

**Black-tailed prairie dog (*Cynomys ludovicianus*) awareness of neighbours'  
vigilance is spatially explicit**

By

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## ABSTRACT

Black-tailed prairie dogs, *Cynomys ludovicianus*, gauge neighbour vigilance through jump-yipping, a contagious, multimodal display where individuals vocalize while jumping upward. Jump-yip bouts were recorded using three camcorders across 27 sites within the Dakotas to examine how instigator location and spatiotemporal pattern of conspecific response within bouts influence instigator vigilance, thereby testing whether instigator knowledge of conspecific vigilance is spatially explicit. Video files were analyzed to determine if instigators disproportionately devoted personal vigilance following jump-yip bouts toward areas of conspecific non-responsiveness over areas with conspecific response. Paired-sample tests indicated that instigators oriented vigilance toward non-responsive areas significantly more than areas of responsiveness after both current ( $Z = -4.74$ ,  $P = 0.0001$ ) and past jump-yip bouts ( $Z = 0.42$ ,  $P = 0.0001$ ). Instigators direct personal vigilance toward areas where predators may go undetected, demonstrating spatiotemporal awareness of conspecific vigilance, and thus utilizing both public and personal information to minimize predation risk.

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## INTRODUCTION

Communicative signals provide individuals with public information, which augments personal information about one's environment and experiences, shaping fitness-enhancing behaviour (Stephens, 1989; Valone & Templeton, 2002). Enhanced access to public information thus constitutes one of the many benefits of social grouping (Valone & Templeton, 2002), which also include increased foraging efficiency (Clark & Mangel, 1986; Hamilton, 1964; Hoogland, 1995), territory maintenance (Box, 1973; Macdonald, 1983), reproductive benefits (Blumstein & Armitage, 1999; Muller & Manser, 2008; Woolfenden, 1975), enhanced navigational accuracy (King & Sueur, 2011; King, Sueur, Huchard & Cowlshaw, 2011) and reduced predation risk (Hoogland, 1979; Pulliam, 1973; Thompson & Hare, 2010). Communication exists in many forms but requires a signal and the reception of that signal, which makes communication both influential and meaningful (Marler, 1998; Ruxton & Schaefer, 2011). Acoustic calls contain information regarding an individual's age, sex, identity, social dominance, reliability and skills, all of which contribute to group spatial dynamics (Bousquet, Sumpter & Manser, 2011; Hoogland, 1995; Lima & Zollner, 1996). Where signals pertain to predators, individuals must assess both the urgency of response associated with signals, and the reliability of the signaler to respond appropriately (Frings & Frings, 1977; Hare & Atkins, 2001; Tyack, 2008). Alarm calls serve to alert group members to the presence of potential predators (Blumstein, Steinmetz, Armitage, & Daniel, 1997; Owings & Morton, 1998), and can inform group members of a predator's location (Davis, 1984; Greene & Meagher, 1998; Thompson & Hare, 2010), induce responses (Marler, Evans & Hauser, 1992; Seoraj-Pillai & Malan, 2015; Warkentin, Keeley & Hare, 2001), and recruit additional callers, thus deterring attack (Furrer & Manser, 2009; Graw & Manser, 2007). From those calls, receivers extract information regarding the signaler's location (Sloan, Wilson & Hare, 2005), state of vigilance and attentiveness (Hare, Campbell & Senkiw,

2014; Shelley & Blumstein, 2005), and reliability (Hare & Atkins, 2001; Magrath, Pitcher & Gardner, 2009), which allows group members to make informed decisions about environmental risks. Because individuals rely on conspecifics to detect predators, selection favors prey that remain aware of their neighbours' vigilance levels in order to detect (and/or avoid) predators that might otherwise approach undetected (Beauchamp, Alexander & Jovani, 2012; Di Blanco & Hirsch, 2006; Hare et al., 2014).

Vigilance and anti-predator behaviour is essentially universal among animals and yet varies with group size, density, habitat, and perceived predation risk. The threat posed by predators is a major determinant of prey distribution and foraging behaviour (Lima & Dill, 1990; Urban & Richardson, 2015), and the time and energy devoted to vigilance typically comes at the expense of time and energy devoted to foraging (Caraco, 1979; Hamilton, 1971; Lima & Dill, 1990; Schall & Pianka, 1980). Threats are temporally and spatially diverse, and predators preferentially attack less vigilant prey, solitary prey or prey on the periphery of a group (Hamilton, 1971; Lima & Zollner, 1996; Packer & Abrams, 1990; Sparrevik & Leonardsson, 1995). Foraging animals manage their risk of predation by foraging in proximity to other individuals, partaking in intermittent scanning bouts ('many-eyes' effect' (Lack, 1954)), detecting predators early and deterring predators and/or moving to avoid predators (Bednekoff & Lima, 1998; Pulliam, 1973; Roberts, 1996). As group size increases, individuals devote more time to foraging (Elgar, 1989; Hare et al., 2014; Roberts, 1996), less time to vigilance (Pulliam, 1973; Kildaw, 1995), and more time to monitoring conspecifics within the group (Hirsch, 2002). Fixed head orientation and eye gaze are the primary physical traits observed when an individual is considered vigilant (Cantwell, Johnson, Kaschel, Love, Freeberg, 2016; Clark & Dukas, 2003; Elgar, 1989, Lima & Dill, 1990), and directionality of scanning can be

influenced by group density within a colony (King, Sueur, Huchard & Cowlshaw, 2011). Previous studies of degus (Ebensperger & Wallem, 2002), spiders (Henschel, 1998), and forest primates (van Schaik, van Noordwijk, Warsono & Sutriyono, 1983) support the hypothesis that grouped animals detect predators earlier than solitary animals, and multiple vigilant individuals in a group allow the entire group to benefit from this collective vigilance (Treves, 2000).

Vigilance behaviour can emerge in patterns, often resulting from the ecological constraints species face (Eftimie, 2013; Schleidt, 1977) and animal aggregations are defined by directionality of movement, centers/edges, leaders/followers, and arrangements within a habitat (Edelstein-Keshet, 1997). These arrangements have been documented for various taxa; e.g. fish schools sorting collectively (Couzin, Krause, James, Ruxton & Franks, 2002); bird flocks displaying parallel grouping (Heppner, 1997); and bat colonies clustering both for roosting and feeding (Tuttle, 1976; Wilkinson & Boughman, 1998). Within-group spatial position or the localized center of density is especially important for animals who navigate to find new food sources and stay in relatively compact groups (Di Blanco & Hirsch, 2006; Edelstein-Keshet, 1997; Robinson, 1981). Spatial dynamics of animal aggregations can be particularly difficult to research in that an individual's current position is likely correlated with its previous position (and thus non-independent). Further, movement itself generates variation in group size and in sample size (Edelstein-Keshet, 1997; Patterson, Thomas, Wilcox, Ovaskainen & Matthiopoulos, 2008). Unlike species with a diverse suite of predators and multiple escape options (Greene & Meagher, 1998), ground-dwelling animals are often constrained to their territories and do not have the option to fly, run great distances, or climb out of reach of presumptive predators (Blumstein & Armitage, 1997; Caro, 1994; Hoogland, 1995; Macedonia & Evans, 1993; Murie & Michener, 1984). The limited escape option of rushing down a burrow requires colonial burrowing species

to refine skills related to both the detection and deterrence of predators (Hoogland, 1995; Manser & Bell, 2004, Stromberg, 1978), through frequent assessment (Hoogland, 1981; Warkentin, Keeley & Hare, 2001), responsiveness, and the ability to adjust to recent cues in one's environment (Leger, Owings & Boal, 1979; Marler et al., 1992; Owings & Morton, 1998).

Responsiveness to collective behaviours/calls, where signals pass among group members ensuring the transmission of a behavioural change, benefits social groups via coordination of migration (Edelstein-Keshet, 1997), enhanced thermoregulatory efficiency (Gerum et al., 2013), escape (Heppner, 1997; Sirot & Touzalin, 2009), and coordinated defense (Graw & Manser, 2007; Sirot & Touzalin, 2009). Collective behaviours likely have a learned component requiring response facilitation, where an act is demonstrated, thus increasing the probability that another group member will perform the same act (Krueger & Flauger, 2007; Sumpter, 2006). Pairing this with the context in which it takes place, an observing individual will learn when it is appropriate to perform that act (Krueger & Flauger, 2007; Rendell et al., 2011), leading to species-specific behaviour including contact calls, chorusing and duetting. Contact calls (back and forth repetitive calling with individually-distinctive sounds promoting localization), chorusing (communal vocal efforts by a group) and duetting (a male/female pair communicating using song), are particularly interesting in that they require synchronous participation from multiple group members, and may attract the attention of nearby predators (Brown, Dooling & O'Grady, 1988; Giacoma, Sorrentino, Rabarivola & Gamba, 2010; Haimoff, 1984; Morris, 1980; Muller & Manser, 2008; Party, Streiff, Marin-Cudraz & Greenfield, 2015). Although an individual acting in unison with the group may experience a cost if that individual abandons a resource too early, or experience diminished returns by postponing a personally profitable activity, King & Cowlshaw (2009) emphasize that following the group ultimately proves most beneficial. Collective calls serve to

enhance the cohesion of a pair or group of individuals, facilitating the detection and deterrence of predators (Couzin, 2009; Treherne & Foster, 1981), which can be seen in birds that mob (Curio, Ernst & Vieth, 1978; Sandoval & Wilson, 2012), meerkats that act as sentinels (Townsend, Zottl & Manser, 2011), and Thomson's gazelles that inspect predators (FitzGibbon, 1994). Awareness of the attention of other group members can lead to group-level collective vigilance where all members are aware, potentially responsive, and reciprocate in providing information about perceived threats (Griffin, 1981; Hare et al., 2014; Sherman, 1977; Sumpter, 2006).

Collective behaviour research across a range of species that utilize personal and public information facilitates an understanding of how individuals within social groups are able to measure group size and density and use these measurements to their advantage (Beauchamp, 2003; Bednekoff & Lima, 1998; Bousquet et al., 2011). Collective behaviour and decision making in humans was once considered unique (Griffin, 1981), though we now know that collective behaviour is common among non-human animals (Couzin & Krause, 2003; Sumpter, 2006), where acting as an efficient, cohesive and communicative unit proves beneficial (Slobodchikoff, 2012; Sumpter, 2006). The signals employed in animal communication may be referential, goal-oriented, semantic, or displacement-based, and share similarities across taxa that allow personal and public information to be utilized (Couzin & Krause, 2003; Sumpter, 2006). Thus, many studies concerning collective communicative behaviours highlight the benefits to individuals who aggregate with each other (Beauchamp et al., 2012; Hoogland, 1995; Parrish, Hamner & Prewitt, 1997). Our understanding of the cognitive abilities of non-human animals continues to grow, and with an understanding of how/why groups cooperate and make informed decisions with 'accurate' public information, we can better understand the evolution of animal cognitive abilities (Couzin, 2009; Sueur, Deneubourg & Petit, 2011).

I observed jump-yipping, a collective behaviour, in wild black-tailed prairie dogs (BTPD), *Cynomys ludovicianus*, living in large social colonies (commonly referred to as “towns”) throughout the Great Plains area of North America (Figure 1). They maintain a stable system of territories within prairie grassland habitats encompassing burrow systems and foraging habitat (Hoogland, 1995; Murie & Michener, 1984). Colonies, towns and villages are all synonymous terms used to describe their expansive communities that can surpass thousands of individuals containing multiple family groups called “coteries” (Hoogland, 1995). Coteries contain somewhere around 26 individuals occupying roughly 0.3 ha of habitat space within visual and acoustic range of neighbouring coteries. Movement between coteries is typically restricted by territorial aggression (Hoogland, 1995; King 1959). Coteries consist of an interior with burrows and an outer periphery with short grass where prairie dogs forage (Garrett, Hoogland, & Franklin, 1982; Hoogland, 1995). Subcolonies of semi-isolated or visually-obstructed individuals are termed “wards”, which often occupy less suitable habitat (Hoogland, 1995; King, 1959). BTPDs do not hibernate, although they are less active during the winter, and can be seen during the summer aboveground at dawn and often remain aboveground until dusk (Hoogland, 1995). Most individuals are active during the day, including juveniles who emerge from the burrow in early spring, typically in April/May depending on the weather (Hoogland, 1995). Individuals partake in a variety of activities aboveground, including foraging, playing, maintaining burrow entrances, gathering grass and watching for predators (Hoogland, 1995). At the entrance to each burrow is a large mound of soil, and prairie dogs frequently use these mounds as predator lookouts (Hoogland, 1995; King, 1959). BTPD towns once extended across most of the Great Plains, with undisturbed colonies historically containing thousands of individuals and extending for ~60,000 square kilometers (Hoogland, 1995; National Geographic,

2018). Ranching and agricultural practices (poisoning), sylvatic plague and recreational shooting have reduced the current estimated occupied habitat to approximately 21% of the area prairie dogs historically occupied, and total population has declined severely in the last 150 years (Avila-Flores et al., 2012; Hoogland, 1995; Luce, 2003; Summers & Linder, 1978; Vermeire, Heitschmidt, Johnson & Sowell, 2004). Increasing awareness of prairie dog cognition and their ecological importance is invaluable, as they are a fundamental component of prairie ecosystems, yet their existence is threatened by continued efforts to hunt and poison them as ‘pests’ (Hoogland, 1995; Luce, 2003; Slobodchikoff, 2012).

