

# Effects of phenology and sex on social proximity in a gregarious ungulate

E. Vander Wal, P.C. Paquet, F. Messier, and P.D. McLoughlin

**Abstract:** Structure in sociality is known to relate to intrinsic and extrinsic factors. Less understood are the mechanics of sociality expressed as fine-scale behaviours that maintain hierarchies, mediate competition, or transmit pathogens. A recent novel approach to quantifying fine-scale social behaviour has been to use proximity-logging biotelemetry collars. This technology continuously records data whenever collars are within a predefined distance of each other, at times of day, and in habitats where traditional ethological approaches to focal-individual sampling of behaviours are unfeasible. We tested a series of expectations on fine-scale ( $\leq 1.4$  m) interaction rates and durations consistent with competing hypotheses of seasonal and sexual segregation for elk (*Cervus canadensis* Erxleben, 1777). Female–female dyads interacted 4 times more frequently than male–male dyads (mean interaction rate per year: female–female = 62 vs. male–male = 14;  $P < 0.001$ ), and male–male interactions were 1.5 times longer in duration than female–female interactions (mean interaction length: female–female = 30 s vs. male–male = 45 s;  $P < 0.001$ ). We propose that fine-scale interactions among members of a population can be modeled as a trade-off between the frequency (quantity) and the duration (quality) of interactions. Our results have implications for understanding sex-based differences in sociality in gregarious herbivores and for disease transmission, which may follow from social intercourse.

**Key words:** behaviour, *Cervus canadensis*, disease, elk, sexual segregation, sociality.

**Résumé :** Il est établi que la structure dans la socialité est associée à des facteurs intrinsèques et extrinsèques. La mécanique de la socialité exprimée par l'entremise de comportements à petite échelle qui maintiennent les hiérarchies, modulent la concurrence ou transmettent des pathogènes est toutefois moins bien comprise. Une nouvelle approche de quantification des comportements sociaux à petite échelle consiste à utiliser des colliers de biotélémetrie qui enregistrent la présence d'autres individus situés à proximité. Cette technologie enregistre des données en continu quand des colliers se trouvent en deçà d'une distance donnée les uns des autres, à des heures du jour et dans des habitats où les approches éthologiques traditionnelles d'échantillonnage des comportements à l'échelle individuelle ne peuvent être utilisées. Nous avons vérifié un ensemble de prédictions concernant la fréquence et la durée d'interactions à petite échelle ( $\leq 1,4$  m) correspondant à des hypothèses concurrentes relativement à la ségrégation saisonnière et sexuelle du wapiti (*Cervus canadensis* Erxleben, 1777). La fréquence des interactions de dyades femelle–femelle était quatre fois plus grande que celle des interactions de dyades mâle–mâle (fréquence annuelle moyenne des interactions : femelle–femelle = 62 contre mâle–mâle = 14;  $P < 0,001$ ) et les interactions mâle–mâle étaient 1,5 fois plus longue que celle des interactions femelle–femelle (durée moyenne des interactions : femelle–femelle = 30 s contre mâle–mâle = 45 s;  $P < 0,001$ ). Nous proposons que les interactions à petite échelle de membres d'une population peuvent être modélisées en tant que compromis entre la fréquence (quantité) et la durée (qualité) des interactions. Nos résultats ont une incidence sur la compréhension des différences basées sur le sexe sur le plan de la socialité des herbivores grégaires et pour la transmission de maladies pouvant découler de rapports sociaux. [Traduit par la Rédaction]

**Mots-clés :** comportement, *Cervus canadensis*, maladie, wapiti, ségrégation sexuelle, socialité.

## Introduction

Sociality, broadly defined as group living, has implications for several ecological phenomena (Krause and Ruxton 2002; Silk 2007). It may arise as an adaptive response to a number of external influences including predation (Hamilton 1971) and social foraging (Rieucou and Giraldeau 2011). Intrinsicly, however, social groups may stratify based on factors such as age (Michelena et al. 2008), relatedness (Wolf et al. 2011), and sex (Pérez-Barbería et al. 2005). Stratification may be a response to limiting the constraints of social behaviours, such as disease transmission. What is less known are the social dynamics that occur within different segregated sex classes. In particular, we address the differences in fine-scale mechanistic social interactions between conspecifics of different classes for a wild species, especially at large spatial and

temporal scales. Here our focus is specifically to test whether fine-scale social behaviours described by proximity meet expectations predicted from alternate scales of social behaviour (e.g., segregation) and how sex and season influence this pattern.

