SEX, FRIENDS, AND DISEASE: SOCIAL ECOLOGY OF ELK (*CERVUS ELAPHUS*) WITH IMPLICATIONS FOR PATHOGEN TRANSMISSION

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by

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ABSTRACT

Many mammals are social. The most basic social behaviour is when the actions of one conspecific are directed toward another, what we call the 'dyadic interaction'. Both intrinsic and extrinsic factors may affect an individual's propensity to interact with other members of a population. I used a social cervid, elk (*Cervus elaphus*), as a model species to test the importance of intrinsic and extrinsic factors of sociality on dyadic interactions. Dyadic interactions not only form the basis for social structure and information transfer within a population, but are also routes of pathogen transmission. My objective in this thesis was thus twofold: to improve our understanding of sociobiology, but also to gain insight into how sociality may underlie the transmission of communicable wildlife disease. I used a hierarchical, autecological approach from DNA, through individual, dyad, group, subpopulation, and ultimately population to explore the effects of intrinsic factors (e.g., sex and pairwise genetic relatedness) and extrinsic factors (e.g., season, conspecific density, habitat, and elk group size) on sociality.

Elk in Riding Mountain National Park (RMNP), Manitoba, Canada, are exposed to the causal agent of bovine tuberculosis (*Mycobacterium bovis*; TB); however, spatial variation in apparent disease prevalence suggests that TB can only persist in one subpopulation within the Park. Using the natural RMNP system and a captive elk herd that I manipulated, I explored factors that influence interaction rates and durations (as a proxy for pathogen transmission) among elk.

Sexual segregation in elk results in seasonal and sex-based differences in interaction rate and duration; with interactions peaking in autumn-winter for both sexes. Female-female dyads interact more frequently than male-male dyads. However, male-

male dyads interact for longer durations than do female-female dyads. Interaction rate and duration did not covary with pairwise relatedness. Conspecific density also had sex-specific results for interaction rate and duration. Whereas male-male dyadic interaction rates increase with density, female-female dyads increase until they reach a threshold and subsequently reduce their interaction rates at high density.

I observed density dependence in interaction rates in experimental trials and from field data. Furthermore, social networks revealed that social familiarity (i.e., heterogeneity of interactions) can be both frequency- and- density dependent depending on the strength of the relationship (i.e., number of repeat interactions). Density also affected the likelihood that an interaction would occur; however, this was modified by vegetation association used by elk.

My results reveal several ecological and evolutionary implications for information transfer and pathogen transmission. In particular, I show that seasonal inter-sex routes of transfer may exist and that transfer is likely to be density-dependent. Finally, I conclude that such transfer is modified by available resources.

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And of course my partner Carissa for being wonderful.

DEDICATION

For my father Jake (1949–2008)

His propensity for critical thought
and
shared enthusiasm for nature
have shaped all aspects
of this research.

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Chapter 1: General Introduction

1.1 Theory

The question of why animals exhibit social behaviour is among the greatest in biology (May 2006; Sherratt & Wilkinson 2009). E.O. Wilson (1975) distinguished ten qualities of sociality. Foremost among them were integration or differentiation of behaviours; group size and structure; connectedness and mixing within and between groups; and information flow. All of these qualities are believed to represent evolutionary trade-offs. To the individuals involved, social behaviours can confer both benefits (e.g., predator detection [Pulliam 1973; Lima 1995; Childress & Lung 2003; Isvaran 2007], predator [Hamilton 1971; Foster & Treherne 1981] and parasite[Mooring & Hart 1992] swamping, increased time to feed [Lima 1999; Blumstein & Daniel 2002]) and costs (e.g., increased probability of detection [Jarman 1974; Hebblewhite & Pletcher 2002], parasitism [Brown & Brown 1986; Cote & Poulin 1995], pathogen transmission [Bonds et al. 2005; Woodroffe et al. 2009], intra-specific competition [Isvaran 2007]). Most interesting to me is the cost-benefit balance that exists at the level of information flow; that is, where interaction between individuals occurs.

The basis of all social behaviours is interaction: when the presence or behaviour of one individual is directed toward another to affect its behaviour (Whitehead & Dufault 1999). At its simplest, social interaction involves two individuals: the dyad. Dyadic interactions are primary routes for information transfer among individuals, which is the proximal benefit of dyadic interaction. But at the same time, a cost may be incurred; in particular, I am interested in what may be the consequences of social interaction for the transmission of pathogens. Analyzing this cost-benefit construct cannot, however, be conducted in isolation: interactions among conspecifics may be affected by critical number of factors, from the density in which a population occurs to where (or in what habitat) interactions take place.