Research on prairie dogs has revealed information-rich signaling within colonies (Waring, 1970; Smith, Smith, Oppenheimer & Devilla, 1977), with Slobodchikoff, Perla and Verdolin (2009) suggesting that prairie dogs have one of the most complex communication systems currently under study. Prairie dogs express a variety of signals: chatter barks, chuckles, repetitious barks, snarls, growls, screams, and tooth chatters, which publicize potential threats, define territories, or are emitted during play/social interactions (Hoogland, 1995; Waring, 1970). BTPD are highly communicative regarding the presence of a threat and typically emit a high-pitched alarm call, which alerts other members to scan the environment for the threatening stimulus (Hoogland, 1995, Waring, 1970). Alarm calls are emitted in the presence of both avian and terrestrial predators (Hoogland, 1995), and the shared effort to communicate about presumptive risks in the environment allow BTPDs to achieve a collective level of vigilance (Hare et al., 2014). Prairie dogs are ideally suited to communication research, as individuals can be reliably located in large numbers within burrow systems, and little effort is required to live-trap, handle and mark them. Their frequent and seemingly complex alarm communication also renders them an opportune model for cognition research.

According to Hoogland (1995), BTPDs are preyed upon by numerous bird-of-prey species (prairie falcon (*Falco mexicanus*), Cooper's hawk (*Accipiter cooperii*), Northern harrier (*Circus hudsonius*), red-tailed hawk (*Buteo jamaicensis*) and golden eagle (*Aquila chrysaetos*)), mammalian predators (American badger (*Taxidea taxus*), black-footed ferret (*Mustela nigripes*), long-tailed weasel (*Mustela frenata*), bobcat (*Lynx rufus*), mountain lion (*Puma concolor*), common gray fox (*Urocyon cinereoargenteus*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), domestic dogs (*Canis lupus familiaris*), humans (*Homo sapiens*)), and snakes (bull (*Pituophis catenifer sayi*) and prairie rattlesnake (*Crotalus viridis*)). Since BTPD colonies are highly conspicuous on flat landscapes, which are easy for predators to traverse, prairie dogs constitute opportune prey. With acute vision and refined auditory senses, vigilance promotes the detection of predators directly and indirectly by gauging the movement and auditory cues emanating from nearby individuals (Hoogland, 1995; Kildaw, 1995; Waring 1970). BTPDs are therefore highly sensitive to changes in group-size, with the removal of individuals from central areas drawing individuals on the edge toward the center of the group, where group members are more densely aggregated (Hoogland, 1979). Additionally, the removal of individuals from a coterie reduced the time remaining coterie members spent foraging and increased the proportion of time devoted to vigilance (Kildaw, 1995). BTPDs use information acquired via personal vigilance, alarm calling, and collective detection both to distinguish and respond appropriately to presumptive predators, thereby reducing their susceptibility to predation (Hare et al., 2014).

BTPDs assess conspecific readiness to react through a contagious multimodal behaviour called a jump-yip (Hare et al., 2014). When jump-yipping, an individual lifts its forepaws into the air with an upright torso and simultaneously emits a vocal 'wee-oo' (Waring, 1970). This posture is held for a second or more as neighbouring conspecifics are stimulated to respond by

displaying additional jump-yips (Waring, 1970). The contagious nature of this display can recruit sequential responses from 40-50 individuals, including even distant group members (Hoogland, 1995). Although jump-yips are often described as passing from one individual to the next, contagious bouts seldom spread symmetrically within a town (Hoogland, 1995). This asymmetrical spread presumably reflects spatiotemporal variation in the awareness of neighbours, as reflected by their response to the jump-yips of their neighbours (Hare et al., 2014). As outlined in Hare et al. (2014), jump-yipping has previously been considered to serve a variety of functions: predator alarm (Anthony, 1955; Hoogland, 1995; Waring, 1970;), an ‘all clear’ signal following threat retreat (Anthony 1955; Hoogland 1995; King 1959; Smith, 1958), deterrence of predators (Smith et al., 1977), territorial disputes (King, 1959; Smith et al., 1977; Waring 1970), and initiation of social greetings (Hoogland, 1995). The cohesive and socially beneficial function of jump-yipping was recently determined by Hare et al. (2014) who found that bouts allow prairie dogs to optimize the trade-off between foraging and vigilance by assessing conspecific awareness. Bout instigators increased time devoted to active foraging and decreased personal vigilance as the latency for neighbouring conspecifics to join in a jump-yip bout decreased, or as the number of respondents and overall duration of conspecific response increased (Hare et al., 2014). Jump-yipping therefore provides a mechanism allowing individuals to monitor the vigilance levels of others. Clark and Dukas (2003) suggested a model for optimal selective attention during vigilance where attention should be devoted to dangerous angles rather than ‘safe’ angles, but did not observe this trend firsthand in a naturally-existing animal populations. Where collective vigilance occurs, the Clark and Dukas model would predict that personal vigilance should be directed selectively toward areas devoid of alert conspecifics within a social group. There are occupied areas within a colony that are devoid of jump-yipping, and

those areas may contain conspecifics that are not always attentive, thus all individuals bordered by those areas may be more susceptible to predators. Where gaps in conspecific coverage exist, whether that is attributable to lack of responsiveness from above-ground conspecifics, or the absence of neighbouring conspecifics in those areas, selection would favor individuals that compensate for that deficit in public information by directing personal vigilance toward those areas over others.

The primary goal of this study was to determine whether instigators of jump-yip bouts orient personal vigilance toward areas of diminished neighbour response to jump-yipping. Such selective attention to areas of reduced conspecific responsiveness would reveal that BTPDs' awareness of their neighbour's vigilance is spatially explicit. I also examined the temporal dimension of prairie dog awareness of their neighbour's vigilance by testing whether selective attention is manifested in response to just the most recent jump-yip bout, or is extrapolated from neighbour responsiveness during past jump-yip bouts. Further, I tested whether selective attention was limited to situations in which a bout instigator was confronted with neighbours that didn't respond or included areas where potential respondents were absent altogether. Finally, with the increase in risk experienced by individuals on the periphery of a group, I tested whether peripherally-located versus centrally-located jump-yip bout instigators relied differentially on personal versus public information. I tested whether selective attention based on spatiotemporal variation in conspecific responsiveness was more pronounced in central individuals (that have access to a plethora of public information) compared to peripherally-located individuals, who would presumably focus the majority of their personal vigilance toward the edge, owing to the increased risk of a predator approaching undetected from the edge as opposed to the center of the group (Elgar, 1989; Rattenborg, Lima & Amlaner, 1999).

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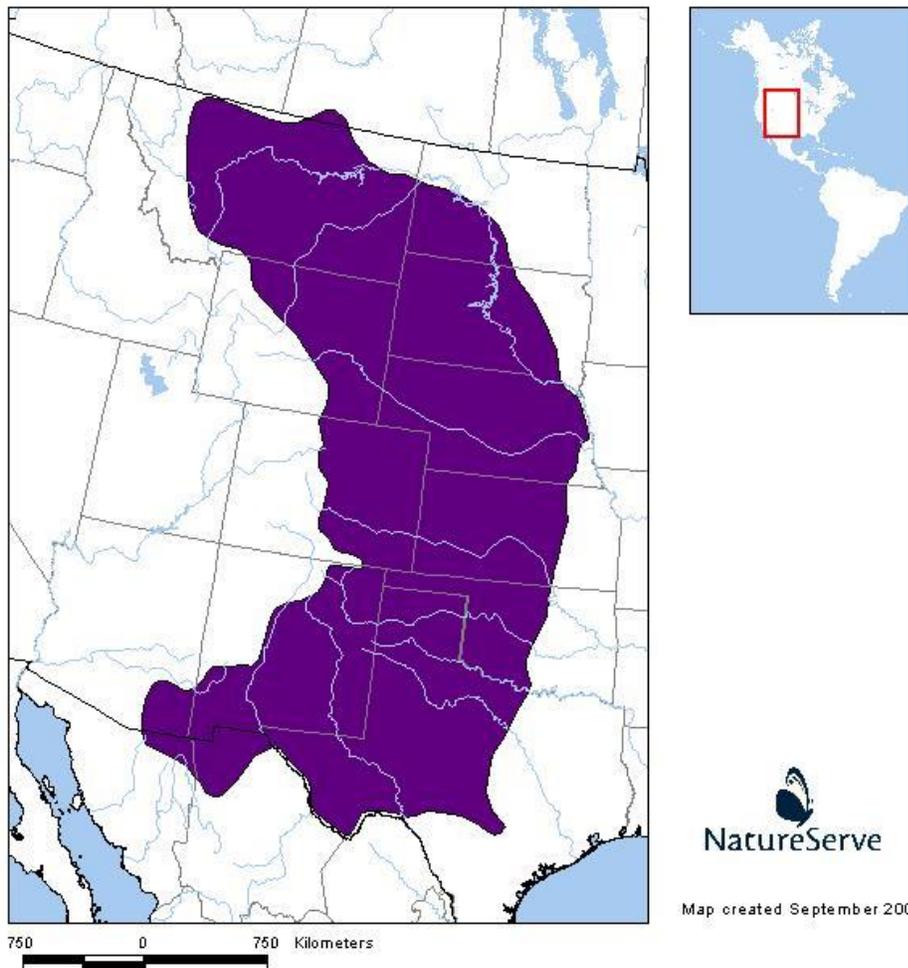
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Figure 1. Black-tailed prairie dog range across North America, where purple shading indicates year-round residence.



## **METHODS**

### **Study Site**

My observational study used video cameras to record the behaviour of free-living, unmarked BTPDs from a vehicle (navy blue 2005 Hyundai, Elantra), which was parked on roadside pullouts beside prairie dog towns throughout North and South Dakota. Using the vehicle as a blind at a pullout is a method that ensures prairie dogs acclimate to the presence of the vehicle and human observer (Hare et al., 2014; Johnson & Collinge, 2004; Lehrer, Schooley & Whittington, 2012). My work was conducted under an “Abbreviated Protocol for Minimal Animal Involvement” granted by the University of Manitoba’s Fort Garry Campus Animal Care Committee, and I received permission/permits from the six National Parks/Grasslands where I conducted research. Video-recording commenced on 1 May 2017 and continued until 15 May 2017. I did not record on 8 May due to high winds (42 kph) and scattered rainstorms.

Video-recording took place in Theodore Roosevelt National Park (N46°56', W103°31'), Grand River National Grasslands (N45°45'0", W102°30'12"), Badlands National Park (N43°45', W102°30'), Buffalo Gap National Grasslands (N43°29'57", W102°53'21"), Wind Cave National Park (N43° 33' 22", W103° 28' 38"), and Custer State Park (N43°44'45", W103°25'5") (see Table 1). These parks were chosen after careful review of aerial surveys and/or population surveys of prairie dogs in the area (Hare et al., 2014; Hoogland, 1995; Knowles, Proctor & Forrest, 2002; North Dakota Game and Fish Department, 2016; Sidle, Johnson & Euliss, 2001). All North/South Dakota prairie dog populations are long-standing natural populations that pre-date the establishment of the parks (Knowles et al., 2002; Virchow & Hygnstrom, 2002); however, with the creation of the National Park System, which monitors populations, records of prairie dogs on my study sites date back to 1946 for the oldest Park (Wind Cave) to 1998 for the

most recently instated protected grassland area, Grand River (Hoogland, 1995; Luce, 2003; National Park Service, 2018; United States Department of Agriculture Forest Service, 2018). The elevation throughout this region ranges from 1525m to 3050m (North Dakota Base and Elevation Maps, 2016; South Dakota Base and Elevation Maps, 2016), and includes a minor mountain range, rolling hills, eroding sedimentary rock formations, rivers, wetland reservoirs, and mixed-grass prairies (Reading & Matchett, 1997). Prairie dog burrows were primarily located on flatter landscapes (Hoogland, 1995) surrounded by prairie grasslands with a mix of brush, wildflowers and desert succulents growing in clay-loam and glacial-deposited soils (National Park Service, 2015; Reading & Matchett, 1997). Prairie dogs create an exposed area where scarlet globemallow (*Sphaeralcea coccinea*), black nightshade (*Solanum nigrum*), pigweed (*Amaranthus spp.*), wheatgrass (*Agropyron spp.*), buffalo grass (*Bouteloua dactyloides*), rabbit brush (*Ericameria nauseosa*) and sagebrush (*Artemisia tridentate*) are systematically clipped down (Hoogland, 1995; Johnson & Collinge, 2004). Prairie dogs that colonize tall grass prairies of mixed vegetation tend to forage throughout the day (Hoogland, 1995), however, seasonally they may not come aboveground before 0900 hrs CST. The chosen sites in the Dakotas varied in size from 11,706 ha (Wind Cave National Park) to 239,574 ha (Buffalo Gap National Grasslands).

Pilot data collection took place from 29 March through 26 April 2017 at Winnipeg, Manitoba's FortWhyte Alive (N49.8203°, W97.2251°). FortWhyte Alive consists of a prairie grassland, mixed aspen-oak forest and open-water ponds. The prairie dog colony at FortWhyte Alive was introduced in 2008 (K. Froese, FortWhyte Alive, personal communication, January 27, 2017). Prairie dogs in the area occupy a grassy area between a bison pen and open water, and are further constrained by the roads in the area and buildings. Thirty jump-yip bouts were

initially recorded at FortWhyte Alive to ensure that the multi-camcorder method adopted could resolve group-wide response properties and that a viable sample of jump-yip bouts would be obtained if few additional bouts were obtained from sites in North and South Dakota. A maximum of four jump-yip bouts were recorded per day to limit pseudoreplication within this small, pilot population (Hare et al., 2014; Senkiw, 2007). Trials were terminated if humans entered camera view, as FortWhyte Alive staff explicitly requested that the public not be filmed. Pilot data were not included in my final analysis, as an adequate sample size was obtained from observations of natural populations subjected to less human disturbance in the subsequent field season.