Sexual segregation is common for social mammals, especially ungulates (for a review see Ruckstuhl and Neuhaus 2005). Bowyer (2004) calls sexual segregation niche separation among the sexes, leading to characteristic spatiotemporal differences in diet and habitat use (i.e., ecological separation; Mysterud 2000). Sexual segregation may decrease predation risk or reduce intraspecific competition between the sexes (Ruckstuhl and Neuhaus 2000), and some facets of competition and social preference are expressed as dyadic behavioural interactions (Bon and Campan 1996; Beck and Peek 2005). Based on principles of spatial density and dispersion, we hypothesize (Table 1) that dyadic interactions would be limited

Received 5 October 2012. Accepted 9 May 2013.

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**Table 1.** Annual sex-specific expectations (expected increase or decrease) and justifications for changes in interaction rates and duration for female and male elk (*Cervus canadensis*), and whether or not data reflected expectations.

Sex	Expectation		Data reflected expectation		Justification
	Interaction rate	Interaction duration	Interaction rate	Interaction duration	
Female–female	Increase	Decrease	Yes	Yes	Female elk live in larger groups than males (Franklin et al. 1975; Vander Wal 2011), which may result in more hierarchical interactions and opportunities for aggression. Interactions will be aggressive and thus short (Weckerly 1999)
Male–male	Increase	Decrease	No	No	Male interactions will be infrequent at small spatial scales because of the costs of aggression (Weckerly 2001) and visual cues establishing hierarchies (Clutton-Brock 1982) despite the importance of monitoring conspecifics (Lung and Childress 2007). Interactions will be short and aggressive (Weckerly 1999) outside of the breeding season
Female–male	Decrease	Increase	Yes	No	As a result of sexual segregation, intersexual interaction will be infrequent and occur primarily during the breeding season (Bowyer 2004). For seasonal expectations see Table 2

between sexes outside of the breeding season. In seasonal environments, animals experience cyclical changes in their surroundings, including, e.g., access to resources (Festa-Bianchet 1988, Green and Bear 1990, Jacques et al. 2009), restrictions to timing of mating and gestation (Loe et al. 2005), and predation risk (Lingle et al. 2008). Similarly, we hypothesize that effects of phenology (Table 2) and sex will be apparent in the fine-scale nature of social interactions.

Here we are concerned with the number and duration of social interactions (obtained from proximity-logging radio collars). These measures of social interactions represent proxies for competitive effects and information transfer between individuals, and are also opportunities for transmission of disease (Krause and Ruxton 2002). Currently, little is known regarding this fine scale of social interaction across seasons and sexes (Cross et al. 2012), as the advent of technology to continuously monitor fine-scale animal proximity is relatively new (Prange et al. 2006).

We posit that sexual and seasonal segregation of male and female elk (*Cervus canadensis* Erxleben, 1777) will result in important differences in rates and durations of fine-scale social interactions between dyads (logged when individuals came within 1.4 m of each other). Expectations of how they might vary follow from examples in the literature that occur at alternate spatial scales (Tables 1, 2). For example, we expect that females will have comparably more intrasex fine-scale interactions than male–male or male–female interactions as a result of living in larger groups (Franklin et al. 1975; Vander Wal et al. 2013a). Because males are known to have short aggressive interactions (Weckerly 1999), we predict that at the fine scale, this will result in comparably shorter interactions than expected for females. We elaborate on these expectations in Table 1. Examples of seasonal expectations include that sexual segregation will result in few fine-scale intersex interactions compared with those within sex; however, this relationship should not hold in and around the mating season (autumn). Explicit expectations for the sex-specific effects of seasonality are further detailed in Table 2.

We discuss our results not only in light of sociobiology, but also dynamics of wildlife disease. In a recent review, Cross et al. (2012) highlight the importance of continuous fine-scale monitoring of animal interaction as a proxy for pathogen transmission. Our study population of elk is a reservoir host for bovine tuberculosis

(*Mycobacterium bovis* Karlson and Lessel, 1970 (bTB); Shury and Bergeson 2011). We recognize the potential for overlap in how individuals socialize and how pathogens may be transmitted. Because of this overlap, sex- and season-specific social interactions may have implications for disease transmission.

## Materials and methods

### Study area and species

Our study area was Riding Mountain National Park (RMNP; 3000 km<sup>2</sup>; supplementary Fig. S1<sup>1</sup>), Manitoba, Canada (50°51'N, 100°15'W). Vander Wal (2011) presents a detailed biogeographic description of the park. In February–March of 2007 and 2008, we captured free-ranging elk ( $n = 106$ ) using a net-gun fired from a helicopter (for details see Cattet et al. 2004). We equipped 47 adult females and 59 adult males with proximity-logging radio collars (Sirtrack Ltd., Havelock North, New Zealand); each animal retained their collar for 1 year. Our methods followed animal care protocol No. 20060067 of the University of Saskatchewan. Loggers were programmed to record the frequency and duration of pairwise interactions whenever two collared elk ranged within  $1.42 \pm 0.20$  m (mean  $\pm$  95% CI) of each other and then logged the data to memory. Collars deactivated recording an encounter when dyads separated for  $>30$  s at a distance of  $1.98 \pm 0.32$  m. Proximity collars were programmed at 1.42 m for technical and biological reasons. Technically, 1.42 m represents a small setting that ensures reliable results (Prange et al. 2006; 1.1–2.8 m). For further information on data treatment see the supplementary methods.<sup>1</sup> Biologically, we tried to ensure that data pertained to elk which were as close as possible such that the distance may represent a meaningful distance for direct pathogen transmission. However, effective transmission distance for bTB in elk is unknown.

