

Black-tailed prairie dog, *Cynomys ludovicianus* (Sciuridae), metapopulation response to novel sourced conspecific signals

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Aggregation of territorial individuals within a species can be facilitated via conspecific signals, wherein settlement implies habitat suitability, ease of resource acquisition and/or increased predator detection. The black-tailed prairie dog is a colonial small mammal with alarm vocalizations that confer benefits via group vigilance against predators and increased foraging time. Although prairie dog alarm calls are relatively well understood, the information embedded in their jump-yip call, which includes both a distinct cry and a bodily gesture, remains less clear. We evaluated prairie dog behaviour in response to conspecific acoustic signals using playbacks of alarm and jump-yip calls at 26 sites in northeastern Wyoming, U.S.A. Recorded calls from an isolated colony were broadcast to a mean of five individuals per site, and behavioural responses were compared against uninfluenced behaviour and a control playback of ambient sounds. The alarm playback caused prairie dogs to increase vigilance 122% and decrease foraging time 23%, demonstrating prairie dogs will shift behaviour based on signals from individuals of an unfamiliar colony. However, the alarm call playback reduced frequency of the jump-yip behaviour only at colonies nearest the recording source. The jump-yip playback caused unfamiliar prairie dogs to display 339% more jump-yips than uninfluenced behaviour. The jump-yip playback did not alter recipients' foraging or vigilance behaviours relative to control treatments, suggesting that although prairie dogs can understand and reciprocate an unfamiliar, single modality signal, they may not shift other behaviours based on this stimulus. As such, the purpose and benefits of the jump-yip call remain unclear. Playback efficacy also had a nonlinear relationship with distance from recording source. Our work improves understanding of communication at the metapopulation level, examines the potential role of the jump-yip and provides insights for how conspecific signals might be used as a management tool.

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Information is routinely perceived, processed and used by animals in the wild to make decisions that reduce uncertainty (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005). Collectively, information is received from multiple sources over varying spatio-temporal scales to acquire food resources, select breeding habitat, locate potential mates or avoid predators (Schmidt, Dall, & van Gils, 2010). Information broadcast through conspecific signals can increase animal reproductive success and survival at the population

level (Courchamp, Clutton-Brock, & Grenfell, 1999). Conspecific cues may contain information about habitat quality (Alatalo, Lundberg, & Bjorklund, 1982; Stamps, 1988), resource availability (Pärt & Doligez, 2003), predator threat and context (Loughry, 1987; Slobodchikoff, Kiriazis, Fischer, & Creef, 1991) and optimal mate selection (Dugatkin & Godin, 1993; Grady & Hoogland, 1986), and an animal may use this information to enhance its fitness. The specific mechanisms underlying conspecific cues vary by species; examples of cue modalities include chemical cues in spiny lobsters (*Panulirus interruptus*; Zimmer-Faust, Tyre, & Case, 1985), visual cues in anole lizards (*Anolis aeneus*; Stamps, 1988) and auditory signals in pied flycatchers, (*Ficedula hypoleuca*; Alatalo et al., 1982). Some animals use a combination of cue modalities, including bird species that perceive both auditory and visual cues (Schlossberg & Ward, 2004).

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Research on conspecific signals in the wild has advanced from basic scientific experiments into more applied investigations of how cues might be used to influence dispersal or breeding success in avian and amphibian species (DeJong, Cowell, Nguyen, & Proppe, 2015; Hahn & Silverman, 2007; James, Stockwell, Clulow, Clulow, & Mahony, 2015; Ward & Schlossberg, 2004). Despite demonstrations of the role of conspecific cues and signals for habitat selection and fitness outcomes (Danchin, Boulinier, & Massot, 1998; Stamps, 1988), the functionality of many cues remains unclear for numerous taxa. Moreover, how the language or dialects used to transmit various conspecific cues and signals may vary over space and time within regional metapopulations is also unknown. Signals used within a metapopulation across a regional landscape can be subjected to spatiotemporal attenuation of their usefulness (Marten & Marler, 1977; Perla & Slobodchikoff, 2002); i.e. they could carry negative implications for dispersing individuals. Basic experiments that document the behavioural responses of regional metapopulations to conspecific signals are needed to shed light on the meaning of various signals and pave the way for future work exploring the potential utility of conspecific cues for regional-scale conservation or management applications.

Prairie dogs (*Cynomys* spp.) represent a model organism for inferring the functionality of conspecific signals in the wild for a social small mammal (Shier & Owings, 2007). Prairie dogs are colonial ground-dwelling rodents that aggregate in small familial territories (i.e. coterries) that are grouped together to form larger conspecific territories (i.e. colonies; Grady & Hoogland, 1986). The prairie dog's complex social and vocal communications make it uniquely suited to respond to conspecific signals, and benefits of gregarious interactions include optimized foraging time as a result of community-level antipredator vigilance (Hoogland, 1979, 2006). Furthermore, the utility and function of conspecific signals within prairie dog communities warrants additional study because prairie dogs provide numerous benefits to other flora and fauna through their roles as ecosystem engineers, foundation species and keystone species (Hoogland, 2006; Jones, Lawton, & Shachak, 1994).

All species of prairie dogs issue alarm calls that are solely auditory cries and have been decoded for vocabulary, cognitive recognition and intercolony dialect (Frederiksen & Slobodchikoff, 2007; Kiriazis & Slobodchikoff, 2006; Slobodchikoff, Paseka, & Verdolin, 2009; Smith, Smith, Oppenheimer, & Devilla, 1977). Unique to the black-tailed prairie dog, however, is the jump-yip call, the embedded message of which remains a source of speculation. The jump-yip, which entails a black-tailed prairie dog rising onto its hindlegs while producing a unique high-pitched call, is a contagious display reciprocated by individuals throughout the colony. Few studies have attempted to decipher the jump-yip and existing studies have generated mixed results. Early research described the jump-yip as a 'territorial call' (King, 1955) whereas more recent qualitative assessments suggested the signal conveys the resolution of a conflict or threat (e.g. a dispute has been resolved or a predation threat has passed; Hoogland, 2006; Smith, Smith, Devilla, & Oppenheimer, 1976). One recent quantitative study concluded the jump-yip vocalization is a 'roll call' used to assess community vigilance against predators and resulted in increased foraging time for the call instigator (Hare, Campbell, & Senkiw, 2014). The benefits to the reciprocators, however, were unquantified and remain unclear.