### **Experimental Design**

I used video recordings of naturally-occurring jump-yip bouts to examine the spatial awareness of jump-yip bout instigators with respect to conspecific responsiveness to bouts, as well as the instigator's spatial location within the group and colony type. Spatial location was a variable used to denote the instigator's within-group spatial position at the conspecific level. Colony type (*town center, town edge, ward center and ward edge*) was a designation of the group's spatial location in the overall town or in relation to the geometric population center within a group. Jump-yipping behaviours were captured with three SONY Handycam™ camcorders (DCR-68; SONY Corp., Tokyo, Japan): two camcorders were mounted on tripods placed 110cm above the ground's surface and situated at the front and rear of my vehicle, each camera with a field of view of 50°, while I operated a third handheld Handycam™ which focused primarily on the bout initiator. Handycams™ have widescreen capture (which could reliably capture prairie dog head orientation at a distance of ~70m and eye-catching jump-yipping behaviour within 100m) and 720 x 480 video resolution. Stationary

tripod-mounted Handycams™ were set to wide angle to capture the broad-scale pattern of colony member responsiveness to the initiation of a jump-yip bout and recorded continuously at each observation site.

I focused particularly on three aspects of prairie dog behaviour; jump-yip bout instigation, responsiveness during a bout, and instigator head orientation following bout termination. An instigator was the first individual after >5 sec absence of jump-yipping, to perform a jump-yip display by lifting its front paws off the ground and into the air with an upright torso and simultaneously utter a vocal “wee-oo”(Waring, 1970). A jump-yip bout consisted of subsequent jump-yips after the initial instigation that were separated by  $\leq 5$  sec from each other, where the total number of respondents consisted of  $\geq 1$  individual (Hare et al., 2014; Senkiw, 2007; Smith, Smith, Devilla & Oppenheimer, 1976). I captured the behaviour of the jump-yip instigator as soon as the instigator was seen (or heard with the idea that I could confirm with stationary camera recordings the true identity of the instigator) for approximately 90 seconds. Individual prairie dogs remained identifiable, as video records were continuous from the start to the end of a bout, although without applying unique marks to individuals, their identity among trials within the same coterie is ultimately uncertain. Preliminary observations from my 2016 field season and pilot trials conducted at FortWhyte Alive indicated that instigators were often standing/alert just prior to bout instigation, and were readily discernible as they began a jump-yip. Most instances in which bout instigation was captured effectively occurred by chance in that I was not specifically focused on the instigator (63 of 91 bouts). The instigator was thus in the view-finder of the handheld camera and brought into focus within 5 seconds of initial jump-yip emission, while immediate recording took place if the instigator was already in focus prior to bout instigation. Recording behaviour for 60s following a

stimulus/response event in this species has been deemed ideal since it minimizes extraneous influences on subject behaviour that might otherwise confound any inference regarding the effect of the factor of interest (Hare & Atkins, 2001; Hare et al., 2014). I employed all occurrence sampling to capture the behavioural contagion and distribution of behaviour as outlined by Altmann (1974). Video files from each camcorder's 80 GB hard drive were archived to a portable hard drive and reviewed daily to ensure meaningful data were being collected.

Multiple instigators' jump-yipping behaviours were recorded from unique towns within each park in North and South Dakota and equipment was moved daily to new towns to minimize pseudoreplication and maximize sample size. Prairie dog towns were spatially separated by more than two kilometers and thus visually/acoustically isolated from each other. Recording start time ranged between 0730 hrs CST and 0930 hrs CST due to fluctuation in weather as well as the remoteness of certain towns and continued each day until between 1330 hrs and 2000 hrs depending on weather conditions. All sites were mapped by taking a waypoint at the center of each observation site with a handheld WAAS-corrected GPS unit (eTrex 10; Garmin Ltd., Olathe, KS) once video recordings for that site had been obtained. Sites were chosen for high densities of above-ground prairie dogs (~20 in sight as I approached in the vehicle), visibility owing to the absence of physical obstructions; avoidance of high traffic areas, roaming bison, or little-to-no shoulder/pull-out area. A portion of a colony, approximately 60m x 60m, with an average of 13 individuals above ground, was recorded during each sampling period. Although the total colony/town is typically much larger, my above-ground sample size remained consistent with previous studies where sampling of jump-yipping behaviour was derived from isolated colonies (Hoogland, 1995; Loughry, 1993), peripheral sections of colonies and/or coterie-sized areas (Hare et al., 2014), or where ~11-30 aboveground individuals could be sampled (Smith et

al., 1976). Video-recording of jump-yipping behaviour continued for 1-2 hour intervals, during which 1-12 viable jump-yip bouts were recorded at a particular site before equipment was moved to a new colony. The number of jump-yips recorded at a site fluctuated due to weather, human visitation, accuracy of capturing the true instigator and time of data collection (prairie dogs are less active during the warmest times of the day). I spent an average of 68 minutes at each site. During the ten-minute acclimation period, a count of above-ground individuals, ambient temperature (Kestrel 3000, Nielsen-Kellerman Co, Boothwyn, PA), extent of cloud cover (cloudy, partially cloudy, mostly sunny, sunny), average wind speed (the average was taken from the 'avg' detected by the Kestrel 3000 during a single 10 second measurement), and primary wind direction were recorded in a field notebook. Observation periods in which individuals appeared to be orienting toward my vehicle (or a visitor's vehicle) and were issuing alarm calls were paused until individual(s) stopped orienting and alarm calling. Additionally, I paused (or ceased) handheld filming when visitors parked and exited their vehicles, recording would resume ten minutes after visitor departure. Observations were occasionally terminated when the site became too frequented by human visitors, which consisted of a person(s) staying within a distance where they could be heard for longer than 15 minutes either with their vehicle running or after exiting their vehicle. Given the availability of possible sites within the parks and the relatively low set-up time, it was most efficient to move to a new site if I was recording in an area continually disturbed by human visitation. Video files containing jump-yips that were preceded by the detection of vehicles and/or human foot traffic (if camcorders were not paused/removed) were not included in my analysis. Most Dakota sites were relatively clear of human foot traffic, as May is early for seasonal National Park visitation.

## **Coding Behavioural Data**

Handycam™ recordings were reviewed both in the field and at the University of Manitoba following completion of data collection in 2017. I coded the stationary Handycam™ recordings first, noting all instances of jump-yipping in an Excel file along with the time each jump-yip was seen/heard in the video file (time of instigation). Where necessary, I used headphones (IER-H500A; SONY Corp., Miyagi, Japan) to ensure response counts were as accurate as possible and to confirm instigator identity. After viewing recordings from both stationary angles, I moved on to watching and coding behaviour of the bout instigators from the handheld camcorder. I matched handheld footage with stationary footage using unique characteristics of a bout, file name/time and environmental contexts to confirm from the three viewpoints that the instigator truly initiated the bout. Beyond verifying instigation, a minimum of one conspecific response was required to be considered a bout, and the orientation of the bout instigator needed to be reliably discernable for 60 seconds following bout termination, with the exception of instances where an individual's head orientation was temporarily (1-3s) blocked by another conspecific or from passing behind an object (burrow) before coming back into view. These bouts were included, so that in total, 91 jump-yip bouts from 27 sites within parks outside of Manitoba constituted the final data set used in my analyses.

## **Behavioural Definitions of Coded Variables**

Definitions and descriptions for the variables considered for analysis are detailed below. The field site was captured by the two stationary camcorder views (Figure 2), and all visible individuals within the plot were designated to quadrants (Q1-Q4) where they were visible at the time the jump-yip bout was initiated relative to the instigator. The *above-ground population* was defined as the number of visible prairie dogs seen in the given area captured by the combined

viewpoints of both stationary camera angles. *Jump-yipping* was behaviourally defined as an individual's forepaws lifting off the ground into the air, with an upright torso and simultaneously uttering a vocal "wee-oo" (Waring, 1970). A *bout* was defined as jump-yips following an initial instigation that were separated by no more than 5s from each other, where the total number of respondents consisted of  $\geq 1$  individual (Hare et al., 2014; Senkiw, 2007; Smith, et al., 1976). Jump-yip bouts were considered independent if jump-yips were separated by more than six seconds. The majority (91%) of bouts included in analysis were 60 seconds to 20 minutes apart, ensuring subsequent bouts were independent of current bouts. 9% of bouts, occurring from eight different field sites with above-ground populations over 19 individuals, were independent of the subsequent bout, but occurred roughly 30s from the previous bout, with each bout lasting less than 2s, where instigators were unique. *Instigator Head Orientation* was a measurement of the instigator's scanning/head orientation in the 60 seconds following bout termination, this measurement served to determine the instigator's vigilance relative to the pattern of conspecific response within the site. Scanning/head orientation refers to an alert instigator, head parallel to the ground (at horizon) with eyes open and facing any of the 90° sections separated by cardinal compass directions in the 360° field surrounding the instigator (termed sections H1, H2, H3, H4; H for 'head orientation') (Hare et al., 2014; Senkiw, 2007). Although the instigator was recorded immediately following instigation for approximately 90 seconds, only the 60 seconds of behaviour following the termination of the bout was quantified for analysis. For scanning/head orientation to be viable for analysis, the instigator had to be evident (obvious) and the instigator's head orientation needed to be distinctly visible. Instances where head orientation could not be reliably determined or the identity of the instigator could not be determined were not included in analysis. Alternatively, angular deviation at fixed time intervals could be quantified to arrive at a

mean vector of gaze direction, and compared to the mean vector of responsiveness using Rayleigh's test. Errors in estimating exact angular deviation from video records, along with the problem of collapsing responsiveness in both the presumptive independent and dependent variables into single mean vectors, however, make this analytical approach less robust and therefore less desirable than the category-based analysis employed. *Responsiveness* was measured by the view provided by the stationary camcorders and consisted of responsive individuals (R) ( $\geq 1$  individuals responding with subsequent jump-yips), individuals who did not jump-yip (no response), and empty space (absence)). Each 90° quadrant (Q1-Q4) relative to the instigator was classified as responsive (R), no response (N) or absence (A). The *instigator's head orientation/scanning* within a 90° section ( $H_x$ ) corresponding with each quadrant ( $Q_x$ ) for each particular bout/trial (H1 orientation corresponded to responsiveness (either R, N, A) in Q1; H2 orientation corresponded to responsiveness in Q2, etc.; see Figure 3). Upon detecting no significant difference between no response and absence, the categories of no response and absence were pooled together and defined as non-response (NR), thereby allowing as robust a test as possible for differential orientation of instigators to areas of non-response versus areas with respondent conspecifics. *Total number of responses* was a count of the number of jump-yip responses both seen or heard within the context of a bout and *number of respondents* was a count of the number of unique individuals seen responding to a jump-yip instigation (some individuals respond multiple times). Jump-yip response *latency* was defined as the most immediate response to the instigation and responses were often heard/seen before the completion of the original instigation, and were assigned a uniform latency of 0.5 seconds if responses occurred within the 1<sup>st</sup> second. Immediate responses following jump-yip bouts are likely most relevant given that conspecific and allospecific behaviours likely exert a more profound influence on an instigator's

response as time increases (Hare & Atkins, 2001; Moeller & Frings, 2014).). Individuals were located on screen and were often visible from both the handheld camera and one of the stationary angles, which made tracking their movements and behaviour easier. *Bout duration* was defined by an absence (audible or visual) of jump-yipping for six seconds following previous jump-yip responses, signifying the termination of a bout (Hare et al., 2014; Senkiw, 2007; Smith et al., 1976). *Previous Responsiveness* measured past responsiveness in quadrants of a particular site and was characterized by the most recent preceding jump-yip bout, where  $\geq 1$  individual can be seen responding in  $\geq 1$  quadrant, and where the previous jump-yip bout was terminated within 60s–10 mins of the current bout. The instigator's head orientation during a current bout then provided two measurements, current responsiveness, which corresponded to responsiveness within the present bout, and previous responsiveness, which corresponded with responsiveness within quadrants in the bout preceding the present bout. This measurement was of interest to understand the persistence of any influence of previous jump-yip bouts relative to current bouts within a particular site and was derived from the initial stationary video coding of jump-yip bouts. Most previous bouts occurred less than five minutes from a current bout, as the natural abundance of jump-yipping in the wild is quite high (approximately 4 bouts/min., 15 jump-yips/min.; Hare et al., 2014; Senkiw, 2007). Current bouts occurring within <60s of previous bouts, previous bouts >10 minutes before current bouts and bouts prior to the first recorded bout of the day were not included in previous responsiveness analysis. The '*alert*' behaviours instigators displayed while orienting were variable, but all included gazing parallel to the ground with the head at horizon level. These behaviours included: standing on the burrow (AB); emerging from the burrow entrance (AE); standing with all four paws on the ground (AF) (termed S4D in previous studies but coined by Steiner, 1971); four paws on the ground while on

the burrow mound (AFB); resting with belly on the burrow mound with eyes open (AR); standing on two legs (AS); foraging (F); moving toward the burrow mound (FB); leaving an interaction with a conspecific (LI); resting with belly on ground and eyes open (RS); trotting (R); and walking (W). AF behaviour was the most consistent behaviour and accounted for 40% of all alert/scanning behaviour. The *instigator's behaviour before jump-yipping* was recorded similarly using the same definitions as above, with the exception of eye gaze, in that a prairie dog could be resting with eyes shut prior to instigating a jump-yip bout or foraging with their head down prior to a bout. *Town center/edge* and *ward center/edge* were initially labeled from aboveground population characteristics of size, relative population density, amount of continuous/unobstructed burrow area as observed at the time of data collection, and habitat features such as a measurable depletion of grass in an area and inactive/escape burrows bordered by noticeable vegetative rings or tree line (Garrett et al., 1982; Hoogland, 1995). Wards differed from towns in that the continuous burrow area was obstructed in some way, either visibly or acoustically from the adjacent prairie dog-occupied areas (Hoogland, 1995; King, 1959). Town and ward edges were defined by discontinuous burrow area, with two or more quadrant areas bordered by habitat 'edge' or unclipped vegetation (Garrett et al., 1982). Town Center/Edge and Ward Center/Edge labels were revisited at the University of Manitoba where GIS maps were accessed along with aerial population surveys and park map data, which displayed total acreage of the colonies in question. Three sites were changed to reflect GIS/park data, which indicated that sites were wards, not small towns as originally labeled. The within-group spatial position of an instigator was defined by the instigator's position relative to aboveground conspecifics in the area being recorded. The *instigator's location* was defined as central (located among neighbouring (~15m

away) conspecifics, burrows with active movement and clipped grass), or peripheral (neighbours >15m away, lack of active burrows and edge vegetation (tall grass, tree line; Garrett et al., 1982).

