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Density dependence in social behaviour: home range overlap and density interacts to affect conspecific encounter rates in a gregarious ungulate

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Abstract Sociality is poorly understood in the context of population processes. We used wild, female elk (*Cervus canadensis*) equipped with proximity-logging radio collars ($n = 62$) from Manitoba, Canada (2007–2009), to test for modifying effects of population density (two areas: 0.42 and 0.22 animals/km^2) on the relationship between two measures of sociality. This included the rate at which collared individuals encountered one another per year (encounters logged as animals ranging to within 1.4 m of each other) and the extent to which animals overlapped in annual home range (proportion of shared minimum convex polygon ranges). Overlap was significantly greater in the high density area compared to that of the low, but not if we only considered individuals that directly encountered each other, implying that familiar individuals will maintain a constant degree of range overlap regardless of density. Encounter rate was nonlinearly related to home range overlap. This relationship was also density-dependent, exhibiting negative density dependence at high proportions of overlap, primarily in the high density subpopulation. Sociality, as defined by two interacting measures of behaviour—encounter rate and home range overlap—exhibits a complex nonlinear relationship; we discuss the implications

of these results as they pertain to sociobiology, resource competition, and pathogen transmission.

Introduction

Sociality is broadly defined as the properties and processes of social existence (Wilson 1975). Ecologists interested in sociality seek to inform us about the ecological and evolutionary factors that promote and maintain interactions between conspecifics leading to group living. Despite broad acceptance that density-dependent processes are fundamental to ecology, density dependence in the study of sociality has thus far received limited attention (but see Bateman et al. 2012; Vander Wal et al. 2012a, 2013a; Cross et al. 2013).

Sociality in group-living species can be quantified through multiple measures, for example, when two individuals directly encounter each other and express social behaviours (i.e., dyadic interactions or encounters). Dyadic encounters provide the foundation for analysing social structure, as interactions form the basis for relationships between individuals (Hinde 1976; Whitehead 1997). From dyadic interactions, a second level of organisation is often assumed to emerge. This occurs at the extent where individuals are observed to share the same area or range. For example, associations of larger movement patterns over longer time periods that reflect group associations and shared (or avoided) space use. The reverse assumption—that such spatial patterns imply fine-scale interactions—may be referred to as the 'gambit of the group' (Franks et al. 2010). Here, individuals seen grouping together (e.g., sharing home ranges or travelling together in a school or herd) are assumed to be directly interacting with every other individual in that group.

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But do high levels of association in space always imply high rates of encounter between animals (dyads)? If a group is formed due to the fusion of two smaller groups, individuals of founding groups are known to interact with one another at different rates after the fusion event (Millspaugh et al. 2004a; Couzin 2006). Also, familial associations (Dubost 1970; Clutton-Brock et al. 1982; Wronski and Apio 2006) may bias the relationship between large-scale overlap in movements and fine-scale interactions. These are considerations internal to the dynamics of a group, but how well spatial overlap and indirect associations match with direct encounters of dyads might also be affected by the extrinsic ecological factors that define the costs and benefits of group living.

Foremost among external factors affecting group dynamics is conspecific density and the process of resource competition, e.g., for food or mates. Density is known to affect group size and composition (Ruckstuhl and Festa-Bianchet 2001; Pépin and Gerard 2008; Vander Wal et al. 2013a). It has further been shown to affect dyadic encounter rates and encounter duration in experimental settings (Vander Wal et al. 2012a), and to increase agonistic behaviour (Pettit-Riley et al. 2002; Moyle et al. 2009). Density is also known to decrease mobility (e.g., 'social fence' hypothesis (Matthysen 2005)), necessitating an increase in home range overlap with higher abundance (e.g., rodents (Ostfeld et al. 1985; Ferron and Ouellet 1989; Erlinge et al. 1990; Steury and Murray 2003), felids (Nielsen and Woolf 2001), and ursids (Dahle and Swenson 2003)). Conversely, very low population densities may have consequences to social behaviour and breeding ecology, giving rise to Allee effects (Brashares et al. 2010). If densities directly follow from resource availability (i.e., habitat *sensu* Morris (2003)), nonlinearity in range separation (territoriality) may be apparent, with overlap occurring at low and very high levels of density (food abundance (see White 2004 for review)), but not moderate levels where the relative costs of food or territory defence are low. This situation has been observed in bears (McLoughlin et al. 2000), bats (Chaverri et al. 2007), and birds (Carpenter and Macmillen 1976). Recognising the complex nature of how home range overlap is determined and how density might affect encounter rates, what can we expect for the relationship between range overlap and the rate of direct encounter between dyads as density increases? This aspect of sociality is poorly understood.