Prairie dogs exhibit phenotypic variation at local and regional scales within a population (Gibert, 2016). Gunnison's prairie dogs, *Cynomys gunnisoni*, for example, have unique dialects at the local and regional scale (Perla & Slobodchikoff, 2002), with attenuation of the acoustic structure of alarm calls occurring as geographical distance increases across a region (Slobodchikoff, Ackers, & Van Ert,

1998; Slobodchikoff & Coast, 1980). Although dialect and attenuation of alarm and jump-yip calls by black-tailed prairie dogs may be presumed based on research with Gunnison's prairie dogs, it has not been confirmed. If spatiotemporal attenuation occurs in black-tailed prairie dog metapopulations, it could have significant implications for dispersing black-tailed prairie dogs, as individuals may encounter dialect variation or mismatch when encountering new populations. Determining whether behavioural responses vary with distance from a playback source could provide inference for whether further research on signal attenuation in this species may be a fruitful line of inquiry.

We investigated behavioural responses to conspecific signals used by black-tailed prairie dogs through a field experiment within a black-tailed prairie dog metapopulation. We used auditory playbacks of alarm and jump-yip calls to determine (1) an animal's ability to perceive signals originating from an unfamiliar individual (noncolony member), (2) effects of a single-modality display of a multimodal signal, (3) whether recipients of the jump-yip alter vigilance time or foraging time after receipt of conspecific signals and (4) whether behavioural responses vary based on distance from the playback recording location. We predicted that prairie dogs would (1) demonstrate recognition of cues from an unfamiliar individual by increasing vigilance and decreasing foraging time in response to the alarm call playback, when compared to a control of uninfluenced behaviour (no-playback) and a second control playback of ambient sounds (hereafter, control), (2) demonstrate recognition of the jump-yip call by issuing the jump-yip in response to the jump-yip playback, despite the absence of an accompanying visual display, (3) increase foraging time and reduce vigilance time during the jump-yip playback call and (4) display weaker behavioural responses to playbacks of the alarm and jump-yip calls as colony distance from the playback recording location increased. We reasoned that findings supporting these predictions could illuminate the functionality of conspecific signals by black-tailed prairie dogs and specifically, the mystery of the jump-yip call.

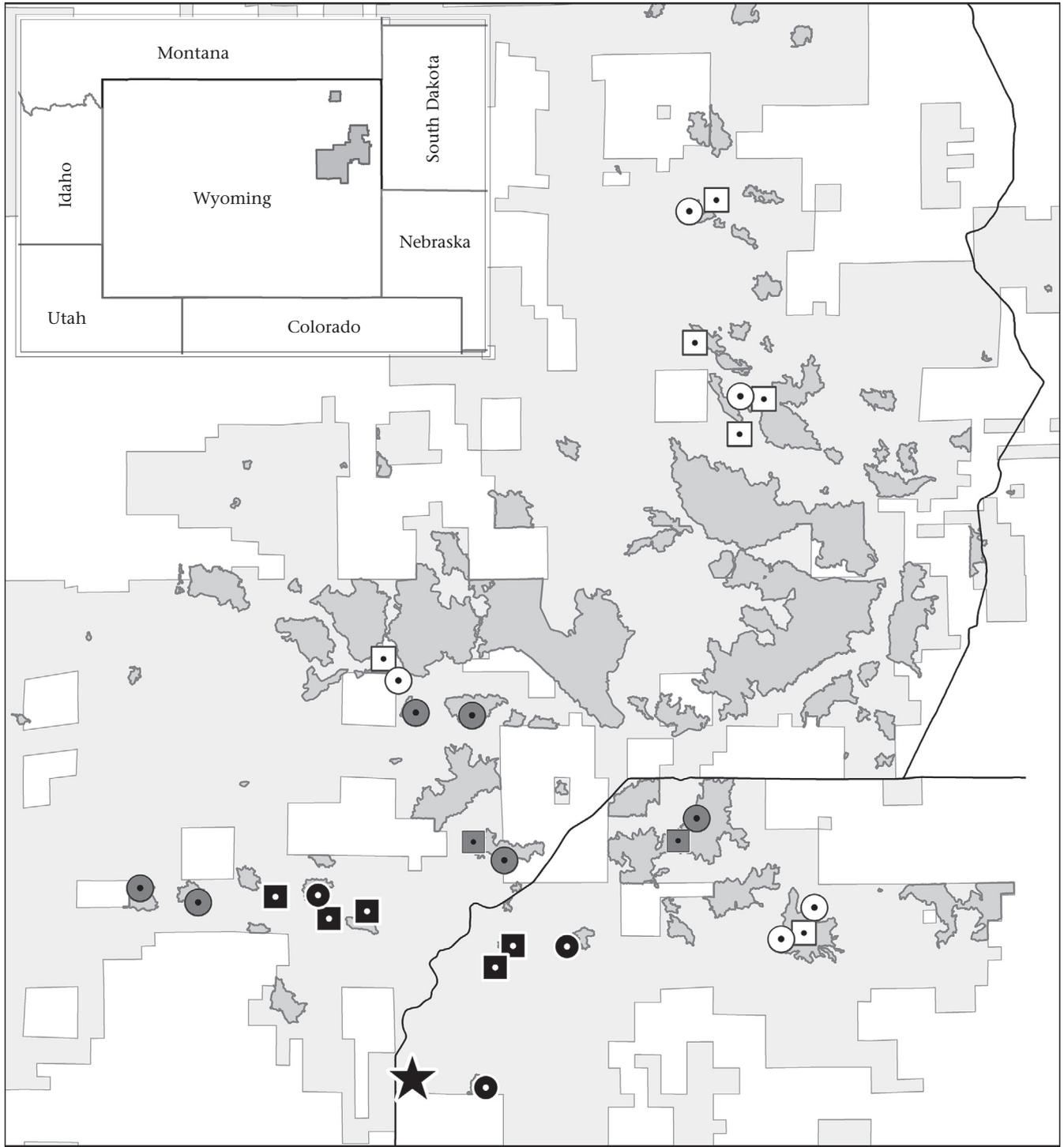
METHODS

Site Description

Our study was conducted in the Thunder Basin National Grassland (Thunder Basin) in northeastern Wyoming, U.S.A., on public land managed by the U.S. Forest Service. Thunder Basin is a 1.7-million-acre mosaic of privately owned land (64.4%) and public land managed by the U.S. Forest Service (29.3%) and the state of Wyoming (6.3%). Precipitation averages 250–300 mm annually (Porensky & Blumenthal, 2016), and Thunder Basin is situated on the ecotone of northern mixed-grass prairie and sagebrush steppe. Elevation within Thunder Basin ranges from 1097 m above sea level in the south to 1585 m above sea level in the north. These rangelands are managed for domestic livestock grazing, wildlife habitat, recreation and mineral extraction. Prairie dogs are often lethally managed on most private lands and largely protected from recreational shooting and poisoning on public lands, however, in 2017 the U.S. Forest Service lifted all shooting restrictions for prairie dogs on publicly owned land.