### **Data Analysis**

Video was analyzed at the University of Manitoba. All jump-yip bouts used for final analysis included one or more visible respondents, a visible and discernable jump-yip instigator, and no human interaction such as foot-traffic or vehicular encroachment. R version 3.3.1 (R Core Team, 2013) was used for analysis. Data exploration followed the recommendations of Zuur, Ieno and Elphick (2010), and thus included histograms to assess whether data conformed to the assumption of normality, boxplots to determine outliers, and a Bartlett's test to determine homogeneity of variance. I did not consider removing any statistical outliers from my sample, yet I wanted to be aware of outliers and the possible affect those 'extreme' values may have on sample means and the power of paired-sample tests (Zumbo & Jennings, 2002). To assess whether overall vigilance rates varied significantly among populations across the range sampled, a Bartlett's test was employed to test for homogeneity among total scanning within four populations (Theodore Roosevelt, Grand River, Badlands/Buffalo Gap, and Wind Cave/Custer). A non-significant p-value ( $t_{(3)} = 2.54$ ,  $P = 0.47$ ) confirmed that group variance was homogeneous and thus samples from all locations were pooled together for the analysis of spatial awareness and spatial location. It is common with discrete count data to have a high frequency of 'zeros'. My zeros are due to a lack of observed scanning by the instigator rather than a lack of information, making them 'true zeros'. For all analyses, sample size varied among analyses because of the number of bouts that are applicable from within the overall sample ( $n=91$ ), with bout instigators constituting the unit of replication for each bout, and their scanning quantified relative to conspecific response, or the lack thereof, in the four quadrants surrounding them. For

example, paired tests comparing non-responsive areas and responsive areas in ward centers required instigators to reside in ward centers, of which 23 bouts out of 91 are applicable.

### **Analysis of Spatial Awareness**

45 bouts were used in the analysis of instigator scanning between areas of no response versus areas of absence, as there were only 45 instances where a bout contained an area of both no response and absence. The independent variable consisted of the type of the response deficit; either no response from conspecifics, or absence of above-ground conspecifics. The dependent variable consisted of scanning in the 60 seconds following the termination of a jump-yip bout. A histogram of the differences between the groups did not appear to depart from normality and the groups were determined to have homogeneity of variance ( $\chi^2_{(44)} = 1.10, P = 0.30$ ). Thus, a paired-sample t-test was used to contrast the differences between the groups. I expected that instigators would spend more time scanning areas of no response than areas of absence, due in part to an awareness that conspecifics who didn't respond may be more susceptible to predation and due to a predator's strategy to prey on dense groupings of individuals (Cresswell, Lind, Kaby, Quinn, & Jakobsson, 2003; McPhee, Webb & Merrill, 2012). Additionally, terrestrial predators are especially conspicuous on open/empty habitat where prairie dogs live (Hoogland, 1995).

91 bouts were used in the analysis of scanning between areas of R and NR. The independent variable consisted of response type, either R or NR and the dependent variable consisted of time in seconds that the instigator spent scanning/orienting in the 60 seconds following the termination of a jump-yip bout. Scanning of all responsive quadrants was totaled for each bout as was non-responsive scanning so that two groups indicating responsiveness could be compared; R versus NR. A histogram plotting the residual differences between these groups appeared to be normal, however the homogeneity of variance assumption was not met ( $\chi^2_{(90)} =$

56.62,  $P = 0.0001$ ). Thus, a Wilcoxon signed-rank test was used to contrast the differences in time devoted to scanning areas with responsiveness versus non-responsiveness.

I expected instigators would spend more time orienting and/or scanning toward areas of non-responsiveness than areas of responsiveness due to the greater vulnerability that areas of non-responsiveness present.

91 bouts were used for a chi-square test of homogeneity testing for the distribution of response type (response, no response and absence) within each of the four quadrants. For each bout, a quadrant was scored as either responsive, no response or absent, thus indicating the distribution of response/non-response type across all quadrants. The null hypothesis states that the distribution of response type among each quadrant is equal (Garson & Moser, 1995), whereas I predicted that the distribution will differ due to variability in habitat, presumed predator presence and group density.

77 bouts were used in the analysis of the amount of scanning between areas of previous NR and previous R. The independent variable consisted of previous response type, either previous R (amount of time a current instigator spent scanning the quadrant(s) of previous response was used for this variable) or previous NR (amount of time a current instigator spent scanning the quadrant(s) of previous non-response was used for this variable). NR does represent the cumulative non-responsiveness from both no response and absence. The dependent variable consisted of scanning in the 60 seconds following the termination of a jump-yip bout.

A histogram of the differences between the groups appeared to be normally distributed, however the homogeneity of variance assumption was not met ( $\chi^2_{(76)} = 15.34$ ,  $P = 0.0001$ ). Thus, a Wilcoxon signed-rank test was used to contrast the differences between the groups. I expected

instigators would spend more time scanning areas of previous NR than areas of previous R given that past areas of vulnerability may still be temporally relevant for vigilant instigators.

80 bouts were used in the analysis of scanning between areas of previous NR and current NR. The independent variable consisted of non-response type, either previous NR or current NR. The dependent variable consisted of scanning in the 60 seconds following the termination of a jump-yip bout. Group variances did not depart from homogeneity ( $\chi^2_{(79)} = 0.14, P = 0.71$ ), however, a histogram of the differences between the groups appeared to depart from normality. Thus, a Wilcoxon signed-rank test was used to contrast the differences between the groups. I expected instigators would spend more time scanning areas of current NR than areas of previous NR given that the most recent contextual information is usually favoured over less recent information (Hare & Atkins, 2001; Hare et al., 2014; Macedonia & Evans, 1993). All scanning duration data are presented as Mean  $\pm$  SE unless otherwise noted, and differences were considered statistically significant where  $P \leq 0.05$ .

### **Analysis of Spatial Location**

23 bouts initiated by instigators within a town centre (TC), 34 bouts initiated by instigators at a town edge (TE), 23 bouts initiated by instigators at a ward centre (WC) and 11 bouts initiated by individuals at the ward edge (WE) were used to test for any difference in the allotment of vigilance to areas of R and NR among instigators across those 4 different social settings. The dependent variable was the duration of scanning in the 60 seconds following the termination of a jump-yip bout. A histogram displaying the differences between R and NR did not appear to conform to a normal distribution. Thus, a Wilcoxon signed-rank test was used to contrast the differences in time dedicated to scanning areas of R versus NR. I expected instigators residing in populations from central towns and wards would scan areas of R and NR

differently, as instigators residing in central towns theoretically reside in areas with more conspecifics and thus have access to more accurate shared information from group members allowing them to focus on areas devoid of conspecific response, where presumably, predators may approach undetected. Unlike those in central areas, instigators residing in peripheral towns and wards may not scan areas of R and NR differentially, owing to their heightened risk of predation associated with living on an edge, the reduced number of nearby conspecifics, or habitat features that adversely affect predator detection and/or alarm signal reception (Hoogland, 1995; Snowdon & de la Torre, 2002).

76 bouts were used to analyze the difference in scanning devoted to areas of R and NR among central instigators, and 15 bouts were used to analyze the difference in scanning devoted to areas of R and NR among edge instigators. The dependent variable was the amount of time devoted to vigilance in the 60 seconds following the termination of a jump-yip bout. A histogram of the differences between time devoted to scanning areas of response versus non-response for central instigators suggested that these data were not normally distributed, and thus a Wilcoxon signed-rank test was used to contrast differences in vigilance directed to areas of R versus NR for centralized instigators. I predicted that centralized instigators would scan areas of R and NR differentially, as it is central individuals that benefit the most by relying on the vigilance and warnings provided by neighbours, and therefore it would be expected that they focus personal vigilance on areas where they perceive a vulnerability owing to the absence of conspecific responses (Lack, 1954; Pulliam, 1973). Differences in the duration of vigilance devoted to areas of response versus non-response among edge instigators appeared to depart from a normal underlying distribution, and thus a Wilcoxon signed-rank test was used to contrast the differences in vigilance devoted to those areas for edge instigators. I predicted that edge

instigators would not scan areas of NR and R differentially, as they are foraging in the area type imposing the highest risk of predation (Elgar 1989), and thus should devote vigilance to all areas regardless of conspecific responsiveness. As was the case with the data addressing spatial awareness, scanning duration data exploring effects of colony type and an instigator's location within a group are presented as Mean  $\pm$  SE unless otherwise noted. Differences were again considered statistically significant where  $P \leq 0.05$ .

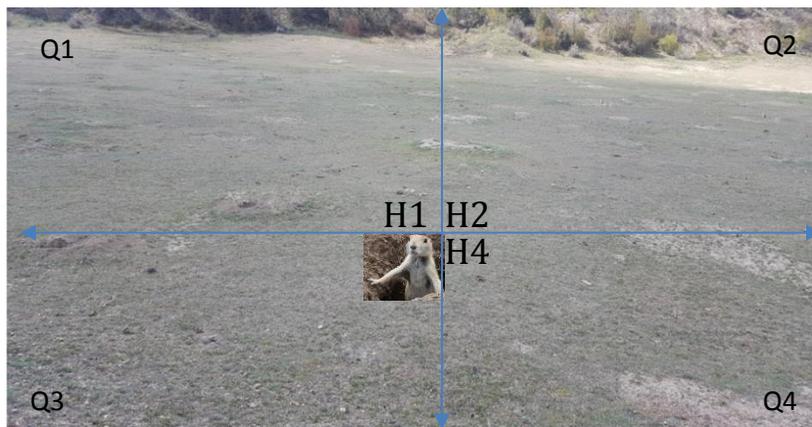
Table 1. Black-tailed prairie dog populations studied and their geographic locations within the National Park/National Grassland observed in this study.

<b>Location</b>	<b>GPS Coordinates</b>
Theodore Roosevelt National Park	46°56.022'N 103°31.132'W 47°57.253'N 103°30.585'W 46°58.732'N 103°29.489'W 46°58.756'N 103°28.931'W 46°57.091'N 103°30.421'W 46°56.965'N 103°30.193'W 46°55.876'N 103°30.816'W
Grand River National Grasslands	45°42.914'N 102°14.060'W
Buffalo Gap National Grasslands	45°42.480'N 102°12.341'W 43°44.730'N 102°11.917'W 43°46.112'N 102°11.921'W 43°52.782'N 102°14.330'W 43°48.818'N 102°9.521'W 43°48.289'N 102°8.212'W 43°43.161'N 102°13.201'W 43°44.532'N 102°28.788'W
Badlands National Park	43°46.112'N 102°11.920'W 43°54.889'N 102°20.284'W 43°54.162'N 102°19.529'W
Wind Cave National Park	43°31.223'N 103°29.084'W 43°34.423'N 103°29.269'W 43°37.536'N 103°29.538'W 43°37.603'N 103°26.313'W 43°32.199'N 103°29.816'W 43°33.014'N 103°28.376'W 43°34.429'N 103°23.237'W
Custer State Park	43°34.428'N 103°23.238'W

Figure 2. Example of combined stationary camcorder viewpoints, where above-ground conspecifics are either responsive or non-responsive within an area.



Figure 3. A hypothetical jump-yip instigator who is scanning H3 and where responsiveness corresponds to Q3.



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## RESULTS

### Descriptive characteristics of bouts analysed

In all cases, prairie dogs reduced alarm calling and postural orientation toward the vehicle after approximately ten minutes of no activity from myself or movement of the vehicle. Activity and response rate (ranging from 1-12 responses) of aboveground individuals varied among bouts, with an average of four jump-yip responses, an average of 13 individuals aboveground during a bout, with an average of 31% of aboveground individuals displaying a response to a bout. 84% of instigators were clustered among visible neighbours and active burrows (central), and 16% of instigators were distanced ~15m or more from visible active burrows and/or were surrounded by edge vegetation (peripheral).

### Awareness

A paired-sample t-test compared time spent alert in the 60 seconds following a jump-yip bout in the direction of non-responsive areas, areas without aboveground prairie dogs (absent areas) versus areas where prairie dogs were aboveground but did not respond to the instigation of a jump-yip bout (no response areas). Instigator scanning did not differ between absent and no response areas (Figure 4;  $t_{(44)} = 0.925$ ,  $P = 0.180$ ). A Wilcoxon signed-rank test was employed to compare scanning in the 60 seconds following a jump-yip bout in the direction of quadrants designated as non-responsive (combined no response and absence) versus responsive. Instigators spent significantly more time oriented toward areas of non-response (NR) ( $20.02 \pm 20.46$ ; mean  $\pm$  SE) than to areas of response (R) ( $5.85 \pm 9.69$ ) following a jump-yip bout (Figure 5;  $Z = -4.74$ ,  $P = 0.0001$ ,  $d = 0.50$ ). A chi-square test was used to test for any relationship between quadrant area and response/non-response type (response, no response and absence) over the 91 jump-yip

bouts documented. The distribution of response type was not equally distributed among quadrants ( $\chi^2_{(6)} = 33.72$ ,  $P = 0.00001$ ; Table 2).