Quantifying the relationship between home range overlap and encounter rate is of vital importance to studies on the evolution of sociality and to assess the risk of pathogen transmission, especially in studies where home range overlap is used as a proxy for encounter (or even contact) rates (see Whitehead and Dufault (1999) for review; Robert et al. 2012). Here, we test the prediction of increased encounter rate with increasing home range overlap. From this prediction, we constructed a hierarchical set of competing models (Tables 1 and S1). These include that patterns in encounter rate can be

Table 1 *A priori* models and model selection for dyadic encounter rate per year (response variable) as a function of proportion of home range overlap (HRO) for female elk in two subpopulations of Riding Mountain National Park, Manitoba, Canada (2007–2009): the east low density subpopulation (0.22 elk/km^2) and the west high density subpopulation (0.42 elk/km^2). Models compose three concepts of increasing complexity: (1) simple linear relationships (M_1, M_2) or additive effects (M_3) can describe the relationship between HRO, density, and encounter rate; (2) a feedback exists between HRO and density (M_4); and (3) nonlinearity in encounter rate by HRO results from possible competitive effects or avoidance (M_5); or the global model (M_6). See Supplementary Table S1 for further details

Models	Independent	ΔAIC^a	$AIC_w{}^b$
M_1	HRO	>10	0
M_2	Density	>10	0
M_3	HRO+Density	>10	0
M_4	HRO+Density+HRO*Density	>10	0
M_5	HRO+HRO^2+Density	0	0.61
M_6	HRO+HRO^2+Density+HRO*Density	0.9	0.39

[a] Change in Akaike's Information Criteria value

[b] Akaike's Information Criteria model weight

explained by home range overlap and subpopulation density independently (M_1, M_2) or their additive effect (M_3). Alternately, home-range overlap interacts with density to create a positive feedback (M_4) or, possibly due to competitive effects, nonlinearity exists between home range overlap and encounter rate (M_5). Finally, we evaluate a global model encompassing both the home range overlap by density feedback and the nonlinearity predictions (M_6). We test these models using wild, female elk ($n = 62$) equipped with proximity-logging radio collars from two discrete subpopulations in Riding Mountain National Park (RMNP), Manitoba, Canada (2007–2009), which vary markedly in their density. Female elk are highly gregarious, and we assumed that the higher the overlap in home range, the more strongly individuals were associated with the group using that range (Franklin et al. 1975; Millspaugh et al. 2004a). We discuss the implications of our findings as it relates to the density dependence of sociality and the applications to sociobiology and modelling the dynamics of communicable disease (e.g., in the elk of RMNP which are affected by bovine tuberculosis, TB).

Methods

Study site and animals

Riding Mountain National Park, Manitoba, Canada (RMNP, 3,000 km^2, Fig. S1) lies on the ecotone of the Boreal Plains and Prairie Parkland biomes (Rowe 1972; Caners and Kenkel 2003). An elevation gradient exists in RMNP: the eastern portions of the park rise 475 m from the Manitoba lowlands

up the Manitoba escarpment. As a result, variation exists in the habitat. At high elevations, the boreal forest dominated by mixedwood forests includes spruce (*Picea Marianna* and *P. glauca*), pine (*Pinus banksiana*), and aspen (*Populous tremuloides*) that are interspersed with waterways, open fens, and bogs. At lower elevations, open marshes and remnant fescue prairie are interspersed in a matrix of aspen parkland and mixedwood forests. RMNP is essentially a closed system surrounded by an agricultural matrix (for further details, see Vander Wal 2011).

