoidance (3) and attraction (4) at control (Cont) and treatment (Flad) units. In our final two steps, we developed a reference level of activity from data prior to fladry installation (season 1) across all units and at control units in all seasons (5) before asking specific questions in regard to change in coyote activity at units inside (In) and outside (Out) fladry enclosures (6).

difference in coyote activity in response to fladry (Table 3). Furthermore, models consistently described a decreased level of activity inside fladry and increased level of activity outside fladry. We found that coyote activity at units within the enclosure declined after fladry installation and remained at this lower level for the duration of the fladry experiment ($\hat{p} = 0.03$, 95% CI [0.01, 0.06]; Fig. 4). Prior to fladry installation, coyotes used approximately 80% of the units, 1–

2 days per month, whereas post-fladry installation, coyote use of units within enclosures dropped to 32%–50% and they frequented those areas <1 day per month (Table 3, Figs 3 and 4). Outside fladry, we found that coyote activity initially increased ($\hat{p} = 0.14$, 95% CI [0.08, 0.24]) following fladry installation, before decreasing over the course of the next 60 days to activity levels similar to the reference level after ~50 days of application (Table 3, Fig. 4).

Discussion

Our study represents the first experimental field test and ecological application of fladry on coyotes and demonstrated that fladry excluded coyotes from protected areas for an average of 37 days ($SE = 12$ days). The benefit of decreased coyote use in protected areas was contrasted by increased coyote use outside the protected area. This could be important if the protected resource (e.g. black-footed ferrets) could travel outside the protected area. This highlights the importance of utilizing monitoring techniques that can provide deeper insight into the behavioral reaction of the mesocarnivore being managed.

We used a dynamic occupancy approach to assess fladry efficacy beyond the number of days the tool was effective and found that fladry decreased coyote spatial and temporal use within protected areas. Measures of use, avoidance and attraction provided information about which units coyotes used and how to 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). Relative to control units, coyote use of protected areas within fladry exclosures was reduced across both post-installation seasons. Use inside fladry exclosures decreased during the first 30 days of our experiment, and surprisingly, further decreased another 23% during the final 30 days (Fig. 3), suggesting that it may be beneficial to install fladry in advance of a critical protection period. 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. $\hat{\epsilon} = 0.37$). More interestingly, the patterns underlying attraction varied substantially inside and outside of fladry exclosures. Inside fladry exclosures coyote attraction was zero (i.e. $\hat{\gamma} = 0.00$), suggesting that when coyotes

Figure 3 We tested the efficacy of modified turbo fladry for excluding coyotes *Canis latrans* from portions of prairie dog *Cynomys ludovicianus* colonies in South Dakota, USA from August to December 2018. Coyote uses probabilities (Ψ) and associated 95% confidence intervals were derived for camera units on treatment colonies inside fladry exclosures (Inside Fladry) and outside fladry exclosures (Outside Fladry) during each season: pre-fladry (Reference) and two post-installation seasons representing the first 30 days of fladry application (Fladry 30) and second 30 days of fladry application (Fladry 60).

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 to previously unused areas was high (i.e. $\hat{\gamma} = 1.00$). This implies that even though we found coyotes avoided a subset of previously used units outside fladry exclosures (i.e. as described by our avoidance estimate), coyotes also explored previously unused areas surrounding the exclosure. However, when interpreting these results, it is important to consider that initial coyote use of prairie dog colonies was generally high (i.e. $\hat{\Psi}_1 = 0.80$).

Our estimates of coyote activity yielded information about how coyotes interacted with fladry at a fine temporal scale (Table 1). Although the 95% confidence intervals between estimates of activity during reference/pre-fladry time periods and post-fladry time period overlapped (Fig. 4), we believe our results support a biological impact of fladry on coyote activity. In the post-fladry installation period, 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 different pattern, where activity initially increased by more than 170% after fladry installation before gradually declining to

Table 3 We tested the efficacy of modified turbo fladry for excluding coyotes *Canis latrans* from portions of prairie dog colonies in South Dakota, USA from August to December 2018

Model	AIC _c	ΔAIC _c	w _i	−2Log (L)	K
$p_2 \& p_3 \ln(\cdot), p_2 \& p_3 \text{Out}(T)$	879.70	0	0.27	860.55	9
$p_2 \& p_3 \ln(\cdot), p_2 \& p_3 \text{Out}$ (seas $\times$ T)	880.30	0.60	0.20	856.59	11
$p_2 \ln(T), p_3 \ln(P), p_2 \& p_3 \text{Out}$ (seas $\times$ T)	880.72	1.01	0.16	854.68	12
$p_2 \& p_3 \ln(\cdot), p_2 \text{Out}(T), p_3 \text{Out}$ (P)	881.04	1.33	0.14	861.88	9
$p_2 \& p_3 \ln(\cdot), p_2 \& p_3 \text{Out}(\cdot)$	881.59	1.88	0.10	864.67	8
$p_2 \& p_3 \ln(T), p_2 \& p_3 \text{Out}$ (seas $\times$ T)	881.84	2.13	0.09	855.80	12
$p_2 \& p_3 \text{Flad}(\text{str} \times \text{seas} \times T)$	885.09	5.38	0.02	854.31	14