Figure 4. Boxplot displaying the time instigators spent alert/scanning in the minute following a jump-yip bout in the direction of either absent areas and no response areas. The black horizontal line within each box represents the median, while the upper and lower bounds of the box represent the interquartile range. Whiskers encompass times that fall within  $(1.5 * (\text{upper quartile} - \text{lower quartile}))$ , delineating outlying data points that are plotted individually outside the range of the whiskers

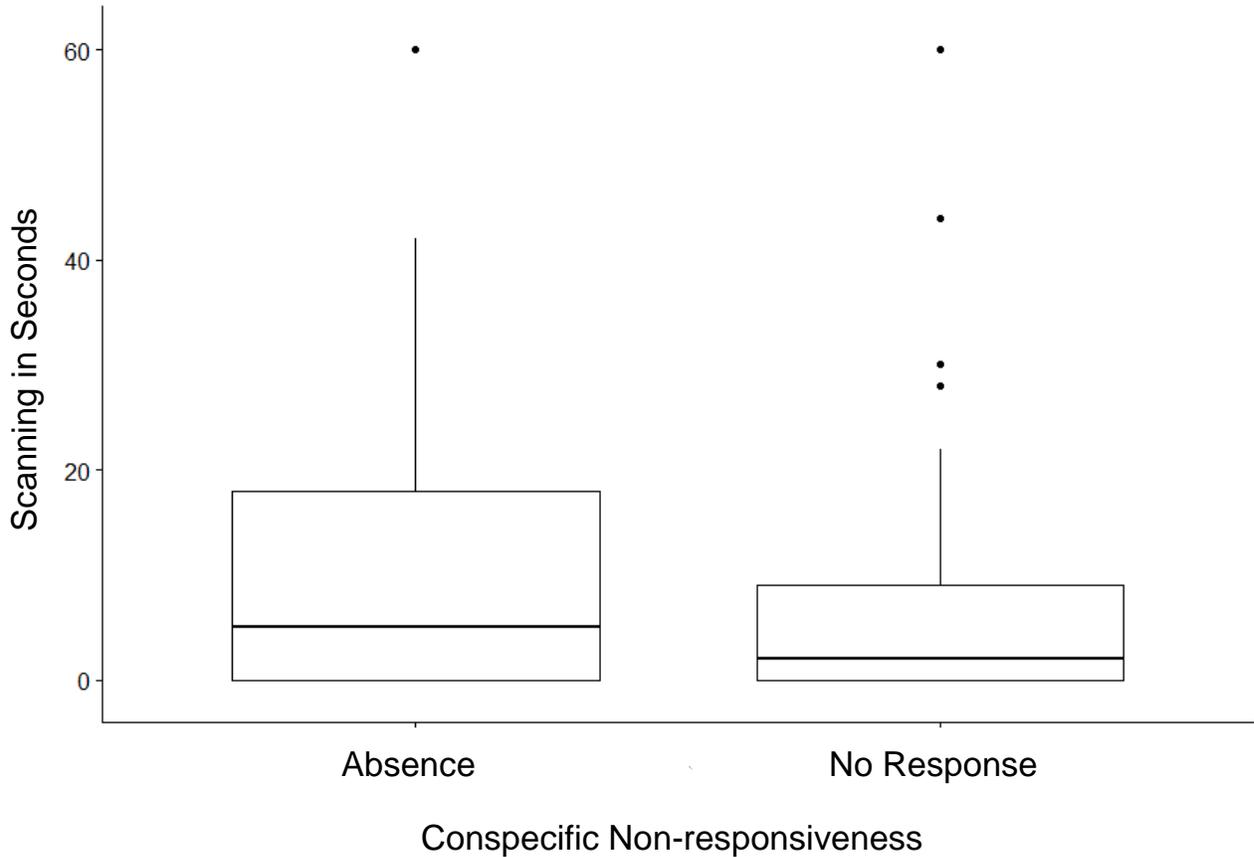


Figure 5. Boxplot displaying the time instigators spent alert/scanning in the minute following a jump-yip bout in the direction of non-responsive areas and responsive areas. The black horizontal line within each box represents the median, while the upper and lower bounds of the box represent the interquartile range. Whiskers encompass times that fall within  $(1.5 * (\text{upper quartile} - \text{lower quartile}))$ , delineating outlying data points that are plotted individually outside the range of the whiskers.

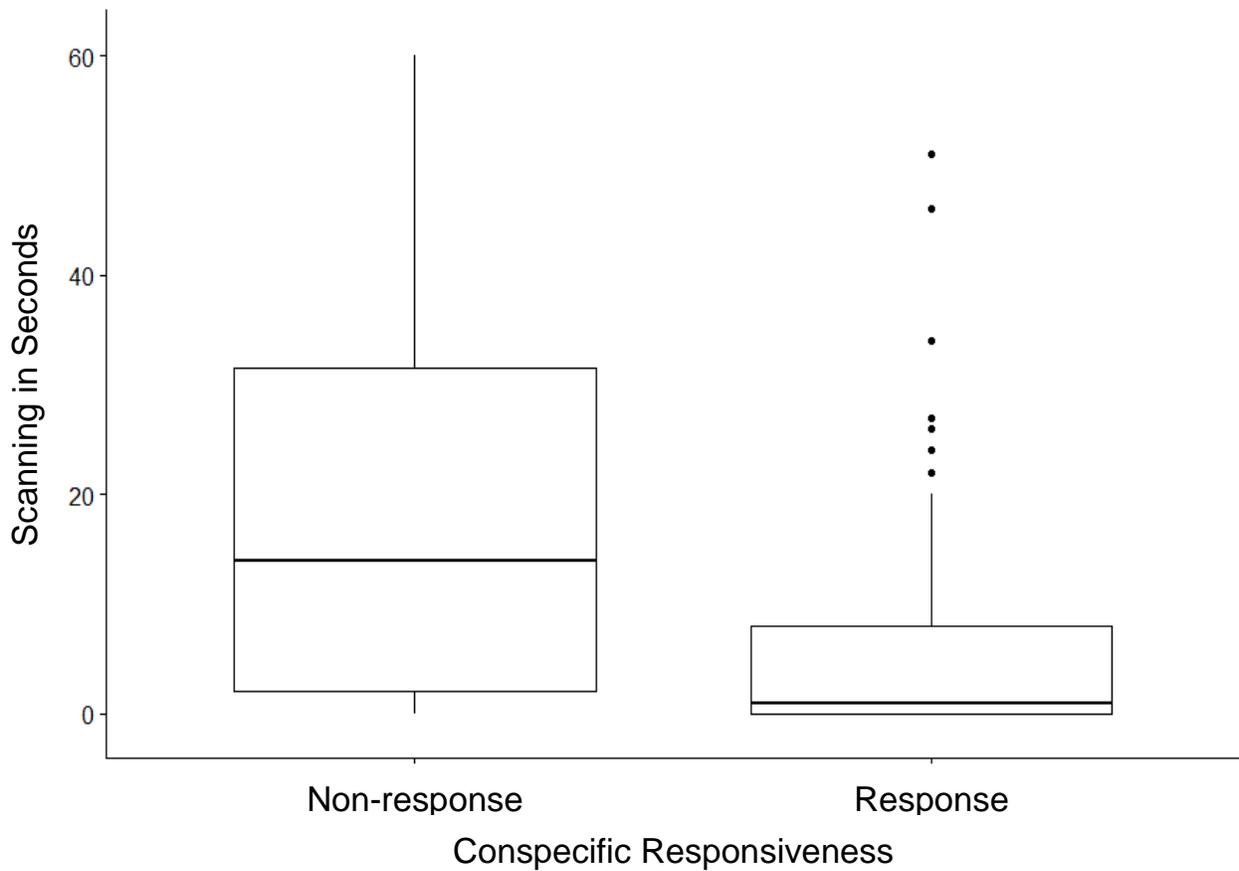


Table 2. Distribution of response types (response, no response and absence) across the four quadrants (Q1-Q4) over the 91 jump-yip bouts documented.

	Response	No response	Absence	Total
Q1	42	29	20	91
Q2	39	38	14	91
Q3	18	30	43	91
Q4	27	41	23	91
Total	126	138	100	364

$\chi^2 = 33.72$ , **df = 6**, **P( $\chi^2 > 33.72 = 0.00001$ )**

A Wilcoxon signed-rank test compared scanning in the 60 seconds following a jump-yip bout in the direction of areas of previous non-response and areas of previous response. Instigators spent significantly more time oriented toward areas of previous non-response ( $21.25 \pm 20.45$ ), than toward areas of previous response ( $7.74 \pm 14.19$ ) to a jump-yip bout (Figure 6;  $Z = 0.42$ ,  $P = 0.0001$ ,  $d = 0.02$ ). A Wilcoxon signed-rank test detected no significant difference between the amount of scanning directed toward areas of previous non-response versus areas of current non-response (Figure 7;  $Z = -0.29$ ,  $P = 0.77$ ,  $d = 0.03$ ).

Figure 6. Boxplot displaying the time instigators spent alert/scanning in the minute following a jump-yip bout in the direction of areas that were past areas of non-response and response. The black horizontal line within each box represents the median, while the upper and lower bounds of the box represent the interquartile range. Whiskers encompass times that fall within  $(1.5 * (\text{upper quartile} - \text{lower quartile}))$ , delineating outlying data points that are plotted individually outside the range of the whiskers.

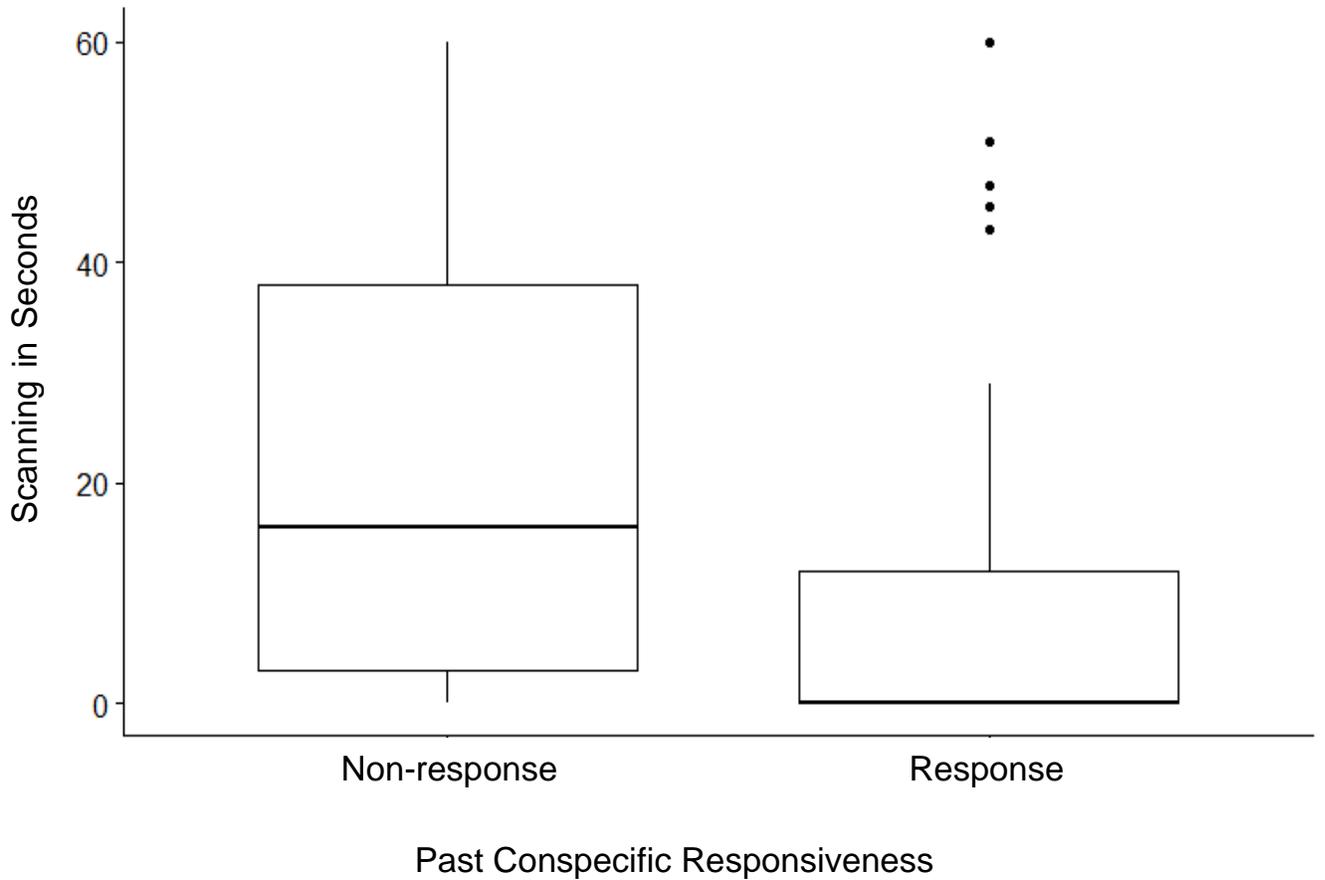
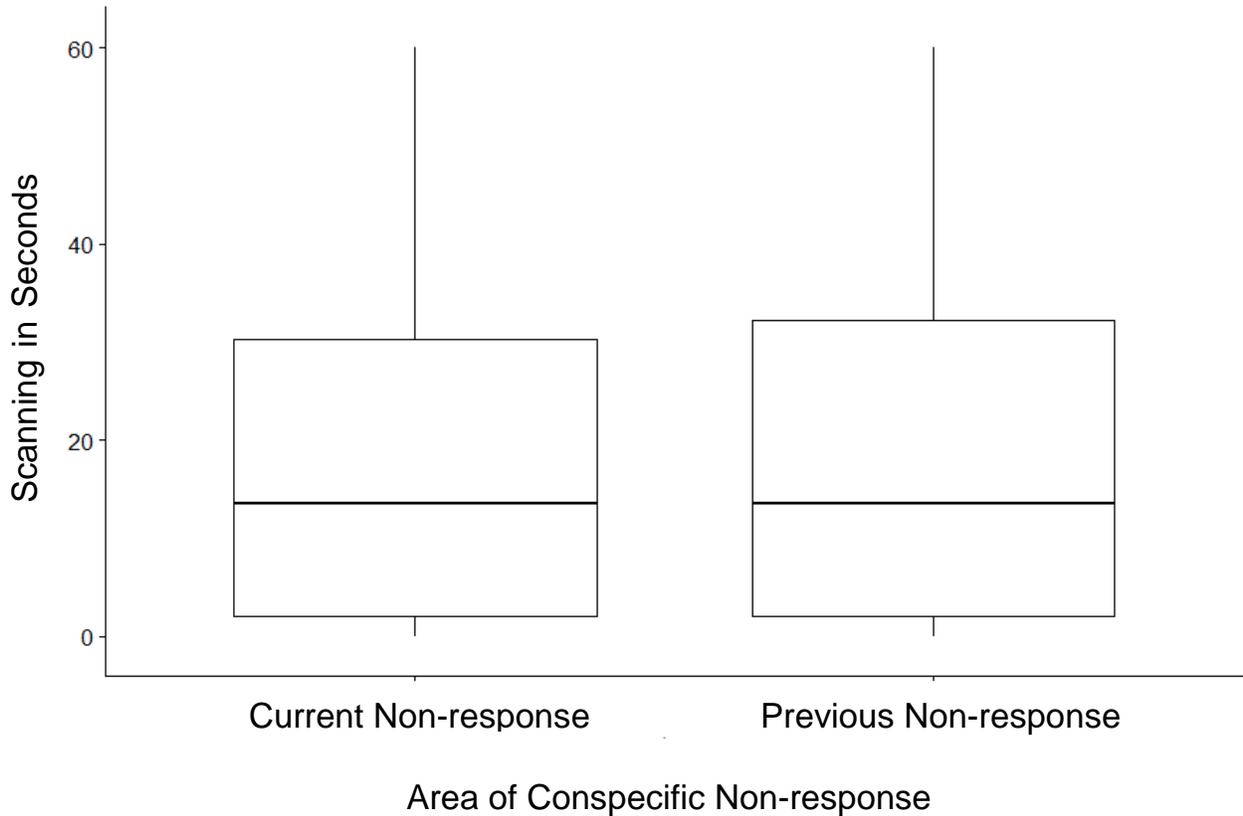