RMNP is a refuge for many species of wildlife, including a population of free-ranging elk. There are two distinct subpopulations of elk in the park (Vander Wal et al. 2012b, 2013b) which occur at different densities: east 0.22 elk/km^2 and west 0.42 elk/km^2 (hereafter 'low' and 'high' relative density, respectively). Subpopulation densities were derived from a 3-year average (2007–2009) of a 25 % coverage aerial survey of visible elk (Parks Canada unpublished data, see Vander Wal 2011 and Vander Wal et al. 2013a for details of survey design).

Elk are considered the reservoir host for bovine tuberculosis (TB, *Mycobacterium bovis*) in the region (see Brook and McLachlan (2006) and Shury and Bergeson (2011) for details). Presence of TB has had considerable economic impacts on the region (Nishi et al. 2006; Brook and McLachlan 2006) as elk are known to co-mingle with cattle (*Bos taurus*; Brook et al. 2013). TB is, however, predominantly restricted to the western subpopulation of RMNP elk (Shury and Bergeson 2011; Vander Wal et al. 2012b).

Proximity-logging radio collars

Proximity-logging radio collars (SirTrack, Havelock North, New Zealand) are a recent technology which quantify encounters between two marked individuals whenever they are within a pre-determined distance from one another (see Cross et al. 2012 for review). Measures of spatial proximity (hereafter encounters) between individuals are used to infer social behaviours such as interactions and direct contact between individuals (e.g., see Ji et al. 2005; Prange et al. 2006; Walrath et al. 2011; Cross et al. 2012; Robert et al. 2012, 2013; Vander Wal et al. 2012a, b; Vander Wal et al. 2013c for examples). Traditionally, studies have relied on radio-tracking data to infer dyadic encounters between individuals, with an encounter (typically referred to as a 'contact') being defined as broadly as two individuals logging spatial locations within 100 m of each other (White and Harris 1994; Ramsey et al. 2002; Schauber et al. 2007; Kjaer et al. 2008). The advent of proximity collars has greatly improved our ability to continuously detect close spatial associations (Ji et al. 2005; Prange et al. 2006; Goodman 2007; Cross et al. 2012) at scales, in locations, and at times previously unavailable and inaccessible with either traditional ethological techniques or satellite- and radio-telemetry.

We programmed proximity collars to record dyadic encounters whenever two collared elk came to within 1.42 ± 0.20 m ($\bar{x} \pm SD$) of one another, (Goodman 2007). For technical reasons (see Goodman 2007), collars deactivated recording an encounter at a distance of 1.98 ± 1.60 m each time a pair separated for >30 s ($\bar{x} \pm SD$, Goodman 2007). As individuals were not observed directly interacting, or physically contacting, we are left to assume that these social behaviours (i.e., indicators of sociality) were being exhibited when the two animals are engaged in an encounter with one another; we assume these encounters do not occur randomly due to the highly social nature of elk. For encounters to be recorded, the elk needed to be within one body length of a collared conspecific. For further discussion regarding proximity collars and data treatment, see Robert et al. (2013) and Vander Wal et al. (2013c).

Animals

We used a net-gun fired from a helicopter (Cattet et al. 2004) to capture female elk ($n = 24$ in 2007 and $n = 15$ in 2008 [high density subpopulation] and $n = 23$ in 2008 [low density subpopulation]). We equipped each animal with proximity collars. Collars were deployed simultaneously and recorded encounters for all dyads within the replicate for 1 year (February–February). The female elk in our study represented a random sample of the adult population, and no correlation between spatial proximity and genetic relatedness was found (Vander Wal et al. 2012b). We relocated the animals several times throughout the year ($\bar{x} = 30.4$) by fixed-wing aircraft (Cessna 172) during daylight hours, usually 0800–1900 h, two to four times per month (see Vander Wal et al. 2011 for details). Animals were collared for equivalent time and collars either dropped off via mechanical release or animals were recaptured and collars removed.