We modeled activity across the first (p_2) and second (p_3) 30 days of our fladry experiment both inside (In) and outside (Out) fladry exclosure stratum (Str) at treatment camera units to test three hypothesized responses. These structures include: (1) a constant ($\cdot$) activity level (no change); (2) a time trend (T) in activity across all 60 days of our experiment ($p_2 \& p_3 \text{Str}(T)$); and (3) a time trend in activity during the first 30 days of fladry application, followed a plateau (P) in activity in the second 30 days ($p_2 \text{Str}(T), p_3 \text{Str}(P)$). We used a general structure, $p_2 \& p_3 \text{Out}(\text{seas} \times T)$, to first test our hypotheses for activity within the exclosures and retained the best-supported structure to then test our hypotheses for activity at units outside fladry exclosures. See the Dynamic occupancy analysis subsection in Results for parameter structures supported in the previous steps of the analysis. Model selection statistics include: AIC_c = Akaike's Information Criterion adjusted for small sample bias; w_i = AIC_c model weights; −2Log (L) = negative log likelihood; K = number of model parameters.

Figure 4 We tested the efficacy of modified turbo fladry for excluding coyotes *Canis latrans* from portions of prairie dog *Cynomys ludovicianus* colonies in South Dakota, USA from August to December 2018. Daily coyote activity, with associated 95% confidence intervals, varied at units inside fladry exclosures (Inside Fladry; red), outside fladry exclosures (Outside Fladry; grey) and at control units (Reference; black). The first 30 days (Days 1–30; before blue vertical bar) reflect detection probability prior to fladry installation across all units. The following 60 days (Days 31–90; after blue vertical bar) reflect changes in activity in response to fladry. Estimates are obtained from the best-supported coyote activity model, $p_2 \& p_3 \ln(\cdot)$, $p_2 \& p_3 \text{Out}(\cdot)$.

reference level after ~50 days of application. This change in activity provides evidence that coyotes, either at the individual or population level, actively explored fladry, where changes in daily activity at units can be attributed to either variation in local coyote abundance or 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 spatial or temporal activity (Sih, Bell & Johnson, 2004; Réale *et al.*, 2007). As a result, increased activity around the outside of our fladry exclosures may have documented the behavior of an individual or individuals learning to overcome fladry (e.g. Young, Mahe & Breck, 2015).

The initial increase in use outside fladry exclosures indicates coyotes may have been attracted to the vicinity of exclosures to assess fladry risk (i.e. risk-assessment, predator inspection; Lima & Dill, 1990; Frid & Dill, 2002), where coarse-scale measures of attraction and avoidance provide information about the risk-assessment process over time (Table 1). Alternatively, fladry may have created a barrier for which activity that normally would have occurred within exclosures was displaced to the periphery of exclosures, therefore resulting in higher detection of coyotes at these locations. This could have resulted because exclosures removed 8 hectares of an average 1430–1520 ha coyote home range (Schroeder, 2007), accounting for a 0.56%–0.53% reduction in home range size. Given the emerging importance in understanding how behavior influences conflict (Blackwell *et al.*, 2016; Breck *et al.*, 2019; Greggor, Berger-Tal & Blumstein, 2020), future studies could better understand intraspecific variation and development of these behaviors by supplementing occupancy data with movement data from marked or telemetered individuals.

Our study used fladry to protect small, high-density portions of prairie dog colonies occupied by endangered black-footed ferrets and decreased coyote use of these areas. Due to inherent challenges associated with monitoring the survival and movements of black-footed ferrets (e.g. small sample sizes, fossorial activity, difficulties affixing transmitters), we could not provide definitive evidence for how coyote exclusion influenced ferret populations, nor is it clear if excluding coyotes from larger areas (i.e. entire prairie dog colonies) provided additional protection to ferrets or increased coyote motivation to enter exclosures. Related to these questions is the need for increased understanding about how coyote motivation to access wild prey translates to domestic livestock scenarios and vice versa, similar to past studies with wolves (e.g. Musiani *et al.*, 2003). Testing the efficacy of coyote fladry for protecting livestock is an important next step for robust evaluation of this nonlethal tool because coyotes are the primary predator of livestock in the U.S. (USDA APHIS, 2015a,b).

We encourage future nonlethal tool studies to employ an occupancy framework to quantify the behavioral response of carnivores to a given tool. 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 effective for monitoring wildlife across large areas and evaluating nonlethal tool efficacy. Better development of effective tools and understanding of carnivore reactions to them will be critical endeavors as we strive to coexist with threatened and thriving carnivore populations throughout the world.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Study area.

Appendix S2. Local prairie dog density.

Appendix S3. Detection models.

Appendix S4. Coyote use models.

Appendix S5. Avoidance models.

Appendix S6. Attraction models.

Appendix S7. Activity models at control units.