Figure 7. Boxplot displaying the time instigators spent alert/scanning in the minute following a jump-yip bout in the direction of areas that were currently non-responsive and areas that were previously non-responsive. The black horizontal line within each box represents the median, while the upper and lower bounds of the box represent the interquartile range. Whiskers encompass times that fall within  $(1.5 * (\text{upper quartile} - \text{lower quartile}))$ , delineating outlying data points that are plotted individually outside the range of the whiskers.



## Spatial Location

A Wilcoxon signed-rank test was used to contrast the differences in time devoted to scanning areas of R and NR within each colony location type (TC, TE, WC, WE). Instigators residing in town centers spent significantly more time (Figure 8;  $Z = -2.01$ ,  $P = 0.044$ ,  $d = 0.42$ ) oriented toward areas of NR ( $22.43 \pm 22.03$ ), than areas of R ( $10.00 \pm 15.20$ ). Instigators residing in ward centers spent significantly more time (Figure 9;  $Z = -2.71$ ,  $P = 0.007$ ,  $d = 0.56$ ) oriented toward areas of NR ( $18.48 \pm 19.70$ ), than areas of R ( $4.13 \pm 6.33$ ). Instigators residing on town edges spent significantly more time (Figure 10;  $Z = -3.52$ ,  $P = 0.0002$ ,  $d = 0.60$ ) oriented toward areas of NR ( $20.35 \pm 19.67$ ), than areas of R ( $4.56 \pm 7.47$ ). Instigators residing on ward edges did not orient differentially toward areas of NR versus R (Figure 11;  $Z = -1.25$ ,  $P = 0.20$ ,  $d = 0.39$ ).

Wilcoxon signed-rank tests was used to contrast NR/R scanning differences among central instigators ( $n=84$ ), as well as NR/R scanning differences among edge instigators ( $n=16$ ).

Centrally-located instigators spent significantly more time (Figure 12;  $Z = -4.77$ ,  $P = 0.00001$ ,  $d = 0.55$ ) oriented toward areas of NR ( $19.82 \pm 19.85$ ) than to areas of R ( $5.22 \pm 8.38$ ).

Peripherally located instigators did not orient differentially toward areas of NR versus areas of R (Figure 13;  $Z = -0.02$ ,  $P = 0.17$ ,  $d = 0.41$ ).

Figure 8. Boxplot displaying the time instigators residing in a central town spent alert/scanning in the minute following a jump-yip bout in the direction of non-responsive areas and responsive areas. The black horizontal line within each box represents the median, while the upper and lower bounds of the box represent the interquartile range. Whiskers encompass times that fall within  $(1.5 * (\text{upper quartile} - \text{lower quartile}))$ , delineating outlying data points that are plotted individually outside the range of the whiskers.

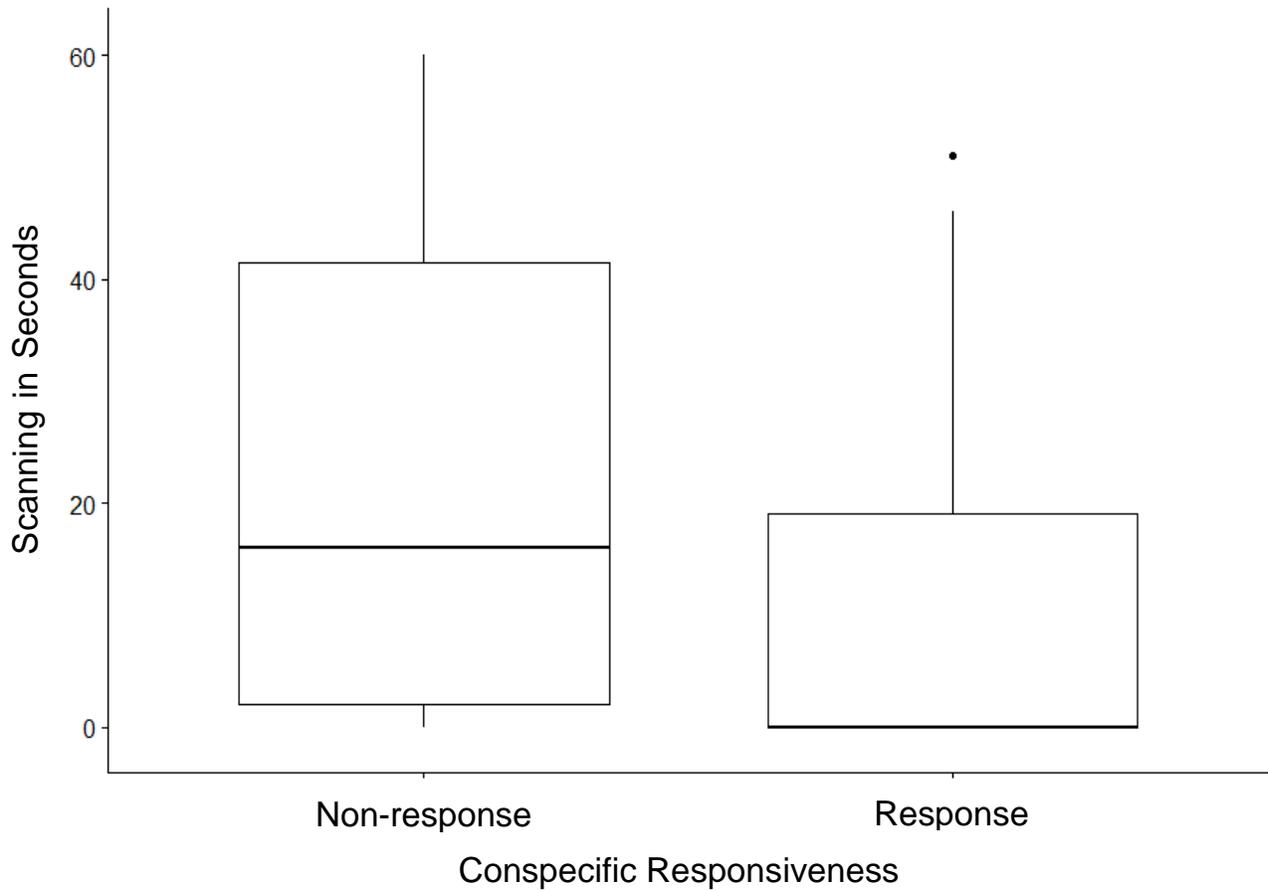


Figure 9. Boxplot displaying the time instigators residing in a central ward spent alert/scanning in the minute following a jump-yip bout in the direction of non-responsive areas and responsive areas. The black horizontal line within each box represents the median, while the upper and lower bounds of the box represent the interquartile range. Whiskers encompass times that fall within  $(1.5 * (\text{upper quartile} - \text{lower quartile}))$ , delineating outlying data points that are plotted individually outside the range of the whiskers.

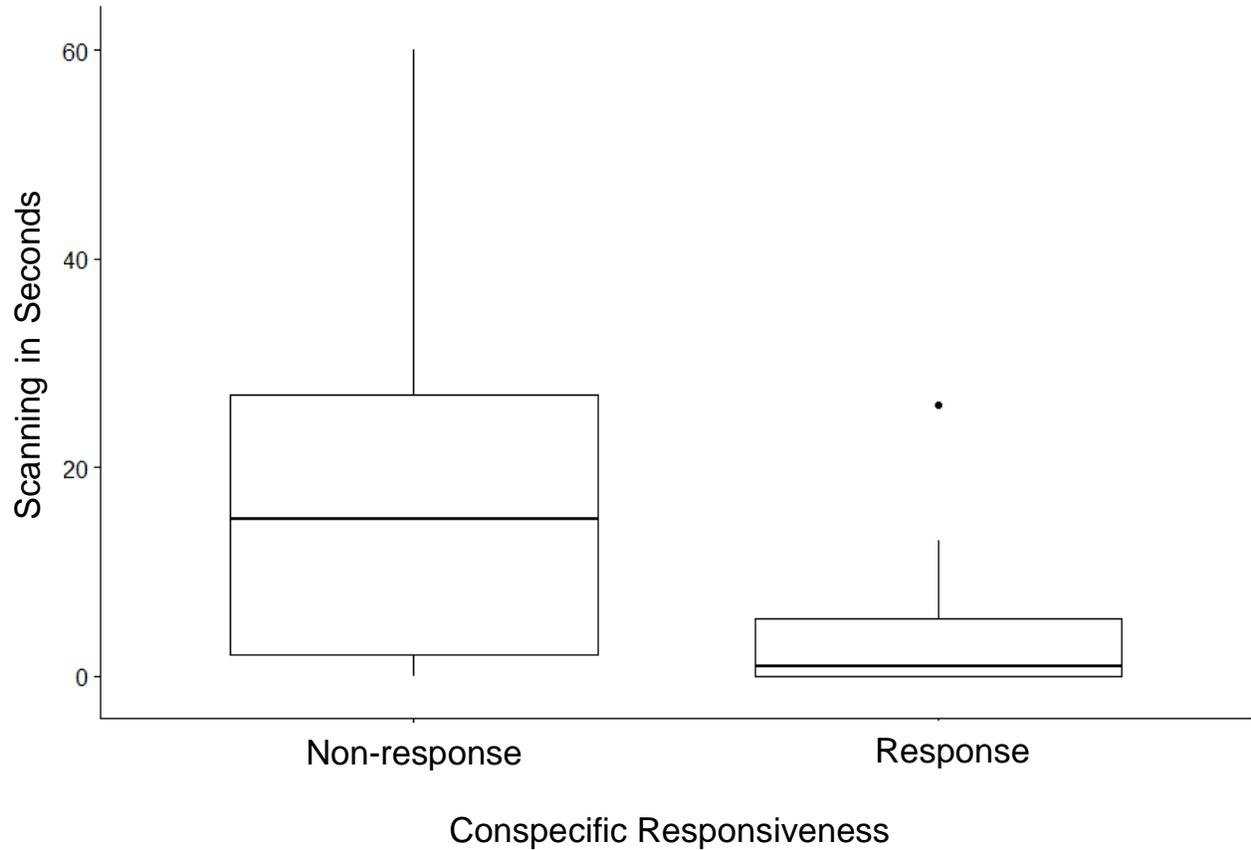


Figure 10. Boxplot displaying the time instigators residing in a peripheral town spent alert/scanning in the minute following a jump-yip bout in the direction of non-responsive areas and responsive areas. The black horizontal line within each box represents the median, while the upper and lower bounds of the box represent the interquartile range. Whiskers encompass times that fall within  $(1.5 * (\text{upper quartile} - \text{lower quartile}))$ , delineating outlying data points that are plotted individually outside the range of the whiskers.