Home range overlap

We determined home range overlap of tracked elk using ArcMap (ArcGIS 9.3, ESRI Redlands California, USA) and the Home Range Tools extension (Rodgers et al. 2005) to calculate 95 % minimum convex polygons. Minimum convex polygons were used due to their ease in comparison across studies and a limited number of relocations (see Fig. S2 for further discussion). We used an index of overlap based on the formula presented by (Millspaugh et al. 2004b):

$$\text{Overlap} = \frac{A_{1,2}}{(A_1 + A_2) - A_{1,2}} \qquad (1)$$

where A_1 and A_2 are the areas of the home ranges of animals 1 and 2, respectively, and $A_{1,2}$ is the area of overlap between

individual 1 and 2. (See Fig. S3 for an example of low, medium, and high range overlap).

Statistical analysis

We tested the relationship between dyadic encounter rate among dyads and home range overlap at the two subpopulation densities using six *a priori* models (Table 1). The simplest of which predicts that univariate tests of whether home range overlap or subpopulation density independently best predict encounter rate (M_1, M_2). Subsequently, we test whether subpopulation density and home range overlap (M_3) and the interaction between the two (M_4) better predict encounter rate. Lastly, we test whether these are better described by including a quadratic term to describe the non-linearity in the relationship (M_5, M_6). Models were ranked based on their parsimony evaluated using Akaike's Information Criteria (AIC; Burnham and Anderson 2002). All models with a ΔAIC<2 were considered indistinguishable. Indistinguishable models were consequently averaged using the R package MuMIn (Barton 2010).

Frequencies of encounters were count data; therefore, all generalised linear models included a Poisson distributed error term. Because logically an animal with no overlap in their home ranges cannot have had fine-scale pairwise encounters, we forced the regression through the origin. We added subpopulation density to the model as a fixed two-level factor ($M_{2–6}$) and its interaction with home range overlap ($M_{4 \text{ and } 6}$). Our dyads were not replicated across years, precluding the use of mixed-effects generalised linear models typically used to control pseudo-replication in pairwise observations. Instead, we randomised the generalised linear model (Manly 1998) to generate a distribution of z-values against which we tested the significance of each covariate. We ran 1,000 iterations of the linear regression with $n=1,000$ randomised samples. This does not fully account for pseudo-replication, but it does ensure that patterns in these data are not statistical artefacts. All statistics were performed in R version 2.15 (2012).

Results

The mean number of encounters per dyad was 65.7±9.2 (both densities pooled). Dyads at high (0.42 elk/km^2) density had more encounters (83.8±12.4, $n=709$) than dyads at low (0.22 elk/km^2) density (16.7±4.4, $n=506$).

The mean home range size of female elk was 42.5±4.5 km^2 ($\overline{x} \pm$ SE) in the high density subpopulation and 34.4±5.9 km^2 in the low density subpopulation. Mean home range overlap per dyad among all dyadic pairs in each study site varied between study areas, with overlap greater in the higher density subpopulation (0.13±0.007) than in the lower density subpopulation (0.07±0.006). However, when non-interacting dyads were excluded from the analysis of home range overlap,

overlap was not different in the two density treatments (high: 0.18±0.008, low: 0.18±0.012; Fig. 1).

Frequency of encounters was nonlinearly related to home range overlap and varied by subpopulation density (Fig. 2). *A priori* models M_5 and M_6, including subpopulation density, home range overlap, its quadratic term (M_5), and the interaction between home range overlap and subpopulation density (M_6), were the most parsimonious (AIC$_w$, $M_5=0.61$, $M_6=0.39$; Table 1). This was despite the additional interaction term in H_6 being nonsignificant ($z=-1.05$, $p=0.29$; Table 2). Home range overlap and subpopulation density all had significant effects in the models ($p<0.001$; Table 2). Results did not differ for models where the intercept was permitted to vary from 0 (data not shown).