Density dependence in ecological processes such as predation (Holling 1966; Bassar et al. 2010), competition (Morris 2003; Stewart et al. 2005; McLoughlin et al. 2006), sociality (Albon et al. 1992; L'heureux et al. 1995), and pathogen transmission (Anderson & May 1979; May & Anderson 1979; Lloyd-Smith et al. 2005) is fundamental to the ecology and evolution of species. Mechanisms that underlie density-dependent phenomena are best tested, however, at the level of the individual (Sutherland 1996). In conjunction with interactions among conspecifics, individuals also interact with the habitats within which they live, and conspecific density is not independent of the resources which comprise habitat (Morris 2003; McLoughlin et al. 2006). Habitat structure forces trade-offs for individuals exploiting resources. Some social behaviours can modify those trade-offs and permit opportunities not available to the individual. Grouping behaviour can facilitate individual access to forage in high risk habitats by sharing risk among individuals in the group (Creel & Winnie 2005). For example information flow among individuals can result in shared predator detection (Hamilton 1971) and differentiation of behaviour (e.g., alleleomimesis minimizing redundant vigilance [Pays et al. 2007]) can maximize nutrient intake while minimizing time spent scanning for predators. However, such conditions are also likely to increase conspecific interactions, and thus pathogen transmission.

In my model species, elk (*Cervus elaphus*), social behaviours, and habitat selection are often sex-specific. Sexual segregation is common in social mammals, especially cervids (see Main, Weckerly, & Bleich 1996; Bon & Campan 1996; Ruckstuhl & Neuhaus 2002; Ruckstuhl & Neuhaus 2005 for reviews). Many gregarious cervids remain in largely sex-specific groupings outside the breeding season. This segregation results in what Bowyer (2004) and Bleich et al. (1997) suggest is niche separation among the sexes, leading to characteristic spatio-temporal differences in diet and habitat use (i.e., ecological separation [Mysterud 2000]). Models predict that sexual segregation will reduce intraspecific competition (Geist & Petocz 1977) between the sexes and decrease predation risk (Ruckstuhl & Neuhaus 2002). Often overlooked, however, is either the effect of parasite and pathogen transmission on sexual segregation, or the effect sexual segregation has on parasite and pathogen transmission.

Pathogen transmission is often predicated on social interactions among individuals that result in contacts which transmit infectious agents (Anderson & May 1979; May & Anderson 1979). Host-pathogen interactions may occur in systems with thresholds (i.e., critical community sizes [Bartlett 1957]) for disease occurrence or fade-out (Begon et al. 2002; Lloyd-Smith et al. 2005). The influence of intrinsic (e.g., sex and relatedness) and extrinsic (e.g., density and habitat) factors on social structure and behaviours is critical to understanding the ecology of pathogen transmission (see Altizer et al. 2003; Cross et al. 2009; Matthews 2009; Tompkins et al. 2011 for reviews).

1.2 Application

Elk have been valued in the Riding Mountain National Park (RMNP), Manitoba, Canada, region prior to European colonization (Green 1933). During the European settlement of the Prairies, elk populations collapsed (O'Gara & Dundas 2002). In the RMNP region this decline was recognized early (Turner 1906) and in fact contributed to the forming of the Park in 1931. In addition to being famous for its elk, RMNP has recently become infamous for its history with respect to bovine tuberculosis (*Mycobacterium bovis*; TB). Tuberculosis was endemic to cattle (*Bos taurus*) from 1880–1960 in the region, and cattle frequently grazed within the area now designated the Park boundaries (Brook 2009). In 1931, bison (*Bison bison*) were translocated from Wainrwight Alberta, and in 1937 one was found dead with TB (Tabluenas 1983; Lees 2004). In 1971, two TB infected wolf (*Canis lupus*) pups were also found dead (Carbyn 1982). From 1991–2003 TB was detected in 11 cattle herds of the region (Nishi, Shury, & Elkin 2006), and again in a single herd in 2008 (Parks Canada, unpublished data). To date, TB has also been detected in elk (n = 35) and white-tailed deer (*Odocoileus virginianus, n* = 7) (Brook & McLachlan 2009).