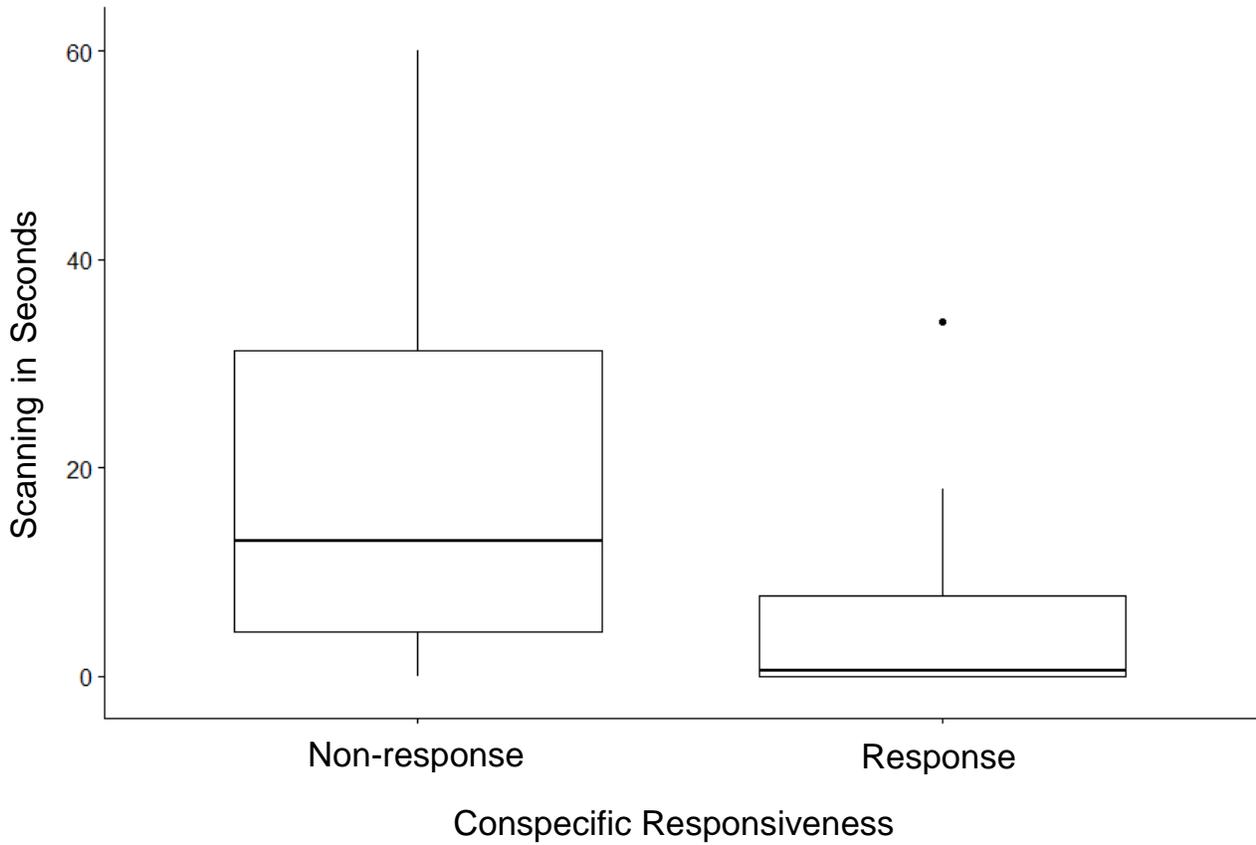


Figure 11. Boxplot displaying the time an instigator residing in a peripheral ward spent alert/scanning in the minute following a jump-yip bout in the direction of non-responsive areas and responsive areas. The black horizontal line within each box represents the median, while the upper and lower bounds of the box represent the interquartile range. Whiskers encompass times that fall within  $(1.5 * (\text{upper quartile} - \text{lower quartile}))$ , delineating outlying data points that are plotted individually outside the range of the whiskers.

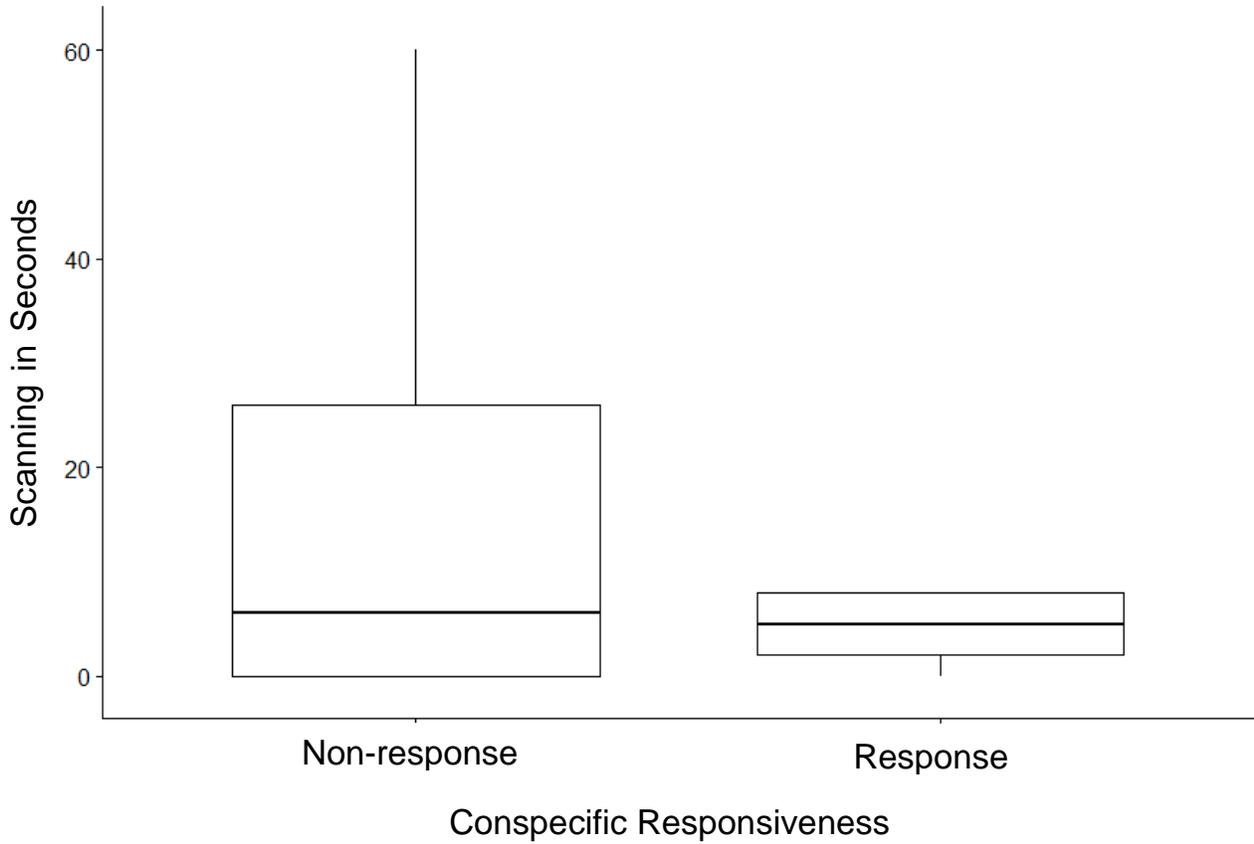


Figure 12. Boxplot displaying the time instigators who are centrally-located to observed conspecifics spent alert/scanning in the minute following a jump-yip bout in the direction of non-responsive areas and responsive areas. The black horizontal line within each box represents the median, while the upper and lower bounds of the box represent the interquartile range. Whiskers encompass times that fall within  $(1.5 * (\text{upper quartile} - \text{lower quartile}))$ , delineating outlying data points that are plotted individually outside the range of the whiskers.

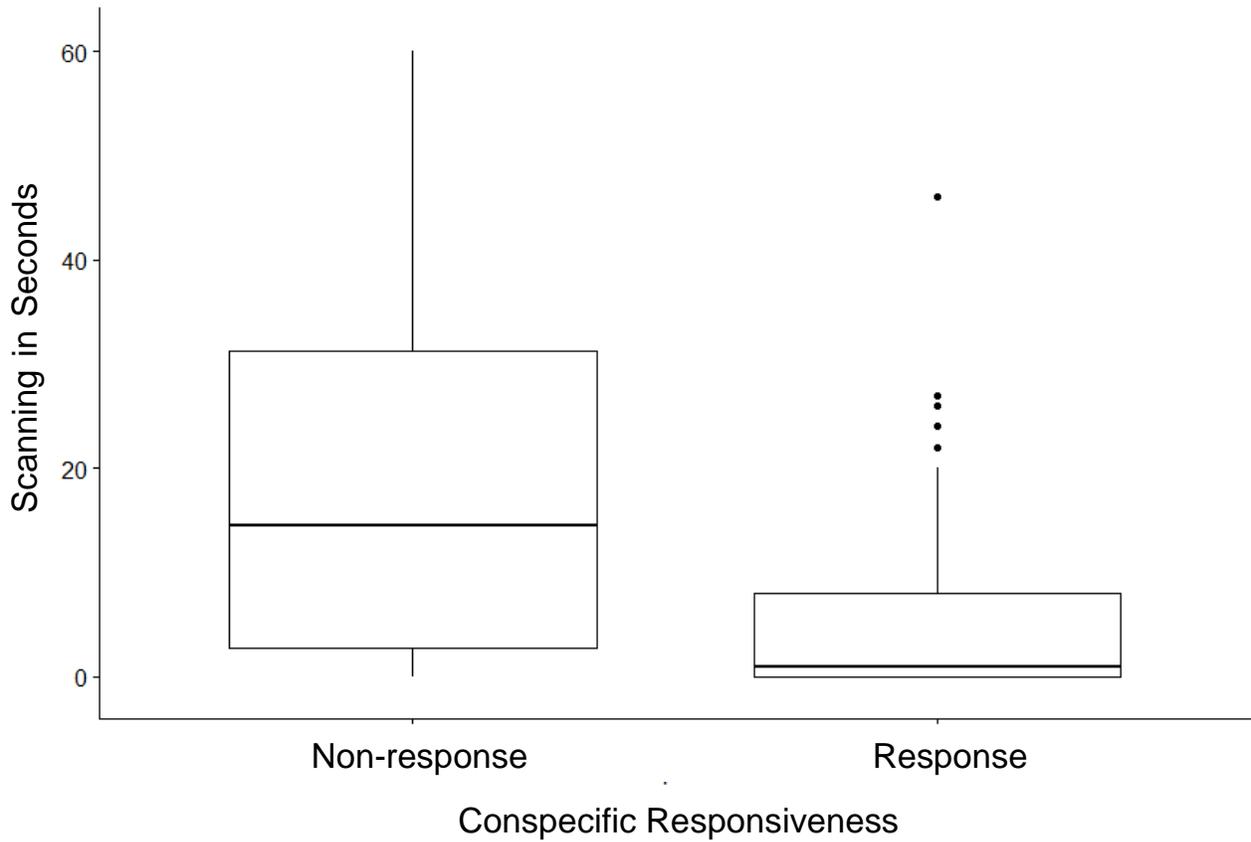
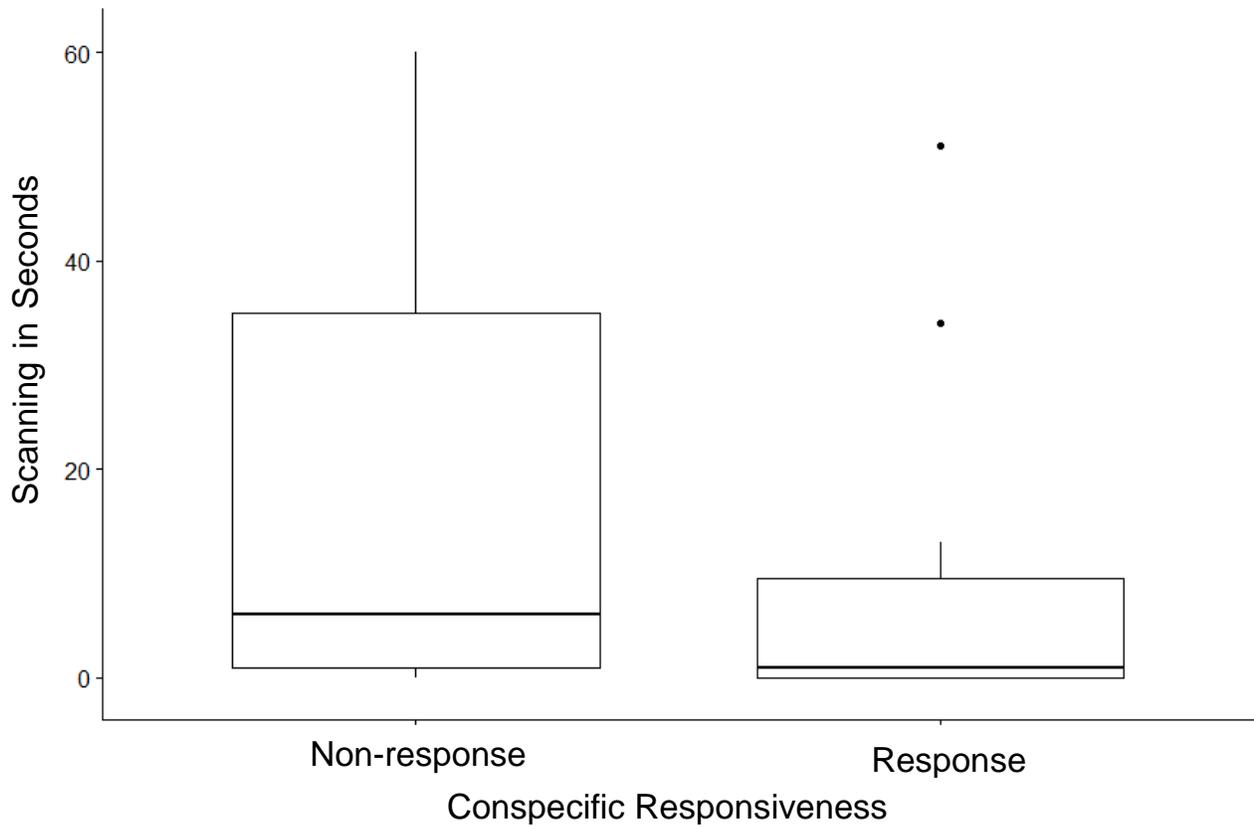


Figure 13. Boxplot displaying the time edge instigators spent alert/scanning in the minute following a jump-yip bout in the direction of non-responsive areas and responsive areas. The black horizontal line within each box represents the median, while the upper and lower bounds of the box represent the interquartile range. Whiskers encompass times that fall within  $(1.5 * (\text{upper quartile} - \text{lower quartile}))$ , delineating outlying data points that are plotted individually outside the range of the whiskers.