Discussion

Density dependence in social behaviour can have important implications for population dynamics (Bateman et al. 2012) and disease prevalence (Lloyd-Smith et al. 2005). In both instances, the mechanisms of these density-dependent effects occur at the fine spatial scale of pairwise encounters, e.g., interference competition or pathogen transmission (Krause and Ruxton 2002). However, the effect of density on these encounters has rarely been explored (but see Vander Wal et al. 2012a; Cross et al. 2013). Here, we described not only density dependence but also how it is modified in a nonlinear fashion
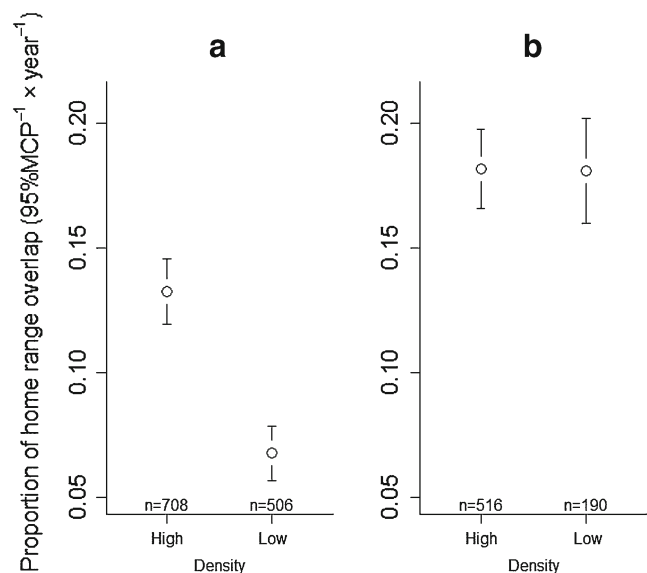
Fig. 1 Mean proportion of home range overlap in female elk of Riding Mountain National Park, Manitoba, Canada (2007–2009). **a** Represents the mean (95 % CI) when all dyads were considered within each study region; **b** the mean proportion of shared space when only individuals with overlapping ranges were considered. Overlapping dyads shared similar home range overlap at both densities, but overlapped with more individuals at higher densities
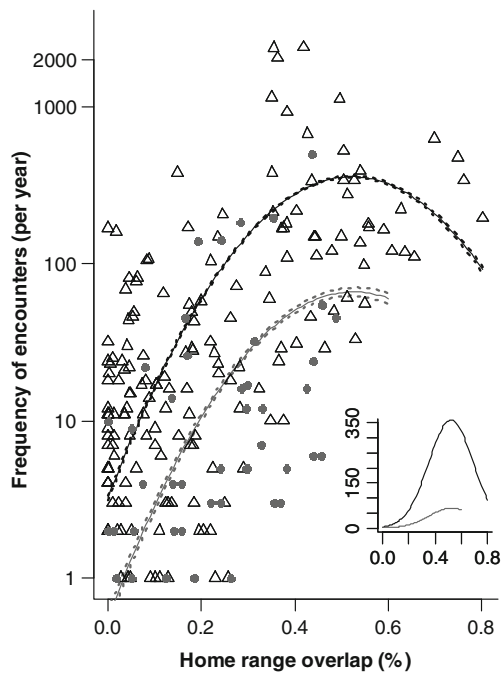
Fig. 2 Encounter rate per dyad versus home range overlap for female elk in Riding Mountain National Park, Manitoba, Canada (2007–2009) for two subpopulations experiencing different densities: high density (0.42 elk/km^2, triangles); and low density, 0.22 elk/km^2 (*grey circles*). Predicted values from a generalised linear model (averaged M$_5$ and M$_6$, see Table 2) are plotted as *lines* with 95 % CI (high density in *black*, low density in *grey*). Inset, predictions plotted in anti-log space, illustrate how encounter rates saturate (for low density, *grey line*) and exhibit negative density dependence (at high density, *black line*)

by shared space use between individuals. For example, due to nonlinear effects thresholds appear where increased home range overlap may lead to a saturated frequency of fine-scale dyadic encounters (Fig. 1, low density subpopulation) or even avoidance of fine-scale dyadic encounters (Fig. 1, high density subpopulation). Saturation of encounters and avoidance