Site Selection Criteria

Experimental sites were randomly selected within prairie dog colonies located on public land managed by the U.S. Forest Service with no evidence of prairie dog shooting. Sites were ≥ 0.8 km from roads or powerlines to minimize confounding behavioural responses to traffic or avian predators, and accessible for



Experiment sites (distance from playback source)

2016	2017	
■	●	Near (0–7250 m)
■	●	Mid (7251–12 000 m)
□	○	Far (12 001–28 139 m)

★ Playback source

■ Public land (USFS)

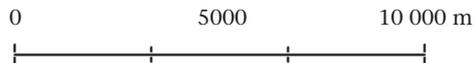


Figure 1. Locations of black-tailed prairie dog colonies, playback recording source and experiment sites within Thunder Basin National Grassland, in northeastern Wyoming, U.S.A. in 2016 and 2017. The distance from playback recording source to experiment site are represented in categories of near, mid and far, and correspond to model construct.

observations from an off-colony location. Sites were separated by at least 1 km within the same year, resulting in all but two experiments being conducted on separate and spatially distinct colonies (Fig. 1). Two experiments were conducted on a single colony but situated >1400 m apart. The distance between site locations ensured experiment playbacks were isolated from one another. This ruleset, in combination with time and access constraints, resulted in experiments on 14 colony sites in 2016, five of which were revisited in 2017, as well as seven new colony sites established in 2017.

Behavioural Observations

We conducted 26 playback experiments during 15 May–30 June in 2016 and 2017. We timed experiments to coincide with peak intercolony dispersal time for male yearlings (Garrett & Franklin, 1988) to address the potential application of using playbacks of conspecific signals to influence prairie dog dispersal behaviour. Each experiment consisted of three observational phases, performed in sequential order: (1) uninfluenced prairie dog behaviour without an audio playback ('no-playback'), (2) prairie dog behaviour during a playback of ambient sounds (western meadowlark, *Sturnella neglecta*, songs and calls), insect noises and other landscape sounds recorded <1.6 km from the recording source for treatments ('control') and (3) prairie dog behaviour during playback of either alarm or jump-yip calls ('treatments'). Each observation type was conducted for 10 min for a total of 30 min at each site. We recorded individual behaviours of prairie dogs using focal sampling (Altmann, 1974; Hirschler, Gedert, Majors, Townsend, & Hoogland, 2016). Each site experienced only one type of treatment playback, either alarm call or jump-yip, and assignment of treatment playback was determined randomly by coin toss (alarm: $N = 12$; jump-yip: $N = 14$).

All playback sounds (control and treatments) were recorded on-location in Thunder Basin in May 2016 from a nonexperimental colony with a Zoom H4nSP 4-Channel Handy Recorder (<https://www.zoom-na.com/>) in a .wav file format recorded in stereo at a frequency of 44 kHz and edited into 5 min soundtracks with approximately 30 s of audio alternating with 30 s of silence using Audacity v.2.1.2 (<http://audacity.sourceforge.net>). The resulting soundtracks were broadcast on a continuous loop using Primos Alpha Dogg Electronic Predator Caller (Primos Hunting, Flora, MS, U.S.A.). Behavioural observations were recorded with a video camera from an off-colony location behind a camouflaged ground blind, and the playback speaker was hidden behind shrubs or tall grass (Fig. 2). Playback volumes were variable between sites due to unique site conditions (e.g. unique distance from focal area to speaker, and wind and topography) and appropriate volumes for each site were determined with a brief test of the control playback during experiment set-up; playbacks were broadcast at an average of 53 dB at an average distance from speaker to focal area of 72 m. We recorded each call type at a single origin to determine how behavioural responses vary with distance, which may be related to prairie dog language variation across a regional metapopulation.

We defined the sample size of each site as the number of individuals visible in the camera field of view within the first 20 s of each observation treatment. Sample size was determined independently for each observation treatment (no-playback, control, treatment) within each experiment. We excluded pups (i.e. juveniles emerged from the natal burrow that year, identified based on size) from our data set because their behaviour can be erratic while they practise social signals. However, we were unable to consistently distinguish between male and female prairie dogs and therefore pooled both sexes in analyses. Individuals too distant to accurately observe or those who entered the camera frame after this time were excluded from observation. Observations concluded