## **DISCUSSION**

Using field-collected video observations of the head orientation of BTPDs following jump-yip instigation, and contrasting vigilance devoted by bout instigators toward areas with responsive versus non-responsive conspecifics, my results reveal that BTPDs selectively monitor areas that lack alert group members. Additionally, my results reveal that this selective scanning is most evident within centrally-located individuals within towns or wards, whereas individuals residing in peripheral wards or peripheral to nearby neighbours do not adjust scanning relative to conspecific presence or responsiveness. These findings indicate that BTPDs are spatially aware of their neighbour's vigilance, adjusting their personal vigilance relative to the threat of presumptive predators escaping detection by conspecifics.

### **Spatial Awareness Influences**

I detected no significant difference between the time jump-yip instigators spent scanning areas with conspecifics that did not respond and areas where conspecifics were entirely absent. This finding reveals that at least in terms of the allocation of personal vigilance, bout instigators perceive those two area types to be of similar importance. Although predators may preferentially approach and attack individuals within areas of high prey density, they may also utilize empty space to travel undetected (McPhee, Webb & Merrill, 2012). I predicted that the presence of even a non-vigilant group member would be more beneficial than empty space, because the presence of an individual at least allows the possibility of that individual becoming vigilant or detecting an approaching predator. It is possible, however, that areas I deemed as "empty space" were only recently vacated, or that individuals present there were not visible to me or the cameras, but that prairie dog group members were aware of their existence.

Jump-yip bout instigators spent more time orienting personal vigilance toward areas of diminished neighbour response than toward areas with response. Previous research exploring

collective behaviour indicates that group members assess each other's vigilance levels (Hare et al., 2014; Roberts, 1996) and that both conspecific actions and experiences affect decision-making in animal groups (Kao, Miller, Torney, Hartnett & Couzin, 2014). Greater white-fronted geese (*Anser albifrons*) estimate flock size and regulate their time budget for foraging accordingly (Lazarus, 1978). Ring-tailed coati (*Nasua nasua*) are least vigilant when in central locations and reduce vigilance as the number of neighbours within 5 meters increases (Di Blanco & Hirsch, 2006). Similarly, wild mustached (*Saguinus mystax*) and saddleback (*S. fuscicollis*) tamarins are less vigilant around close (<2m) conspecifics and tend to increase social behaviours (grooming) around close conspecifics (Stojan-Dolar & Heymann, 2010). The 'many eyes' hypothesis is central to such findings, as group members who are in fact vigilant can reduce their latency to detect a potential threat through the use of predator-associated cues emanating from conspecifics, and thus have more time to forage (Pulliam, 1973; Lack, 1954).

Responsiveness and non-responsiveness within quadrants, as well as the absence of conspecifics altogether, reflects variation in the habitat surrounding bout instigators as the areas observed can be bordered by continuous burrows, vegetation, cliffs or steep slopes, tree line and or roads. Although individuals could be equally dispersed among quadrants, Q3 and Q4 contained conspecifics only 28% of the time bouts were instigated. The habitat features of quadrants likely influence whether conspecifics are present and responsive (Braga & Motta-Junior, 2009; Snowdon & de la Torre, 2002). Q3 and Q4 were closest to the road or pullout where my vehicle was parked and were often bordered by taller, unclipped vegetation. Q1 and Q2 had the highest rates of responsiveness and were usually furthest from any roads.

My results also indicated that there was no difference in the amount of time devoted to scanning areas of previous non-response versus areas of current non-response. This was

expected, as during the time spent at a particular colony, areas devoid of response and those with response often remained more or less consistent. Unoccupied areas typically remained without above-ground occupants, non-responders often remained more or less non-responsive, and more often than not, one or two quadrants would be particularly active where certain unique individuals would routinely instigate or respond to the instigation of jump-yip bouts. This confirms the well-recognized problem of autocorrelation between past and present space use in animal population research (Patterson, Thomas, Wilcox, Ovaskainen & Matthiopoulos, 2008). However, instigators did spend more time oriented toward areas of previous non-response than to areas of previous response, suggesting that they retain at least a short-term memory of past areas of response and non-response. This information would promote a more complete understanding of one's past and present environment, which is apparent in other animals that selectively avoid areas of previous danger (Ferrari, Wisenden & Chivers, 2010; Laundré, Hernández & Altendorf, 2001; Lima, 1998). However, a more comprehensive study documenting spatiotemporal patterns of vigilance within prairie dog towns over a longer time period would be necessary to elucidate the temporal scale over which prairie dogs attend to and adjust their own vigilance relative to the vigilance of their neighbours.

### **Spatial Location Influences**

When considering the spatial location and social environment of instigators relative to neighbouring conspecifics within a site, my results reveal that selection has favoured scanning toward areas of non-responsiveness for jump-yip bout instigators residing in central areas of the site in general, or within towns or wards. Instigators residing on ward edges and those peripherally located to neighbours did not orient differentially toward areas of response versus non-response. This difference is interesting given that the response rate of central instigators and

edge instigators was similar, as were the durations of jump-yipping bouts observed in those areas. If jump-yipping recruitment had been lower for instigators residing in peripheral areas, any difference in the infectious nature of this contagion between central and peripheral areas could be attributed to the greater density of clustered individuals in central areas, where reciprocity is commonly observed among neighbours (Briefer, Rybak & Aubin, 2010; Couzin, 2009). In fact, the number of conspecifics recruited in peripheral areas was not lower than recruitment in central areas, indicating that edge instigators may be constrained by the greater risk of predation they experience and devote greater effort to personal vigilance (Hamilton, 1971; Pulliam, 1973). Instigators residing in ward edges experience pronounced visual obstructions, where the jump-yip signal and response could be distorted by hills and tall vegetation (Garrett, Hoogland, & Franklin, 1982; Hoogland, 1995). Additionally, Hoogland (1995) also notes that fragmented wards are the least efficient at detecting predators. It is possible that edge instigator attention is limited by an awareness of their increased predation risk, perhaps impairing their ability to account for responsive conspecifics in the area. This type of impaired judgement is evident in juvenile salmon, which are slower to respond to food items when the threat of predation is increased (Metcalf, Huntingford & Thorpe, 1987).

Greater access to public information among central individuals is well documented in cases where the information center hypothesis applies (Campobello & Hare, 2007; Ward & Zahavi, 1973). This enhanced access to information in central areas may also select for a greater reliance on public versus personal information among centrally-located individuals. This difference could also result from members who are more successful at outcompeting other members of a prairie town occupying more central positions surrounded by conspecifics (Hoogland, 1979), which would thus experience reduced predation risk relative to more

peripherally-located subordinate individuals (Elgar, 1989; Hoogland, 1995) though without data on the relative dominance of individuals relative to their location within groups, this interpretation remains speculative. Foraging ring-tailed coati are reported to assess vigilance using within-group spatial position cues to assess risk, where dominant individuals often lead a densely clustered group (Di Blanco & Hirsch, 2006). A more comprehensive understanding of how predation risk and patterns of vigilance are distributed within prairie dog towns would require a more in-depth study of prairie dog distribution and movements in the context of predator visitation, which goes beyond the scope of the data at hand.

### **Bias, Limitations and Future Directions**

My results would have been more robust if I had been able to capture a larger area of conspecific response to jump-yip instigation. There were many instances in which the video cameras failed to capture the full extent of the jump-yip response within the colony, and excluded responses of conspecifics that were on the opposite side of the vehicle I used as a blind. Reports of prairie dog jump-yipping bouts including hundreds of individuals within a colony (certainly more than the number of individuals occupying a coterie territory; Hoogland, 1995), suggests that the overall size and distribution of the population may influence the public transfer of information. A camera with a 360° field of view would likely provide a more comprehensive view of overall conspecific response. That said, based upon my efforts to employ a multi-camera DVR-based system during my first field season, obtaining reliable data from this type of system may also prove problematic given the atypical behaviour (retreat to burrows, sustained avoidance of area containing the system, sustained alarm calling directed at tripods and urination/chewing of the system) that prairie dogs displayed when a novel object was placed within their colony.

Another potential confound would be the influence the presence of a human observer and stationary vehicle has on the natural behaviour of prairie dogs. While my deployment of a multi-camera DVR-based recording system in my 2016 field season was an attempt to reduce human presence as much as possible, the camera system itself proved unreliable, and no viable data were obtained. Although the prairie dogs I video-recorded did not orient toward my vehicle and emit alarm calls, I did note that individuals foraging near the road mostly vacated the area after I parked. Thus, although they did not seem particularly alarmed by my presence, they did adjust their distance from me and moved to a different foraging patch. The influence that human behaviour and proximity has on the behaviour of subjects has been reported by Ciuti et al. (2012) who reported that the majority of behavioural variability (80%) in elk, was due to human-based factors (rather than predation, habitat or breeding), and Blumstein et al. (2005) who reported avian species become alert at greater distances from approaching predators when they are in close proximity to humans. Human presence may be an unavoidable influence, as most prairie dog populations are now confined to protected parks, parks are frequented by humans, and many park roads navigate directly through prairie dog towns. My presence may not have applied differentially to conspecific response or non-response, but it could have influenced the absence of conspecifics from Q3 and Q4.

A future study could also build upon the current understanding of prairie dog spatial awareness by manipulating where 'responsiveness' is presumed to come from, given that in the area I studied only 31% of the area constituted 'responsiveness'. With acoustic playback, the orientation of instigator vigilance following a bout could be observed to determine the importance of the instigator seeing jump-yip respondents. There were many situations where instigators were not facing responsive conspecifics either before or after bouts, leading me to

believe the acoustic nature of the call could be enough for an instigator to determine responsiveness within a particular area. Multi-modality is certainly important for this call in order for the display to be conspicuous for group members near and far, and thus ensures that individuals obstructed from hearing the call may see it and individuals obstructed from seeing the call may hear it. It is possible that less recruitment would occur during these manipulated trials, given that recruitment is likely sensitive to the multi-modal nature of the signal, but the question would be whether or not the instigator perceives response if only hearing it. Therefore, it would be interesting to control where acoustic ‘yips’ spatially originate from and manipulate colony responsiveness so that ~50% - 75% of the colony is ‘responsive’, with less area reflecting non-responsiveness, to see if instigators continue to refine their scanning. Additionally, with artificial ‘added’ responsiveness, there may be a decrease in the rate of vigilance from an instigator following bouts, if an instigator perceives more surrounding area to be occupied by responsive conspecifics. This could lead to an increased understanding of the group size effect on vigilance in both towns, wards and clustered individuals and their perceived level of presumed responsiveness while foraging.

Future research would also benefit from working with marked individuals of known relatedness, so that any patterns of response attributable to the relatedness of callers and respondents, or to differential familiarity among those individuals could be documented (Hoogland, 1995). This, however, goes well beyond the scope of the present study where it was deemed that replication at the level of towns was more important to the questions at hand regarding orientation to non-responsiveness than was knowledge of specific individuals. While these considerations acknowledge potential confounding factors and constitute potential refinements of the methods employed, it remains the fact that in spite of such factors, which were

consistent across all groups observed, centrally-located individuals focus their personal vigilance selectively on areas devoid of conspecific response. This finding reveals that black-tailed prairie dog's knowledge of their neighbour's vigilance, derived via the assessment of conspecific response to the instigation of a jump-yip bout, is spatially explicit.

## CONCLUSION

This study is the first to describe spatial awareness through the adjustment of personal vigilance to compensate for areas of non-responsiveness in BTPDs, areas that would presumably allow predators to approach undetected. Jump-yip instigators adjusted their allocation of personal vigilance according to socially-acquired information gathered by attending to responses of conspecific group members within jump-yip bouts. BTPDs rely extensively on public information regarding conspecific responsiveness to the jump-yip, a socially contagious signal, particularly when bout instigators are central. The spatial location of individuals, whether at the town, ward or coterie scale, was a significant factor influencing whether bout instigator's selectively directed personal vigilance to areas devoid of response. Centrally-located bout instigators selectively oriented toward areas of non-response after jump-yipping bouts, while peripheral instigators did not selectively focus vigilance on areas of non-response. Jump-yipping was primarily instigated by central individuals, clumped together within a site, suggesting that instigation is more common among grouped individuals, where group members benefit from the exchange of public information. Density-dependent collective behaviours have been documented frequently among species exhibiting navigational movement (Di Blanco & Hirsch, 2006) in the context of both flocking (Lazarus, 1979) and schooling (Pitcher, Wyche & Magurran, 1982). Edge instigators appear to rely more upon personal information when determining when and where to be vigilant, consistent with their greater risk of predation. The contexts in which prairie dogs exhibit jump-yips, and the patterns of responsiveness that emerge are influential for prairie dog communication and group cohesiveness. The cognitive ability to recognize vulnerabilities within space and time also adds black-tailed prairie dogs to a growing list of animals that show evidence of spatiotemporal awareness when mating (Schwagmeyer, 1994), foraging (Sherry,

Jacobs & Gaulin, 1992) landmark learning (Cartwright & Collett, 1983) maintaining territories (Sherry, 1998), and vigilance (Adachi, 2014; Di Blanco & Hirsch, 2006). Knowing the response characteristics of BTPD jump-yip instigators to the spatial distribution of conspecific responsiveness within their social groups constitutes a significant step toward assessing attentional state, and promoting a more comprehensive understanding of the intricacies of shared information use and cognitive abilities of non-human animals.

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