The spatial variation in apparent prevalence of TB within RMNP (i.e., TB occurs predominantly in western RMNP, rather than east of highway 10) provides a framework for understanding the host-pathogen ecology of TB and consequent management options. Tuberculosis is of concern to local residents (Brook & McLachlan 2006) and has resulted in economic loses to the region (Nishi et al. 2006). As a result of Parks Canada's mandate to "ensure ecological … integrity", tools to confront disease in wild populations may be limited. This apparent conflict exacerbates the need for decisions to be based on sound science developed within the study system.

As an ecologist, I approached the problem of host-pathogen relationships between elk and TB in RMNP from a spatial and sociobiological perspective. I focus on how evolved social behaviours upon which pathogen transmission is predicated are affected by intrinsic (e.g., sex and relatedness) and extrinsic (e.g., season, conspecific density, habitat, and elk group size) factors described below and in Fig. 1.1.

1.3 Objectives

The most basic social interaction occurs at the level of the dyad, i.e., two individuals. This relationship underlies all animal societies. All chapters (and Appendix A) are predicated on dyadic interactions which occurred between focal individuals fit with close-contact proximity biotelemetry collars. My objectives here were two-fold: (1) to explore factors that affect sociality in gregarious cervids; and, (2) to do so in a manner meaningful to understanding pathogen transmission in elk, especially in RMNP. Specifically, I explore factors such as season (Chapter 2), sex (Chapter 2 and 3, Appendix A), conspecific density (Chapter 3–5), habitat (Chapter 5), relatedness (Appendix A), and group size (Chapters 4, 6 and Appendix B) (Fig. 1.1).

1.4 Thesis structure

Underlying the structure of my thesis is a hierarchical autecological approach: from DNA (Appendix A), to individual (Chapters 2-5, Appendix A), dyad (Chapters 2-5, Appendix A), group (Chapters 4, 6 and Appendix B), subpopulation (Appendix A), and ultimately population (Appendix A). The thesis has three major themes, sociality, conspecific density, and information transfer—which is analogous to pathogen transmission. The bulk of the thesis capitalizes on natural variation found within RMNP,

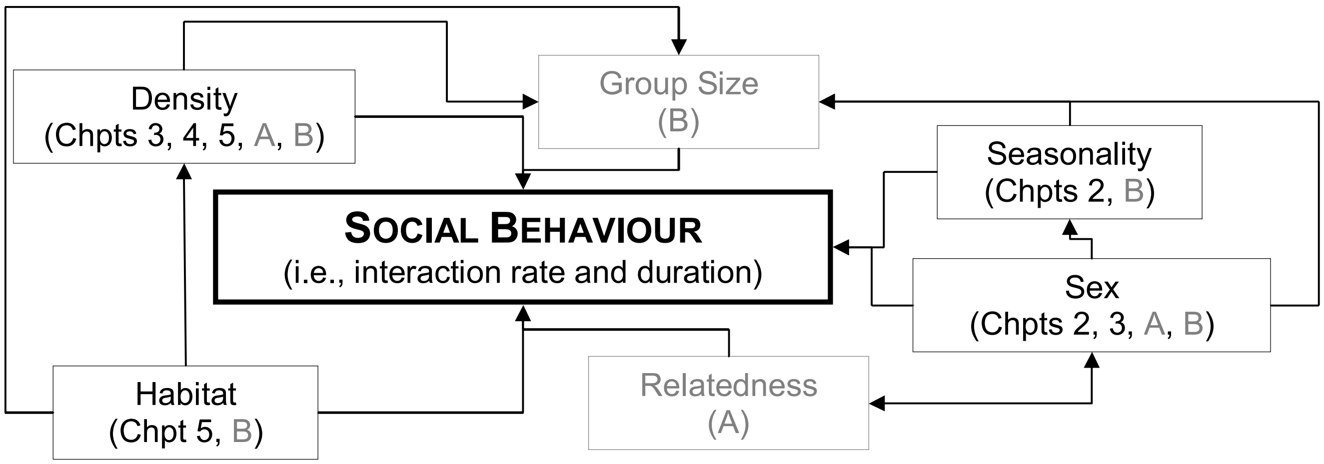

Fig. 1.1 Thesis schematic illustrating interactions among factors that affect social behaviours and their associated chapter or appendix. Factors treated exclusively in appendices are highlighted in grey.

particularly differences in density (landscape scale see Chapters 4, Appendix B and local scale see Chapter 5), resources (see Chapter 5), and apparent prevalence of TB (see Chapter 2, 4 and Appendix A and B) between the western and eastern subpopulation (see Appendix A). However, tests of density-dependent social behaviour are also corroborated via an experimental manipulation (Chapter 3).