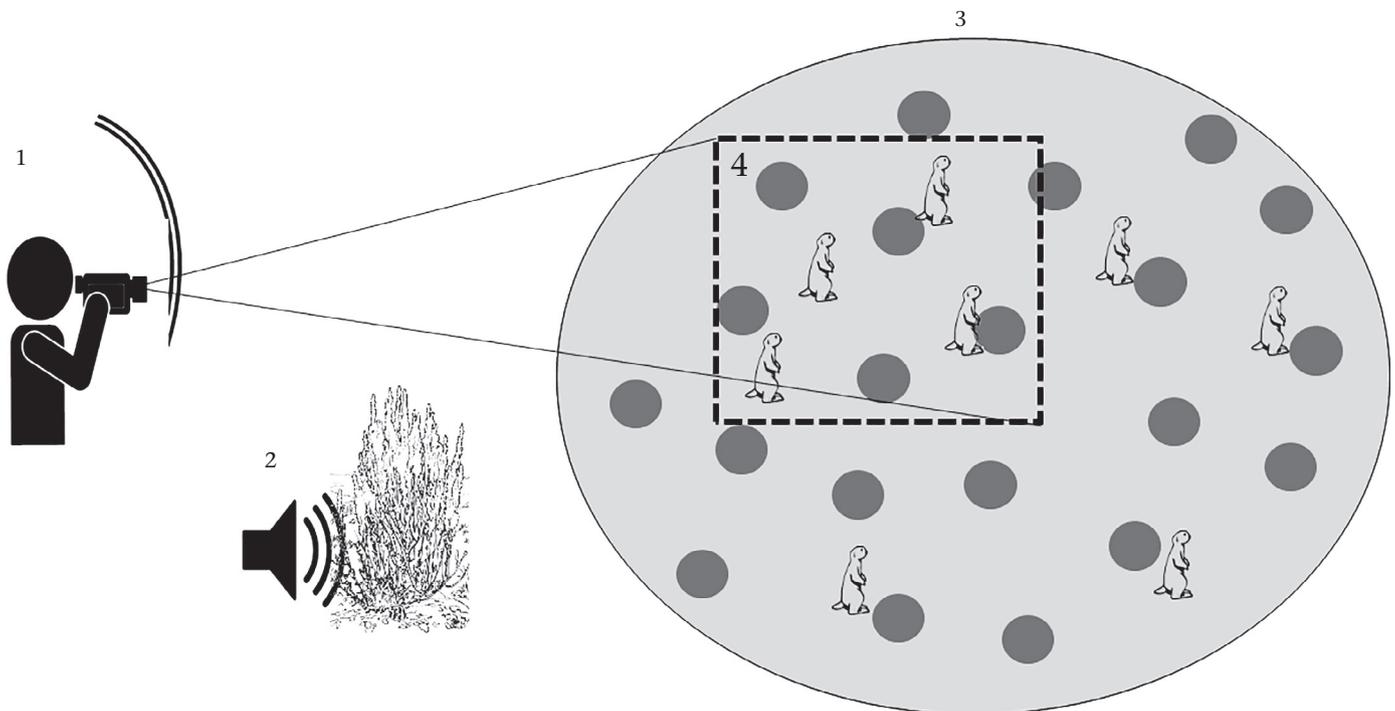


Figure 2. Design of experiment playback, where (1) observers with video cameras were situated at an off-colony location behind a hunting blind, (2) speakers were situated at an off-colony location behind natural cover (i.e. tall grass or shrubs), (3) experiment sites are focal prairie dog colonies and (4) sample size is the number of black-tailed prairie dogs in the camera's field of view within first 20 s of the observation period (in this diagram $N = 4$). Three observation treatment classes were conducted in sequential order (no-playback, control playback and treatment playback) at each colony site ($N = 26$).

Table 1
Description of black-tailed prairie dog behaviours and their categorical classification

Activity	Description
Nonvigilant behaviours	
Foraging	Searching for, or consuming forage. Includes movement between foraging patches and secondary activity of observing surroundings while masticating forage
Resting	Inactivity without vigilant posture (includes sunbathing)
Jump-yip	Performing the jump-yip call
Grooming	Self-grooming
Excavating Burrow	Kicking dirt, nose-pounding of burrow mount, etc.
Socializing	Nonaggressive interactions with other individuals, including group grooming or kissing
Dusting ^a	Dust bath (kicking or rolling in dust)
Passive Watching	Forage intake and mastication has ceased but individual is not exhibited signs of vigilance (as described below)
Fighting	Aggressive interaction with another individual
Vigilant behaviours	
Vigilant watching	Attentively watching surroundings, including running to burrow or posturing for better view of surroundings. All nonvigilant behaviours, as described above, have ceased
Alarm call	Performing the alarm call

^a Dusting has been described as an activity in which prairie dogs partake (Hoogland, 2006), but we did not observe this activity in our observation of treatments.

when the treatment duration of 10 min ended, or the individual was no longer visible (e.g. exited camera frame, went into burrow or behind tall vegetation; Altmann, 1974; Bryan & Wunder, 2014).

Sample size and duration of observation across individuals varied due to our *a priori* ruleset. Although we could distinguish between individuals within a single treatment, we were unable to distinguish individuals across treatment types because they lacked identifying tags or markings. Due to these constraints, our data represent observations of aggregate adult prairie dog behaviour, and not individual responses across treatments. Observations of individuals ranged from 10 s to 10 min in duration across treatments, with an average observation of 5.52 min. Across all treatments and sites, we recorded 388 observations of prairie dog behaviour (Appendix, Table A1).

Ethical Note

Methods of research were approved by the Institutional Animal Care and Use Committee (IACUC) at the University of Wyoming (Protocol no. 20160509LC00237-01) for the 2016 field season and exempted in 2017. Methods of research followed guidelines of the American Society of Mammalogists (Sikes, Gannon, & The Animal Care and Use Committee of the American Society of Mammalogists, 2011). We did not capture, mark, tag, transport or retain any animals during our study. Disturbance of animals in the wild was minimized as all experiment sites were approached on foot and observations were conducted discretely behind a hunting blind. No duress or pain was experienced by observed individuals. Our interactions with the focal species occurred indirectly through playbacks of prairie dog calls.

Data Analysis

We reviewed individual prairie dog behaviour videos in JWatcher v.1.0 (<http://www.jwatcher.ucla.edu/>) to record activity type and duration. The start and end times of prairie dog behaviours were recorded by unique activity type. Activities were grouped as vigilant or nonvigilant behaviour according to energy intake and expenditure associated with each activity (Table 1). For example, prairie dogs commonly clip forage and consume it while standing upright on their hindlegs to survey for predators. Although this activity includes a vigilant component of predator surveillance, forage intake and mastication is not interrupted, and therefore this activity was categorized as foraging (Magle & Angeloni, 2011; Shannon, Angeloni, Wittemyer, Frstrup, & Crooks, 2014; Winnie & Creel, 2007). Conversely, activities

categorized as vigilant behaviour included instances of prairie dogs ceasing normal activities, including foraging, to run to their burrow for safety, thus ceasing forage intake and expending energy in their vigilant activity.