The study of fine-scale proximity as a surrogate for social behaviours has provided a valuable tool to answer questions linked to animal sociality (Ryder et al. 2012, for a review see also Cross et al. 2012). As a result, proximity-logging biotelemetry collars have been successfully employed on various species; e.g., mesocarnivores (Goodman 2007; Prange et al. 2011; Robert et al. 2012) and ungulates (Walrath et al. 2011; Vander Wal et al. 2012b), including with this population of elk (Vander Wal et al. 2012a). Proximity

<sup>1</sup>Supplementary Fig. S1 and Tables S1–S4 are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2012-0237>.

**Table 2.** Seasonal sex-specific expectations (expected increase or decrease) and justifications for changes in interaction rates and duration for female and male elk (*Cervus canadensis*), and whether or not data reflected expectations.

Sex	Season	Expectation		Data reflected expectation		Justification
		Interaction rate	Interaction duration	Interaction rate	Interaction duration	
Female	Winter	Increase	Increase	Yes	Yes	Females group in the winter as an antipredator strategy (Creel and Winnie 2005). Grouping will increase interactions (Vander Wal et al. 2012b)
	Summer	Decrease	Decrease	Yes	Yes	Calving and foraging strategies in females result in smaller nursing groups (Altmann 1951; de Vos et al. 1967; Geist 1982) and solitary behaviours (Franklin et al. 1975), which will decrease the interaction rates among adults
	Autumn	Increase	Increase	Yes	Yes	Breeding harems will result in females being in close proximity to one another (de Vos et al. 1967; Clutton-Brock et al. 1982). Following breeding females will continue to occupy groups into the winter
Male	Winter	Decrease	Decrease	No	No	Small male groups will form after breeding (Geist 1982). Postbreeding males may be in poor condition (Bowyer 1981) and susceptible to predation and disease. Few interactions are predicted based on energy budgets, susceptibility to infection, and maintenance of postbreeding hierarchy aided by antler retention
	Summer	Decrease	Decrease	Yes	Yes	Males may form small groups in summer; however, focus is predominantly on acquisition of nutrients (Geist 1982) and conflict may be avoided as antlers are in velvet (Main and Coblentz 1990)
	Autumn	Increase	Increase	Yes	Yes	Although bachelor groups break apart, breeding activities and establishment of hierarchy will result in the most interactions among males (Geist 1982)
Female–male	Winter	Decrease	—	No	No	Few interactions occur; however, in late winter and early spring, some intersex groups form as an antipredator response and to capitalize on the emergence of early spring grasses and sedges
	Summer	—	—	No	Yes	Inrequent interactions owing to sexual segregation
	Autumn	Increase	Increase	No	No	Interactions will be frequent and will occur primarily between dominant males and breeding-age females (Bowyer 2004). Interaction duration between sex will be longer because of the proximity of breeding harems

collars provide information in dyadic states, not dyadic events (sensu Whitehead 2009); i.e., the nature of the behaviour being expressed by the dyad is unknown. Because 1.4 m represents less than one body length of an elk, we assume that both individuals in a dyad are cognizant of one another and as such are required to adjust their behaviour based on the presence of the other actor. Thus, both actors are interacting (sensu Whitehead and Dufault 1999). We cannot confirm if these interactions result in physical contact. Although we did not confirm the nature of interactions, we assumed that duration of interaction could provide some preliminary information on whether interactions were agonistic (short), neutral, or amicable (longer). For further discussion about proximity-logging data collars see Robert et al. (2013).

In addition to being a source of novel information on fine-scale social behaviours, proximity collars also have been used to make inferences about the transmission of pathogens. Because the elk population of RMNP is a reservoir host for bTB, there have been significant socioeconomic effects in the region (Nishi et al. 2006; Brook and McLachlan 2009). Prevalence levels are low (Shury and Bergeson 2011), which results in challenges studying bTB directly (for a discussion see Vander Wal et al. 2013b). Nevertheless, information is required to manage bTB; for example, information on the fine-scale social interactions of elk can be used as a proxy for potential pathogen transmission (Cross et al. 2012).