I have written each data-chapter (Chapters 2–5) and Appendix A as predominantly stand-alone manuscripts. Firstly, sex-and season-specific differences in dyadic interaction rates compose Chapter 2. The theme of sex-specific differences follows into Chapter 3 where I introduce density-dependent social behaviour via experimental manipulation of a captive elk herd. Density dependence is then tested for both simple dyadic measures and more complex social network metrics using field data (Chapter 4). Conspecific density, however, may be correlated with habitat, thus in Chapter 5 I test how the occurrence of dyadic interactions is affected by resources and local conspecific density. In Appendix A, I explore how genetic relatedness may affect interaction rates and durations within and between subpopulations of elk within RMNP. Finally, Chapter 6 summarizes salient theoretical and applied contributions from the thesis, highlights some group-level phenomena (Appendix B); I also briefly discuss management implications for elk and TB in RMNP.

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Chapter 2: Predicting pathways of pathogen transmission from seasonal and sex-specific strategies of social interactions in a gregarious ungulate

2.1 Abstract

How information is transmitted among members of a population can be viewed as a trade-off between the frequency (quantity) and duration (quality) of interactions. This has implications for the transmission of communicable disease, which may follow from social intercourse. I present an empirically derived model of social interaction from which I infer routes of pathogen transmission for adult elk infected with bovine tuberculosis (TB). Emerging patterns were both sex-specific and seasonal. Female-female dyads and male-male dyads differed in interaction rate (♀-♀ > ♂-♂; $P < 0.001$) and duration (♂-♂ > ♀-♀; $P < 0.001$). Female-male interactions occurred below a modelled isocline for optimal transmission (rates were indistinguishable from male-male dyads [$P = 0.18$], and durations were not different than female-female dyads [$P = 0.35$]). Similarly, the modelled isocline for optimal transmission in autumn and winter exceeded that of summer. Routes of communication and TB transmission in elk are thus likely to occur primarily within—rather than between—sexes, and transmission is likely to occur mainly in autumn–winter. I discuss how my approach can outline pathways of communication in sexually segregated, gregarious species with applications to understanding the spread of communicable disease.

2.2 Introduction

Living in a group is accompanied by costs resulting from increased exposure to parasites (Brown & Brown 1986; Côté & Poulin 1995) and pathogens (Woodroffe et al. 2009); thus, communicable disease should factor into the evolution of gregariousness and sociality (Bonds et al. 2005; Prado et al. 2009). Many transmissible diseases require close-contact interactions among members of a population to spread or reproduce (i.e., transfer from one host to another). Ultimately, social systems can evolve to limit the effect of infectious disease on a species (Prado et al. 2009). Traditionally, our understanding of how pathogens leading to the spread of disease through or between populations was initially predicated on models of homogeneous mixing (Anderson & May 1979; May & Anderson 1979). This, however, is an unlikely assumption. Interactions among members of a population can be constrained in space, time, or by social barriers. For example, sexual segregation may underlie important temporal, spatial, and social impediments to pathogen transmission (Main & Coblentz 1990; Main, Weckerly, & Bleich 1996; Bleich, Bowyer, & Wehausen 1997; Ruckstuhl & Neuhaus 2000, 2002; Bowyer 2004).

Sexual segregation is common in social mammals, especially cervids (see Main et al. 1996 for review). Many gregarious cervids remain in sex-specific groupings outside the breeding season. Several hypotheses are presented for the evolution of sexual segregation, including ideas based on predation risk (Ruckstuhl & Neuhaus 2000) or reproductive strategy (Main et al. 1996); forage selection (Ruckstuhl & Neuhaus 2000) or sexual-dimorphism (Main et al. 1996); and social preference (Main et al. 1996). These hypotheses result in what Bowyer (2004) and Bleich et al. (1997) suggest is niche separation among the sexes, leading to characteristic spatio-temporal differences in diet and habitat use (i.e., ecological separation [Mysterud 2000]). Models predict that sexual segregation will reduce intraspecific competition (Geist & Petocz 1977) between the sexes and decreased predation risk (Ruckstuhl & Neuhaus 2002). Often overlooked, however, is either the effect of parasite and pathogen transmission on sexual segregation, or the effect sexual segregation has on parasite and pathogen transmission.

Here I create a possible set of hypotheses and/or predictions involving the role of parasite and pathogen transmission (Table 2.1), which may contribute directly to the evolution of sexual segregation or follow as an incidental benefit to segregation. I am concerned with how sexual segregation might limit the number and/or duration of interactions between the sexes and act as a barrier to the spread of communicable disease. This includes aspects of how social dynamics within sexes differ, but also how sexual segregation may impart seasonal barriers to disease transmission.