We calculated the proportion of total observation time that each individual spent vigilant and foraging. For each individual, we also calculated a standardized index of jump-yip frequency per 10 min observation period. For each different treatment type within each site, behavioural responses were averaged across all sampled individuals before analysis. We used linear mixed models to determine whether foraging, vigilance and jump-yip frequency varied across observation treatment types and distance from playback source. Our independent variables included treatment type (no-playback, control playback, alarm call playback or jump-yip call playback), distance from source of recording to experiment site, expressed as three categorical values of near (0–7250 m), mid (7251–12 000 m) and far (12 001–28 139 m), and a treatment interaction. Distance cutoffs were determined by identifying natural breaks in the distance data, which were not normally distributed. Our random effects included site and year. Response variables included proportion of time spent vigilant, proportion of time spent foraging and frequency of jump-yip behaviour. All linear mixed effects models were executed in JMP v.12.0.1 (https://www.jmp.com/en_us/software.html). Data were transformed when necessary to meet model assumptions of normality and homoscedasticity, and results are presented as means \pm SE.

To further understand the complexity of prairie dog behaviour to playback treatments, we utilized a partially constrained canonical correspondence analysis (CCA) with supplemental covariates to summarize the variation in relative frequency of multiple prairie dog behaviours in a single analysis considered to be reflective of behaviour composition. This approach allowed us to visualize trends in the composition of behaviours, including the presence/absence and frequency of individual behaviours, and examine how behaviours might be influenced by treatments (Kazmaier, Hellgren, & Synatzske, 2001; Riechert, 1978). We represented behavioural response as a proportion of time spent on each activity type (Table 1). Treatment type (no-playback, control, alarm, jump-yip playbacks) was used as the primary constraining explanatory variable and distance from source of recording to experiment site was used as a supplementary covariate. All constrained axes were tested for significance ($P > 0.05$) using a permutation test with 999 iterations and random seed number generator. Ordination analyses were conducted in Canoco v.5 (<http://www.canoco5.com/>) (ter Braak & Šmilauer, 2012).

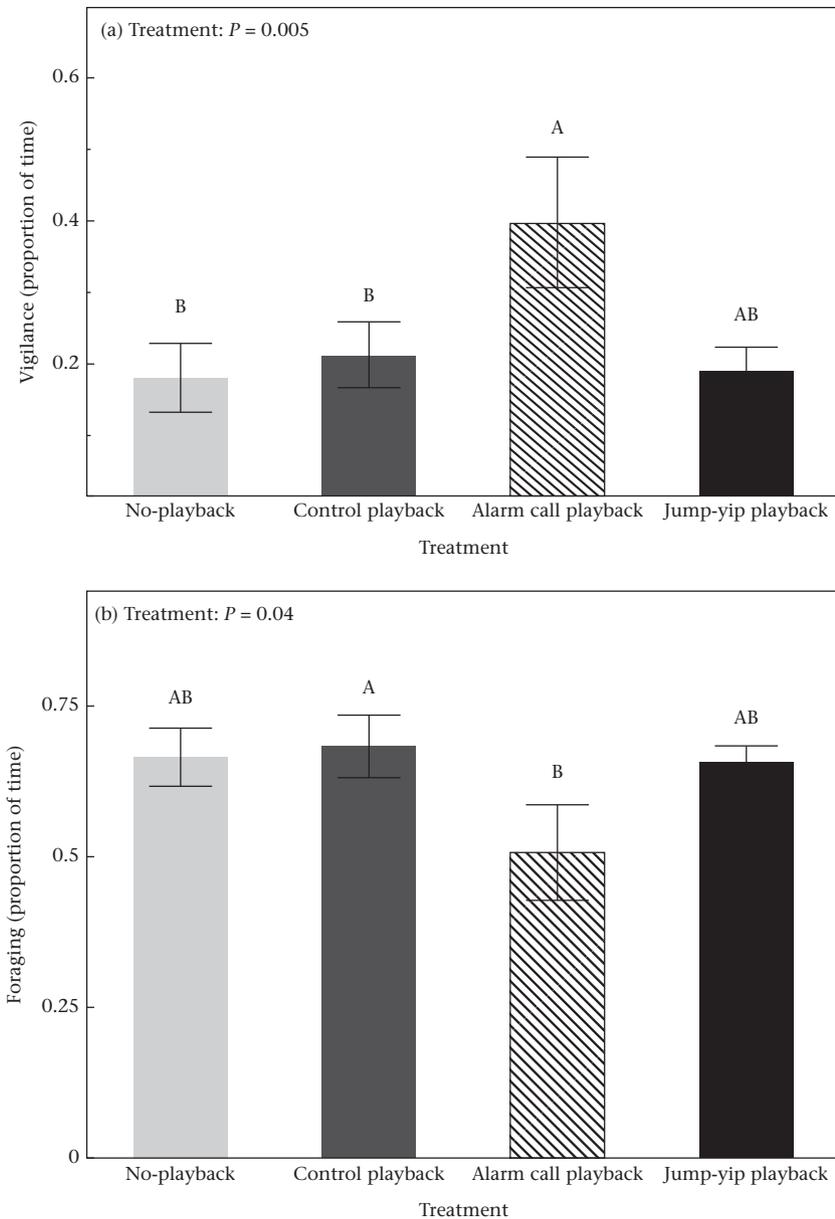


Figure 3. Black-tailed prairie dog average individual proportion of time spent (a) vigilant and (b) foraging, by treatment type. These results are based on data from behavioural observations across 26 sites in northeastern Wyoming, U.S.A. in 2016 and 2017. Error bars show \pm SE.

RESULTS

Proportion of Time Spent Vigilant

The proportion of time prairie dogs spent vigilant was 122% higher during the alarm call playback (0.40 ± 0.1), when compared to the control playback (0.21 ± 0.05) and the no-playback (0.18 ± 0.05 ; $P = 0.005$; Fig. 3a). Vigilance during the jump-yip playback was not significantly different from any other treatment (0.19 ± 0.03). Vigilance responses to playback treatments were not significantly affected by distance to source of playback recording (treatment*distance $P = 0.09$).

Proportion of Time Spent Foraging

Prairie dogs exhibited the greatest proportion of time spent foraging during control playback (0.68 ± 0.05) and decreased their

proportion of time foraging by 23% during the alarm call playbacks (0.51 ± 0.08 ; $P = 0.04$; Fig. 3b). Prairie dogs spent an intermediate amount of time foraging during the jump-yip playbacks (0.66 ± 0.03) and no-playback (0.66 ± 0.05 ; Fig. 3b). Foraging responses to playback treatments were not significantly affected by distance to source of playback recording (treatment*distance: $P = 0.4$).