### Sex-specific dyads

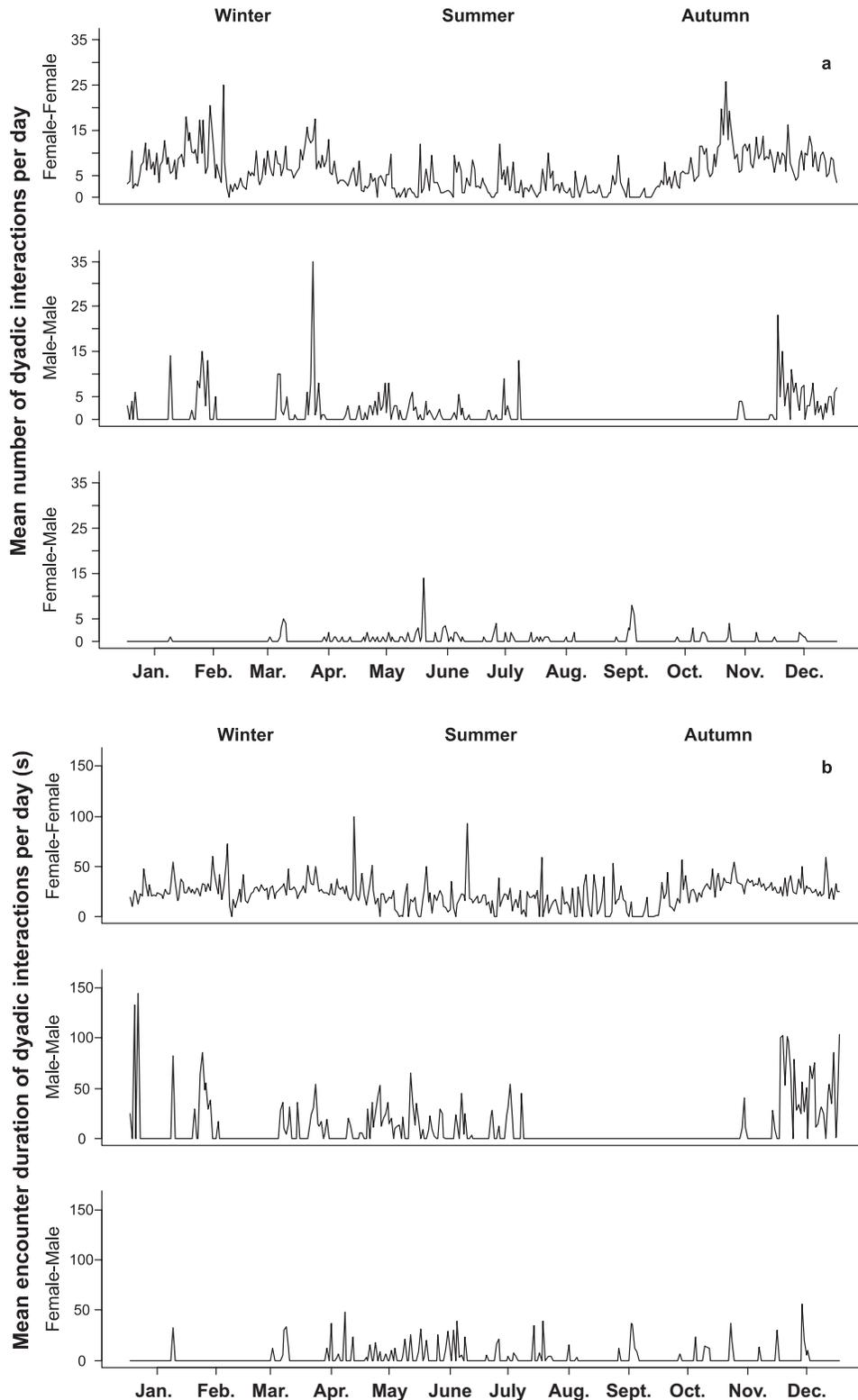
In separate models, we compared the number of interactions per dyad and the duration of female–female, female–male, and male–male interactions. We used a generalized linear mixed model (GLMM; Bates and Maechler 2010; R Development Core Team 2011) to analyze data. We included individual as a random intercept to control for behavioural bias; dyad was added as a random intercept to account for pseudoreplication of pairwise interactions. We performed post hoc comparisons of all fixed effects using *P*-adjusted pairwise *z* scores.

We ran models on two data sources: number of interactions per year (i.e., a full cycle of seasonal behaviours) and duration of interactions. The number of interactions per year had a data range of three orders of magnitude and was  $\log_{10}$ -transformed. Transformed data maintained a Poisson distribution, but were no longer zero-truncated and presented better model diagnostics. Generalized linear models of number of interaction data used a Poisson distribution and were overdispersed. We normalized data on interaction duration with the natural logarithm transformation, which allowed us to use general linear models with a Gaussian distribution.