Table 2 Averaged (M$_5$, M$_6$ Table 1) generalised linear model with Poisson error distribution for dyadic encounter rate per year by proportion of home range overlap for female elk in two subpopulations of Riding Mountain National Park, Manitoba, Canada (2007–2009): the east, low density (0.22 elk/km^2) and the west, high density (0.42 elk/km^2)

	Coefficient (Unconditional SE)	z-value[a]	P-value
HRO[b]	18.04 (0.13)	135.05 (−40.93–46.24)	<0.001
HRO^2	−17.18 (0.13)	130.10 (−48.00–46.77)	<0.001
Low density	−0.55 (0.04)	−13.62 (331.42–557.47)	<0.001
High density	1.17 (0.01)	60.00 (327.13–531.61)	<0.001
HRO[*]density	−0.14 (0.13)	−1.05 (−51.63–43.03)	0.294

[a] 95 %CI generated by randomising the frequency of encounters in a generalised linear model to test whether the outcome could have been generated randomly and thus may have been a function of pseudo-replication due to pairwise data

[b] Home range overlap

suggests that benefits of social behaviour may become costs when two individuals share a large extent of their home range.

Within the shared space, individuals compete over resources (Rieucau and Giraldeau 2011). Direct competition may require more encounters at higher density than low, regardless of how much range is actually shared between individuals. Weckerly (1999) found that aggressive interactions increased in elk with increasing population density, suggesting that as resources became scarcer, defending them was more important. Conversely, in an experimental manipulation of domestic sheep, Mobæk et al. (2012) found there was no evidence for interference competition or the defence of resources. They did, however, demonstrate that animals at high density (low resource abundance) spent more time active. Being active increases the probability of encountering conspecifics. Indeed, Vander Wal et al. (2012a) found that increasing density increased encounter rates in an experimental setting that was not resource-limited. One hypothesis which follows is that increased encounter rates may be proximally attributed to resource availability, but ultimately a function of social phenomena, such as allogrooming or maintaining a hierarchy.

Nevertheless, the nonlinearity and density dependence of our results imply an important, yet unexplored, interplay between local habitat (e.g., structure, resource availability) and encounter rate—one that might vary geographically across the range of our study species. For example, in ungulates open habitats—such as those found in RMNP—are known to result in larger groupings due to emergent group properties (Gerard and Loisel 1995) or increased predation risk (Hebblewhite and Pletscher 2002). Increased group size has been shown to increase encounter rate (Cross et al. 2013). Increased gregarity also precipitates increased home range overlap. Conversely, complex habitats break groups apart (Haydon et al. 2008; Fortin et al. 2009), decreasing the shared space use between individuals. As a result, open habitats are predicted to increase home range overlap and encounter rates. For elk, open habitats with abundant graminoids are known to be preferred habitats (Christianson and Creel 2007), likely supporting higher densities of animals.

Higher densities of elk also result in larger groups (Vander Wal et al. 2013b). Larger groups may be composed of more familiar individuals, as individuals in larger groups may have been able to associate on a smaller scale with more individuals over longer periods of time than those living at lower densities (smaller groups). Familiar animals will interact with one another at higher rates (Millspaugh et al. 2004a; Couzin 2006). Albeit these individuals are often kin; here, encounters among elk are equally likely to be among unrelated individuals (Vander Wal et al. 2012b). Nevertheless, it may be that females must experience a trade-off between interference competition (direct encounters) with other individuals versus scramble competition (avoiding or sharing less space with

conspecifics and lower home range overlap). Or, similarly, the trade-off may occur along a gradient of conflict within interference competition (e.g., proximal avoidance versus avoiding physical contact). These trade-offs may be contingent on the relationships that exist between animals at different densities, the availability of resources within home ranges, and their seasonal use (see Vander Wal et al. 2013c for details on seasonal encounter rates).