Performance of the Jump-Yip Call

Across distances, prairie dogs significantly increased their performance of the jump-yip call during the jump-yip playbacks (3.12 ± 0.7) when compared to the alarm playbacks (276% increase; 0.83 ± 0.34) and no-playback (339% increase; 0.71 ± 0.26 ; main effect of treatment $P < 0.0001$; Fig. 4). However, distance from the recording source significantly altered the influence of treatment type on jump-yip performance (treatment*distance: $P = 0.01$). At

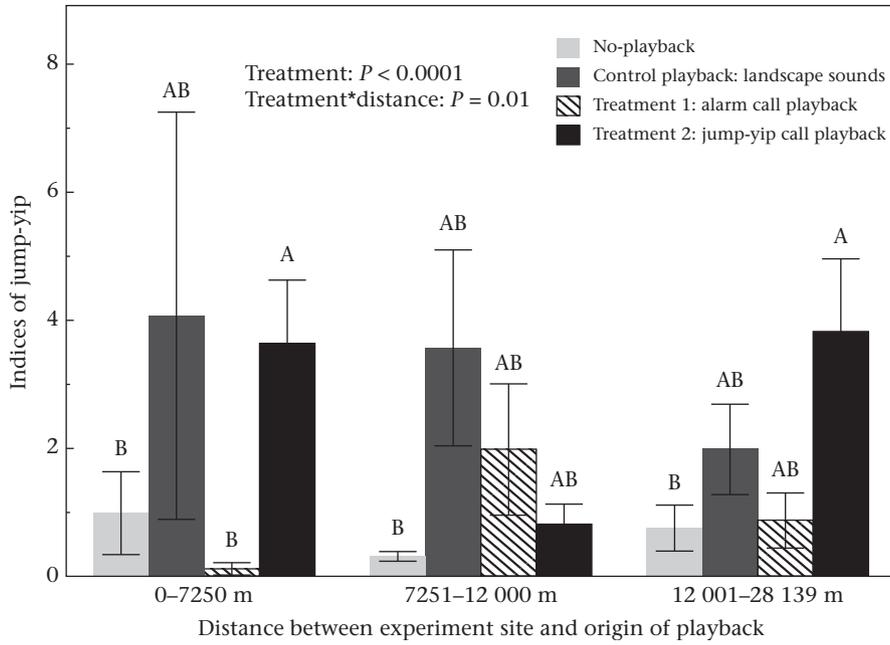


Figure 4. Black-tailed prairie dog frequency of jump-yips performed during each playback treatment. These results are based on data from behavioural observations across 26 sites in northeastern Wyoming, U.S.A. in 2016 and 2017. Error bars show \pm SE.

near and far distances, jump-yip reciprocation during the jump-yip playbacks was significantly greater than jump-yip reciprocation during the no-playback treatment (Fig. 4). Moreover, at the nearest distance, jump-yip reciprocation during the jump-yip playbacks was significantly greater than jump-yip reciprocation during the alarm call playbacks (Fig. 4). Levels of jump-yip reciprocation during all other combinations of playbacks and distance were intermediate (Fig. 4).

Influence of Playback Treatments on Behaviour Composition

In our partially constrained CCA of prairie dog behavioural composition, Axis 1 explained 58% of the fitted variation, was largely a function of the alarm playback, and vigilant activities were spatially distinct in ordination space from nonvigilant activities along this axis (e.g. foraging, resting, grooming; Fig. 5). Vigilance was associated with alarm playbacks, while nonvigilant

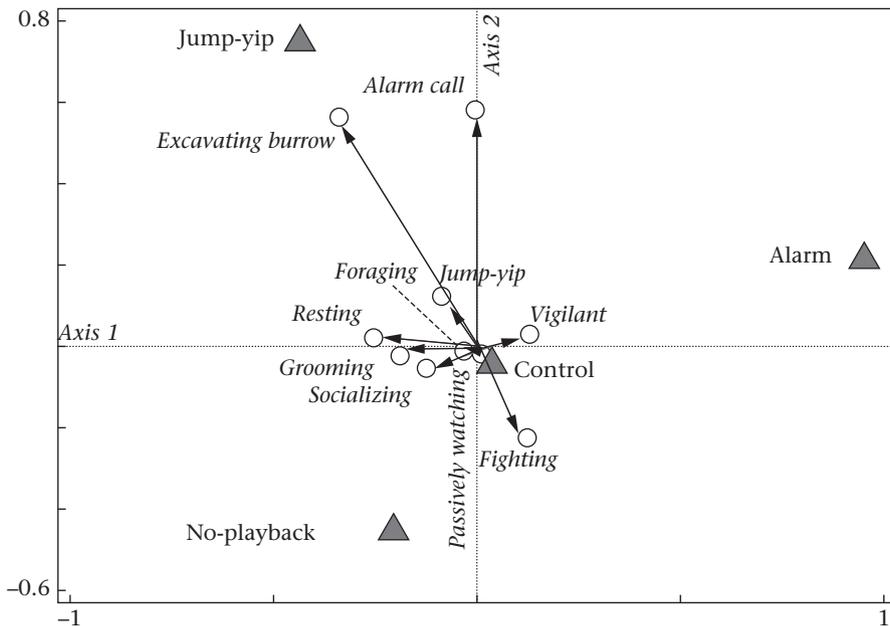


Figure 5. A partially constrained canonical correspondence analysis (CCA) ordination of all black-tailed prairie dog activities during all playback treatments revealed Axis 1 (X axis) explained 58% of the fitted variation, and was largely a function of vigilant activity associated with the alarm call. Axis 2 (Y axis) explained 23% of the fitted variation and was largely a function of the alarm call (for which $N = 2$ observations), excavation, jump-yip and fighting behaviours. Excavation and jump-yip behaviours were associated with jump-yip playbacks, while fighting and socializing were associated with no-playback. Open circles represent sample scores of different response variables (behaviours) along Axes 1 and 2, triangles represent centroids of sample locations corresponding to different explanatory variables (playback treatments), and proximity indicates similarity and correlation in multidimensional space.

activities were associated with the no-playback and jump-yip playbacks. Axis 2 explained 23% of the remaining fitted variation and was largely a function of jump-yip, alarm call, excavation and fighting behaviours (Fig. 5). Alarm calls were associated with both the jump-yip and alarm playbacks. We observed only two instances of focal individuals issuing the alarm call, one during the jump-yip call playback and the second during the alarm call playback. Excavation and jump-yip behaviours were positively associated with jump-yip playbacks, and fighting was negatively associated with jump-yip playbacks (Fig. 5). Fighting and socializing were positively associated with no-playback (Fig. 5). The permutation test for significance of all constrained axes was significant and confirmed our axes explained the observed variation of the prairie dog behaviour composition data relative to our experimental treatments (pseudo- $F = 1.8$, $P = 0.03$).