### Season

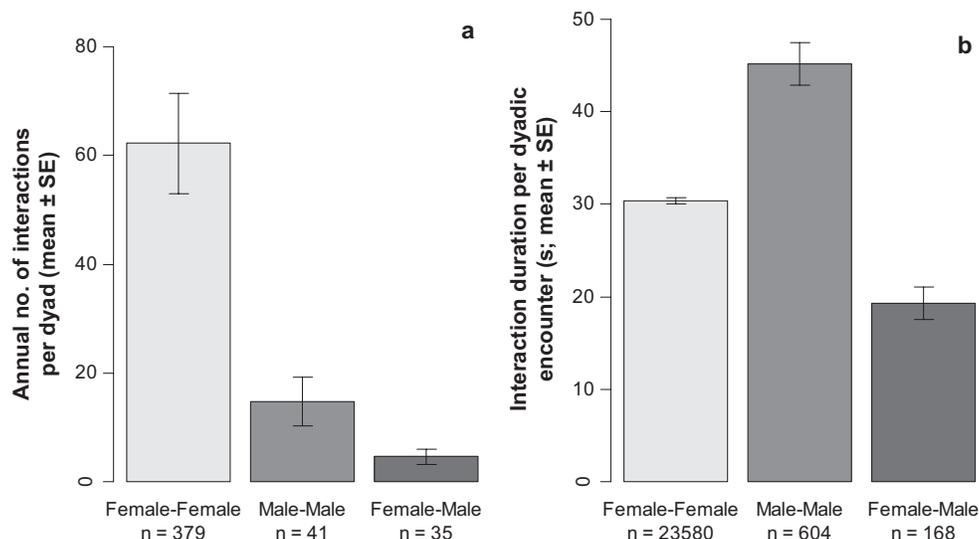
Variation in interaction rate (Fig. 1a) and duration (Fig. 1b) existed for sex-specific dyads. In separate models, we compared the

**Fig. 1.** Annual time series trisected by season for mean count of dyadic interactions (a) and mean duration per interaction (b) from proximity collared elk ( $n = 106$ ) from Riding Mountain National Park, Manitoba, Canada, in 2007–2009 (data pooled by Julian day): female–female dyads ( $n = 379$  dyads,  $n = 23\,580$  events), male–male ( $n = 41$  dyads,  $n = 604$  events), and female–male ( $n = 35$  dyads,  $n = 168$  events).



Proximity collared elk ( $n = 106$ ) from Riding Mountain National Park in 2007–2009 (data pooled by Julian day)

**Fig. 2.** Annual interaction rates (a) and interaction duration (b) among sex-specific dyads from proximity collared elk ( $n = 59$  females and 47 males) from Riding Mountain National Park, Manitoba, Canada, in 2007–2009. Values are means  $\pm$  1 SE.



number of interactions per dyad and duration of interaction among three seasons. Spring–summer was designated as being the snow-free period beginning on 1 May, shortly before calving occurred. Autumn – early winter began at the end of 31 August before mating season and ran to 30 December. Late winter began as day length increased (1 January) until snowmelt and precalving (31 April). We used a combination of GLMMs, similar to interaction rate (above), to model and detect differences among seasons for each sex-specific combination.

## Results

### Sex-specific dyads

Female–female interaction rates varied throughout the year (Figs. 1a, 2a), occurring significantly more frequently than between male–male (4.4 times) and female–male (13.1 times) dyads (all pairwise comparisons at  $P < 0.001$ ,  $n = 455$ ; supplementary Table S1<sup>1</sup>). We failed to detect significant differences between male–male and female–male dyad interaction rates (Fig. 1a, supplementary Table S1<sup>1</sup>). Interaction duration also varied annually (Figs. 1b, 2b). Male–male dyads had significantly longer interaction durations than did female–female (1.5 times) or female–male (2.3 times) pairs ( $P < 0.001$ ,  $n = 24352$ ; Table S2<sup>1</sup>).

### Season

The frequency of female–female interactions (Fig. 3a) was significantly lower in summer than winter (4.0 times) and autumn (6.0 times) (both comparisons,  $P < 0.001$ ,  $n = 379$ ; supplementary Table S3<sup>1</sup>). Mean interaction duration (Fig. 3b) was longer in winter and autumn than summer (1.6 times) ( $P < 0.001$ ,  $n = 23580$ ; supplementary Table S4<sup>1</sup>). Male–male interaction rate (Fig. 3c) was significantly lower in the summer than winter (4.4 times) and autumn (5.0 times) ( $P < 0.003$ ,  $n = 41$ ; supplementary Table S3<sup>1</sup>). Mean interaction duration (Fig. 3d) was longer in winter and autumn (1.8 times) than summer (2.0 times) ( $P < 0.001$ ,  $n = 444$ ; supplementary Table S4<sup>1</sup>). Female–male dyadic interaction rates (Fig. 3e) did not differ among seasons (all comparisons,  $P > 0.05$ ,  $n = 36$ ; supplementary Table S3<sup>1</sup>). Mean interaction duration (Fig. 3f) was longer in winter and autumn (1.4 times) than summer (1.4 times) (all comparisons,  $P > 0.05$ ,  $n = 168$ ; supplementary Table S4<sup>1</sup>).