Albeit infrequently tested (but see Robert et al. 2012), it has been assumed that home range overlap can be used as a proxy for encounter rate (see review by Whitehead and Dufault (1999)). Certainly our findings corroborate this finding; however, with the important caveat that the relationships can be expected to be both nonlinear and density-dependent. Therefore, this assumption may be flawed due to the fact that it is likely site-specific. One area where this assumption has been applied is in wildlife disease ecology.

Sociobiology and disease ecology are quickly finding common ground, as the mechanisms for horizontal pathogen transmission involve individual social encounters (Tompkins et al. 2011). Home range overlap has been used as a proxy for risk of disease transmission (Caley et al. 1998; Ramsey et al. 2002; Schauber et al. 2007). Although our results confirm a correlation between home range overlap and encounter rate, they also caution that the relationship, similar to disease transmission, can be modified by host density. Our results indicate that at high population density, female elk compensate by sharing space with more conspecifics, but share the same amount of space per dyad than at lower density. This may result in increased disease transmission as infected hosts will associate more with susceptible conspecifics, an important element in disease transmission (McCallum et al. 2001). However, as home range overlap increases encounter rates saturate and are predicted to decrease, suggesting that elk are avoiding fine-scale social interactions when shared space use is high (e.g., >40 %). This result varies in magnitude. Nevertheless, it illustrates disproportionally fewer encounters, which therefore may predict decreased pathogen transmission. Some social behaviours, e.g., group size, have been shown to increase the prevalence of directly transmissible pathogens and parasites (Côté and Poulin 1995). Fine-scale social avoidance, however, could be a mechanism to mitigate this transmission. This relationship, however, is also affected by conspecific density. For example, increased density has been shown to increase the risk of parasitic infection, which consequently effects annual reproductive success (Albon et al. 2002).

Our study was a large-scale natural 'experiment' which capitalised on existing natural variation between discrete subpopulations. A strength of our design is that it occurred in a wild population (cf., captive elk used in Vander Wal et al. 2012a). A weakness, however, was failure to replicate density. Although, the relationship between home range overlap and encounter rate was well-replicated, our density treatment was perfectly pseudo-replicated (Hurlbert 1984)—technically

limiting our capacity to make inferences outside of our study system. Given that density has been shown to affect encounter rates (Vander Wal et al. 2012a) and home range overlap (e.g., Steury and Murray 2003; Nielsen and Woolf 2001; Dahle and Swenson 2003), we submit that density likely had a modifying effect on the relationship between home range overlap and encounter rate in our study. However, density itself may be affected by other differences between subpopulations, including habitat, which we do not disentangle here. Indeed, due to density-dependent habitat selection theory, some authors (e.g., Morris 2003) suggest that the definition of habitat needs to include both resources and density.

In summary, our results identified three key findings. First, encounter rate is affected by shared space use; thus, illustrating a possible mechanism to minimise competition and pathogen transmission by avoiding fine-scale encounters when shared space use is high. Second, this relationship is density-dependent, with encounters occurring at dramatically higher rates in high density landscapes. Ultimately, this questions the validity of assuming that shared space use correlates directly with encounter rate. Although a correlation clearly exists, it appears to be context-dependent; as such, we caution against generalising between systems. In addition to these findings, we have identified two important gaps in research into density-dependent social behaviour. The first is to better understand the role of habitat (e.g., structure and resource availability) in shaping social encounters. The second is to highlight the need to integrate data derived from proximity-detecting technology with traditional ethological techniques to identify which social behaviours are being expressed within each encounter.

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Author contributions

EVW conceived and designed the study. EVW collected the data. EVW and MPL analysed the data. EVW, MPL, and PDM interpreted the results. EVW, MPL, and PDM wrote and critically revised the manuscript.