DISCUSSION

Our experimental design spanned 26 field sites over two years and used focal sampling to quantify natural, uninfluenced prairie dog behaviour and responses to playbacks of native, ambient sounds including western meadowlark songs and calls. We then imposed one of two randomly assigned treatment playbacks and recorded the type and duration of behaviours for each of the 388 individuals observed in our experiment. To our knowledge, this is one of the most robust data sets to date exploring black-tailed prairie dog behaviour.

Our study revealed that black-tailed prairie dogs appeared to understand the playback of recorded signals from a presumably unrelated, unfamiliar individual, as indicated by displaying varying degrees of predicted behaviour. Information embedded in prairie dog calls is therefore likely to be beneficial, even if given by nonkin (Hoogland, 1983). Our results also confirmed the alarm signal significantly impacts prairie dog behaviours such as foraging and vigilance, which represent the trade-off between the maximization of resource intake and avoidance of depredation. Findings related to these behaviours are critical for both conservation and management because the majority of daily animal behaviour in the wild can be classified as one of these two activities (Illius & Fitzgibbon, 1994). In colonial species such as our model organism, the use of conspecific signals plays a crucial role in maximizing group vigilance, thus increasing individual foraging opportunities (Hoogland, 1979). Our results suggest that prairie dogs can recognize alarm call signals from an unfamiliar individual, and that this prompts significant increases in vigilance and reductions in foraging time compared to no-playback or behaviour during a control playback of ambient sounds. We found no evidence during the alarm call treatments to support our prediction of attenuation of behavioural response as distance increased between the recording source colony and experimental colonies. We suspect that prolonged exposure to the alarm call playback would not produce the same vigilant response, as prairie dogs are known to habituate to negative stimuli (Hoogland, 2006).

Regarding the lesser-understood jump-yip call, prairie dogs performed jump-yip calls significantly more during the jump-yip playbacks than during other treatments, effectively demonstrating recognition of the recorded jump-yip call despite the absence of an accompanying visual display. However, we did not find evidence to support our hypothesis that prairie dogs would increase foraging time or reduce vigilance time after hearing the jump-yip call. This result is puzzling when considered in conjunction with recent research by Hare et al. (2014), who found that instigators of the jump-yip increased foraging time. Hare et al. (2014) only investigated benefits to the instigator of the

jump-yip, however, whereas our research investigated potential benefits to the recipients. Taken together, these studies indicate that the motivation for reciprocating the jump-yip remains unclear.

We suggest three possible explanations for the observed lack of increased foraging time following the jump-yip treatment. First, prairie dogs may require the full display of the bodily jump-yip to motivate changes in foraging and vigilant behaviour. This hypothesis is unlikely to fully explain our results, however, because although the jump-yips occurred during an audio-only playback, focal individuals were able to receive both audio and visual signals once colony members began to display the jump-yip. Nevertheless, the effectiveness of an acoustic signal versus a visual or combined audiovisual signal should be further explored. For some avian species, a combination of audio playback and visual cue (animal model) is necessary for effective conspecific attraction (Ward & Schlossberg, 2004). For example, yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, responded to conspecific cues and signals where both models and bird songs were utilized, but failed to respond at sites that used either singularly (Ward & Schlossberg, 2004).

Second, the jump-yip call may be encoded with situation-specific information, similar to the alarm call (Loughry, 1987; Slobodchikoff et al., 1991). In that case, prairie dogs may not change their vigilance and foraging behaviour in response to a nonlocal jump-yip recording, either because the jump-yip playback did not match their particular situation, was poorly understood due to difference in dialect or was recognized as a vocalization from a noncolony member and therefore considered less trustworthy (Hoogland, 1983). Our alarm call data suggest some anecdotal support for this hypothesis, as prairie dogs rarely issued alarm calls during the alarm call playback ($N = 1$), despite significantly increasing their vigilance (Fig. 5). This suggests that prairie dogs may be sceptical of an unknown informant and seek to visually confirm the source of alarm before broadcasting an alarm call themselves. Our jump-yip frequency results suggest playbacks were most strongly responded to by individuals in colonies closest to the recording site as these individuals not only increased jump-yip frequency in response to the jump-yip playback but also reduced jump-yip frequency in response to the alarm playback (Fig. 4). This could be a dialect issue as, for example, the dialects of Gunnison's prairie dogs vary by region (interstate) with variation increasing according to geographical distance as a result of dispersal barriers and genetic variation (Perla & Slobodchikoff, 2002; Slobodchikoff et al., 1998). Similar regional dialects may exist for black-tailed prairie dogs and these dialects may vary on finer scales within the same region. Future research should more directly examine dialect variability of the black-tailed prairie dog at relatively fine scales and consider how topographic dispersal pathways or barriers could influence dialect flow.

Third, we suspect foraging time of prairie dogs may be limited by instantaneous intake rate (IIR), or the grams of forage per minute a prairie dog can acquire during foraging activities, and prairie dogs receiving the jump-yip playback may have been unable to further increase foraging time during our relatively short observation durations. The observation in our study that prairie dogs spent similar amounts of time foraging during the jump-yip playbacks as during control playbacks (Fig. 3) supports this idea. The effects and limitations of IIR have been widely studied in livestock animal science. For example, in beef cattle that consume diets high in fibre, which is difficult to digest, maximum forage dry matter intake rate is limited to 1.1% of a cow's body weight (Belyea, Barry Steevens, Whittier, & Sewell, 1993). Although such a limitation has not been quantified for prairie dogs, they consume an

estimated 70 g of forage per day (Koford, 1958), but this may be partially dependent on digestibility of forage (van Langevelde, Drescher, Heitkönig, & Prins, 2008).