### Interaction tactics: rate vs. duration

Social interaction tactics can be decomposed into frequency and duration (Figs. 4a, 4b). Annually, this tactic favours duration

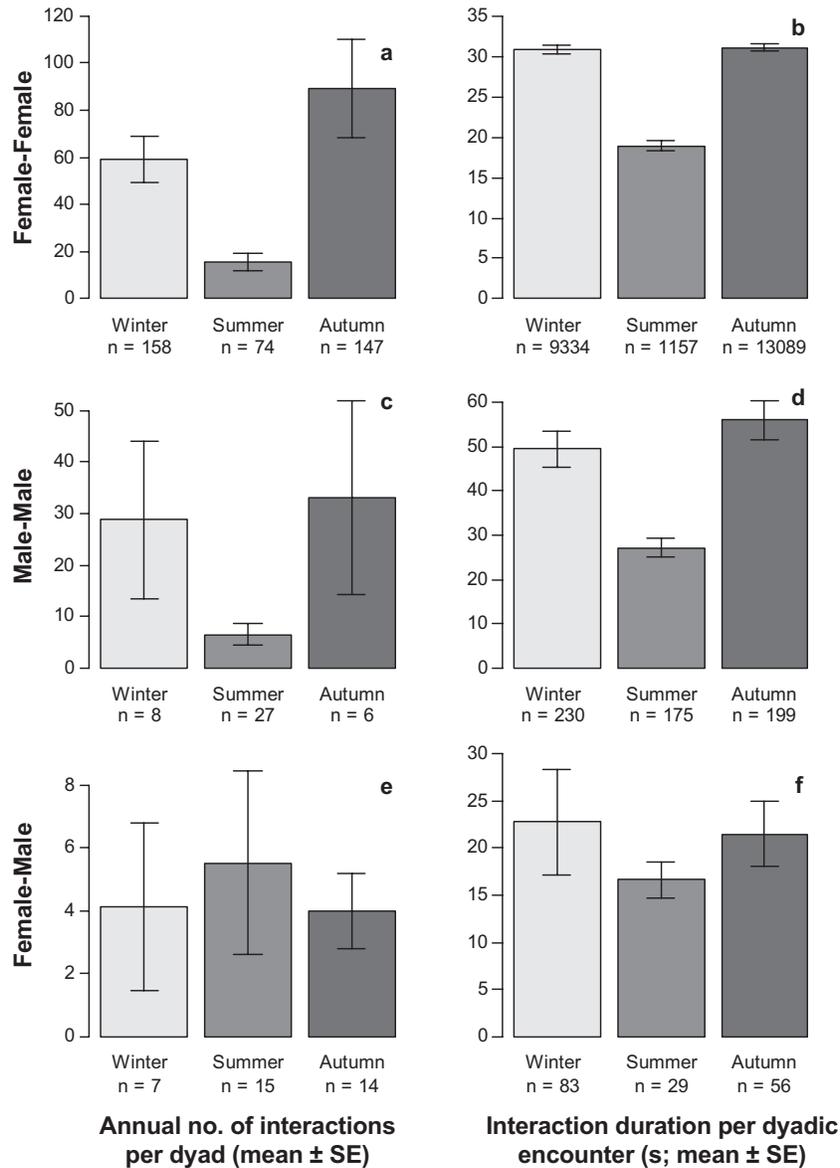
in males and frequency in females along a hypothetical continuum, which represents strategies for social behaviour (Fig. 4a). Seasonally, these tactics maintain the same general principle within sex; however, in summer, they are scaled down, i.e., lower rates and shorter durations (Fig. 4b).

## Discussion

Here we present novel data quantifying continuous-time fine-scale interactions from our observational study of elk. With it, we illustrate three key findings about the effects of fine-scale social behaviours in a sexually segregating ungulate: (1) interactions occur between female–female dyads 4 times more frequently than between male–male dyads; (2) male–male interactions were 1.5 times longer in duration than female–female interactions; and (3) seasonal differences are apparent in both sexes between summer and autumn–winter, but not between autumn and winter. These observations suggest that social interactions have a distinct phenology and that there may be a trade-off between interaction frequency and duration.