We did not find consistent support for our hypothesis that the strength of prairie dog behavioural responses to playbacks of alarm and jump-yip calls would decline as distance from source of playback recording increased. The distance from the source of recording did not significantly influence the proportion of time spent foraging or vigilant, while the effect on jump-yip reciprocation was inconsistent (Fig. 4). Although we had *a priori* reasons for suspecting behavioural responses may be distance dependent, there may be factors contributing to and confounding these results that we did not examine, including dialect plasticity, wind, vegetation structure and/or elevation. Given the unanticipated nonlinear relationship between distance from source and jump-yip reciprocation, we hypothesize that distance may not be the most appropriate metric of dispersal potential in this landscape. Instead, topographic features such as high hills, sagebrush-dominated habitats and intermittent escarpments may act as barriers to dispersing individuals (e.g. Sackett et al., 2011). Future research in this landscape could use a resistance surface modelling approach to investigate the role of topography and other potential dispersal barriers as modifiers of behavioural responses.

Our focal sampling method allowed for the observation of rare or less common prairie dog behaviours (Hirschler et al., 2016). Overall, nonvigilant behaviours and activities were associated with no-playback and the control and jump-yip call playbacks (Fig. 5). We found that prairie dog expressions of vigilant behaviour were associated with alarm call playbacks whereas nonvigilant behaviours such as resting and grooming were more common during no-playback. Foraging and passively watching were associated with our control playback. Interestingly, fighting behaviours decreased during the jump-yip playback and burrow maintenance and jump-yip calls increased. Burrow excavation and maintenance are necessary to maintain the integrity of burrow systems for shelter from the elements, avenues of escape during attempted predation events and other services such as food storage, mating, birthing and pup rearing. However, burrow excavation and maintenance is a risky behaviour for prairie dogs and leaves individuals vulnerable to predation events. Prairie dogs may take advantage of information from jump-yips to conduct more excavation and other necessary but risky behaviours, which may yield fitness benefits.

We observed several other unexpected trends and results in our experiments, and two are of particular note. Of the 26 experiments we conducted, 12 were randomly assigned the alarm call as a playback treatment, yielding a total of 59 individuals in our focal sampling who received the alarm call playback. However, we observed only a single individual issuing the alarm call during any treatment type. Prairie dogs encode information describing the type, location and description of a perceived threat into their alarm call (Frederiksen & Slobodchikoff, 2007; Kiriazis & Slobodchikoff, 2006; Slobodchikoff et al., 2009), which in turn are repeated in chorus by colony individuals as group vigilance. However, the absence of chorus alarm calling during our experiment suggests the information encoded in our alarm playback was perhaps not perceived as an active threat to our focal individuals. Prairie dogs may need to visually confirm a perceived threat before reciprocating an alarm call. Alarm calls issued by unfamiliar, nonlocal individuals may also be poorly understood and therefore rarely reciprocated.

A second unexpected result of our data was the increased foraging time during control playbacks. Vocalizations are a form of public information (Danchin, Giraldeau, Valone, & Wagner, 2004) that can be utilized by eavesdroppers to enhance vigilance and

detection of risk (Beauchamp, Alexander, & Jovani, 2012) and such eavesdropping has been documented to occur between species and across different taxa with shared predators (Carrasco & Blumstein, 2012; Templeton & Greene, 2007; Valone, 2007). Prairie dogs, with their gregarious alarm calls, can serve as information sources for heterospecific eavesdroppers like burrowing owls (Bryan & Wunder, 2014). Our control playback was composed of ambient sounds recorded on site, including a significant proportion of western meadowlark songs and calls. The significant increase in foraging time during the control playback of western meadowlark songs and calls suggests prairie dogs may eavesdrop on meadowlarks as a form of predator vigilance. This may be the first documented instance of prairie dogs relying on public information as a form of predator vigilance. Interspecific playbacks represent another fruitful avenue for future research on the use of audio signals as tools for passively influencing black-tailed prairie dog behaviour.

The influence of conspecifics on habitat selection, and its associated fitness benefits, have been studied at both the individual and population level (Safran et al., 2007), and in both experimental laboratory and field settings (see Campomizzi et al., 2008 for a review). Researchers have demonstrated that conspecific cues and signals can be used to induce settlement of unoccupied areas of suitable habitat, and subsequently lead to high nesting success and site fidelity, in avian species (DeJong et al., 2015; Hahn & Silverman, 2007). Additionally, conspecific signals have been successfully used to expand amphibian species distribution (Buxton, Ward, & Sperry, 2018; James et al., 2015). Across taxa, these examples share commonalities of being territorial, colonial and highly gregarious species – ideal attributes for making information-based decisions through conspecific cues and signals. Our model, the black-tailed prairie dog, shares these conspecific commonalities; however, our findings suggest that the use of prerecorded conspecific signals to influence habitat selection within prairie dog metapopulations warrants further study.

Prairie dogs provide essential benefits to wildlife through their roles as ecosystem engineers, foundation species and keystone species in the grasslands of North America (Hoogland, 2006; Jones et al., 1994). The conservation and management of colonial animals often hinges on understanding how organisms communicate (Alatalo et al., 1982; Danchin et al., 2004; Dugatkin & Godin, 1993; Pärt & Doligez, 2003; Safran et al., 2007; Stamps, 1988). Our work adds clarity to the function of conspecific signals within black-tailed prairie dog metapopulations and identifies factors that may influence conspecific signal use and interpretation.

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Supplementary material

Supplementary material associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.anbehav.2019.02.004>.

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Appendix

Table A1

Total number of behavioural observations of black-tailed prairie dogs by site and year, across treatment types (no-playback, control, alarm and jump-yip)

Site name	Observation records across treatment type
2016	
2016-1	16
2016-2	15
2016-3	16
2016-4	17
2016-5	18
2016-6	22
2016-7	11
2016-8	19
2016-9	15
2016-10	8
2016-11	15
2016-12	10
2016-13	5
2016-14	6
2017	
2017-1	20
2017-2	23
2017-3	36
2017-4	32
2017-5	5
2017-6	12
2017-7	9
2017-8	9
2017-9	10
2017-10	8
2017-11	10
2017-12	21
Total observations	388