Our results meet some, but not all, expectations regarding frequency and duration of interactions. For example, our findings suggest that female–female interactions occur more frequently than male–male interactions. As our study is observational, we cannot definitively disentangle why this difference exists. One possible biological explanation for short but frequent social interactions in females may lie in the lack of obvious visual cues, such as antlers. Thus, behaviours that include social bonding and aggression to reassert hierarchies (Weckerly 1999) will occur more frequently. Upon shedding their antlers, males briefly exhibit similar behaviour. During this time, males are known to become aggressive, disperse, or create discord within groups (Knight 1970; Geist 1982). This spike in male–male interactions is apparent in our time-series data (Fig. 1a; late March), but is not obvious over longer time scales (Fig. 3c). Furthermore, female elk live in larger groups than males (Franklin et al. 1975; Vander Wal et al. 2013a), which may result in more hierarchical interactions and opportunities for aggression. Conversely, smaller groups of males and the clear visual queue of antler size result in fewer fine-scale interactions. Less-frequent interactions among males may also relate to the fact that males typically have lower movement rates (van Beest et al. 2013), which would result in less mixing among conspecifics, further reinforcing local hierarchies.

**Fig. 3.** Female–female, male–male, and female–male annual dyadic interaction rates (*a*, *c*, and *e*, respectively) and interaction durations (*b*, *d*, and *f*, respectively) compared within sex-specific combination among seasons (winter, summer, and autumn) from proximity collared elk ( $n = 59$  females and  $n = 47$  males) from Riding Mountain National Park, Manitoba, Canada, in 2007–2009. Values are means  $\pm$  1 SE.



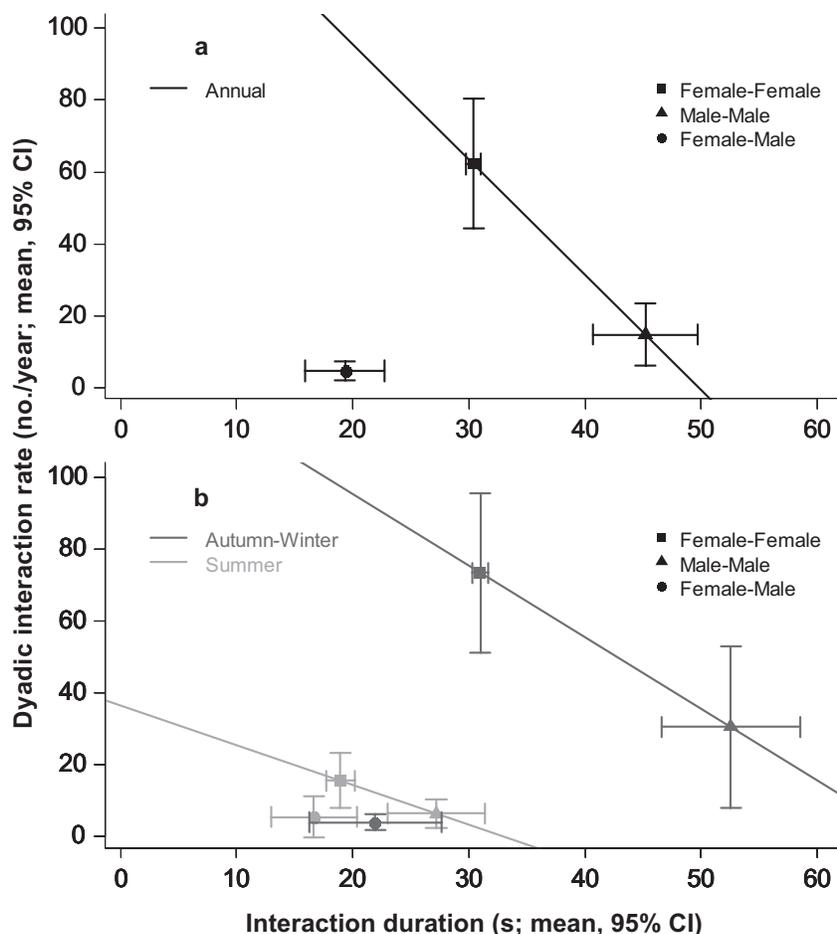
We note that collared males could co-occur in a group without logging interactions (if spaced out  $>1.4$  m); however, when interactions between males did occur, they lasted for longer than all-female interactions. This is contrary to our expectation that males would exhibit short, aggressive interactions when in contact with each other. The cost of agonistic social behaviours may be higher for males than females; for example, possible injuries in males either to formative antlers, or from mature antlers (Geist 1986; Weckerly 2001). Males are also often preoccupied with intrasex vigilance (Childress and Lung 2003) and interactions between males are costly (Weckerly 2001). Thus, male interactions appear to be infrequent, but may be decisive (i.e., requiring longer durations) to minimize repeated costs of reasserting hierarchies within groups.

The trade-off in social tactics between interaction frequency and duration (highlighted in Figs. 4a, 4b) suggests that there are sex-specific approaches to fine-scale social behaviour. These behaviours that are critical for information transfer among members of a population (Krause and Ruxton 2002) and are likely used

to maintain hierarchies (Weckerly 1999) that affect access to resources and mates. The time constraints hypothesis (Dunbar et al. 2009) suggests that animals are limited in the number of behaviours they can express. For example, in ungulates some behaviours such as feeding and vigilance cannot be done simultaneously (Fortin et al. 2004), contrary to vigilance and ruminating (Fortin et al. 2004; Robinson and Merrill 2013). Social behaviour comprises an additional behaviour competing for space in an animal's time budget. For social behaviours, there appears to be sex-specific tactics used. These alternate tactics may be indicative of sex-specific costs related to social behaviour and are likely to be influenced by social environment. Females, which form larger groups, will be more limited in their interaction duration, as it may be spread across more individuals. Conversely, because male groups are smaller (Vander Wal et al. 2013a), more time can be dedicated to each interaction.

Furthermore, these tactics appear to scale with season. Seasonality is a driving factor in sexual segregation (Bonenfant et al. 2004). Seasonality places constraints on activity and placement.

**Fig. 4.** The relationship between sex-specific (female–female, male–male, and female–male dyads) interaction rates and durations for elk ( $n = 106$ ) from Riding Mountain National Park, Manitoba, Canada, in 2007–2009. Error bars are 95% CI. Isoclines are derived from annual (a) and seasonal (b) dyadic interaction rates and interaction durations. The annual model (a) illustrates the trade-off between rate and duration of dyadic interactions for female–female and male–male dyads, with female–male dyads occurring at both lower rate and duration. This relationship is less distinct in the seasonal models (b), where female–female, male–male, and female–male summer interaction rates and durations are all less common and shorter.



For example, females with offspring may be limited in their mobility during summer, while males may move more to obtain adequate resources in preparation for the hypophagia during the mating season (Geist 1982; Apollonio and Di Vittorio 2004). Results for seasonal female–female interactions agreed with expectations based on group sizes, forage rates, and the behavioural changes of having a young at heel. Conversely, results for male–male interactions varied from expectations. Male–male dyads interacted with similar frequency in winter and autumn (both at rates higher than summer), rather than with reduced frequency in winter. Social ungulate aggregations can be affected by resource use (Fortin et al. 2009). In winter, for example, elk will feed on forage found in open habitat, which can increase the likelihood of grouping (Gerard and Loisel 1995) and thus interacting. However, following green-up, animals disperse into more complex habitats to feed (Knight 1970; Christianson and Creel 2007), which should decrease the likelihood of dyadic interactions (Vander Wal 2011).

Disease ecology and sociobiology are rapidly finding common ground on several fronts (Tompkins et al. 2011). Management of disease may hinge on better understanding the mechanics of sex-based sociality, and we propose that studies like ours may offer a first step in developing better models of disease transmission. The dichotomy between interaction rate and duration in females and males highlights an important aspect of potential disease trans-

mission: successful transmission may result from both frequency and durations of interactions. Albeit our sample animals were not afflicted with bTB, in our case, females interacted more frequently with each other, but males interacted for longer durations. We recorded female–male dyadic interactions; however, these interactions had quantity indistinguishable from male–male interactions (i.e., low) and duration indistinguishable from female–female interactions (i.e., low). We cannot rule out that transmission might occur from female to male or vice versa. However, given the dichotomy in fine-scale interactions between females and males and that female–male interactions always occur below the isocline which joins male–male and female–female social interactions in space (Figs. 4a, 4b), transmission may occur predominantly within rather than between sexes.

In summary, quantifying fine-scale interactions has the potential to provide information on benefits and constraints of social behaviours, in particular highlighting novel trade-offs in social tactics between interaction frequency and duration. Here, we investigated whether fine-scale interactions ( $\leq 1.4$  m) would conform to expectations based on known patterns of seasonal and sexual segregation at larger spatial scales. This was not universally the case, suggesting that there may be a disconnect between scale and sociality that merits further investigation. Our study was observational and therefore we could not test explicitly what are the causal factors of that affect the feedback between social behaviour

and scale. Furthermore, proximity-logging technology does not provide data on which behaviours occur when two animals are interacting. We suggest that future studies consider combining traditional ethological approaches to the study of behaviour with proximity collars to better describe the linkage between proximity or dyadic event and specific types of behaviour, or dyadic state.

## Acknowledgements

Funding and logistic support was provided primarily by Parks Canada, the Natural Sciences and Engineering Research Council of Canada, and PrioNet Canada. P. Simpson and B. Simpson adroitly flew elk relocation flights and C. Wilson, T. Vandenbrink, and T. Shury efficiently and safely handled elk. R. Grzela, S. McKay, R. Robinson, S. Johnstone, J. Dillabough, B. Blackbird, S. Boychuk, S. Helms, A. Ledden, and M. Benson assisted with monitoring collared animals. Thank you to T. Sallows, D. Bergeson, and K. Kingdon at Parks Canada for their commitment to this research, and to R.K. Brook and F. van Beest for comments on the manuscript.

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