Sexual segregation is closely tied to the periodicity of mating opportunities, which is also linked to the seasonal changes in an organism's environment (Loe et al. 2006). Animals in seasonal environments experience cyclical changes in their surroundings, including, e.g., access to resources (Festa-Bianchet 1988; Green & Bear 1990; Jacques, Jenks, & Klaver 2009), restrictions to timing of mating and gestation (Loe et al. 2005), and predation risk (Lingle et al. 2008). Behavioural adaptations exist to deal with seasonal vagaries. For example, accumulating resources when they are readily available and living off stored resources (fat deposits) allows animals to survive times of dearth, which may also be accompanied by lower body condition (Focardi et al. 2008).

Table 2.1 Implications of the three main hypotheses for sexual segregation on pathogen transmission and information transfer

Hypothesis	Support	Predictions for Pathogen Transmission/ Information Transfer
Predation risk (Ruckstuhl & Neuhaus 2000) or Reproductive strategy (Main et al. 1996)	Females with smaller body size, and calves at heel are more susceptible to predation than males. Post-rut males are more susceptible to predation and would be conspicuous among a group of females were predators present (Geist 1982)	Times of segregation occur when females and males are both under great physiological stress. Lactating females and post-rut males have lower body condition and avoiding large groups of conspecifics could reduce the probability for contracting transmissible disease.
Forage selection (Ruckstuhl & Neuhaus 2000) or Sexual-dimorphism-body-size hypothesis (Main et al. 1996)	Maximizing forage intake requires selecting food with different passage rates due to unequal rumen size (Clutton-Brock, Guinness, & Albon 1982; Bowyer 2004). Lactating females selecting more digestible forages than males preparing for breeding competition Different rumen size and food selection result in unequal rumination times creating asynchronous feeding cycles that further discourage inter-sex grouping (Conradt 1998).	Different movement rates associated with forage intake rates discourage sympatry and thus reduce the probability of pathogen transmission.
Social preference (Main et al. 1996)	Little evidence exists to support the social preference hypothesis (Romeo, Lovari, & Festa-Bianchet 1997; Ruckstuhl & Neuhaus 2000), which states that males form single sex groups as an evolved behaviour for information transfer. Young males learn fighting skills, breeding season determinants, establish dominance hierarchies, etc. Young females gain information about rearing young in female only groups.	Pathogen transmission is analogous to information transfer (Wilson 1975) and a by-product of information or gene transfer; such that the social preference hypothesis predicts the possibility of sex-specific routes of pathogen transmission may be favoured over inter-sex transmission routes.

Lower body condition predisposes individuals to predation or infection (Jorgenson et al. 1997; Pelletier & Festa-Bianchet 2004).

Behaviours, such as grouping, are used to mitigate seasonal predation risk as poor body condition in late winter often correlates to increased group size in gregarious cervids (Childress & Lung 2003; Fortin & Fortin 2009). Grouping is thought to dilute individual predation risk (i.e., the selfish herd hypothesis [Hamilton 1971]). Aggregating in this condition, however, likely increases the probability of contracting communal diseases (Côté & Poulin 1995; Altizer et al. 2003).

Seasonal aggregations can also be driven by resource use (Fortin et al. 2009). In winter, cervids such as elk feed on forage found in open habitats (Christianson & Creel 2007). However, following green-up, animals disperse into more complex habitat to feed on forbs (Knight 1970). Such seasonal fission-fusion responses create opportunities for wider pathogen transmission from within groups to between groups (Brown & Brown 2004). Seasonality also results in constraints to reproduction, gestation, and parturition; such that reproductive females are limited in their mobility and males need to improve quickly their body condition in preparation for mating competition (Geist 1982). Females maximize fitness by investing in rearing young, whereas males maximize fitness by increasing their mating opportunities (Vos, Brokx, & Geist 1967). Each outcome requires different strategies, which balance foraging, predation, and pathogen risks.

Irrespective of seasonal and sexual segregation, pathogen transmission occurs at a local spatial and temporal scale: where two individuals encounter one another (i.e., dyadic interaction). Interactions need to include an infectious and a susceptible individual and the interaction must result in successful pathogen transmission. Furthermore, body condition and immune response can affect how susceptible an individual is to disease (Beldomenico & Begon 2010). Little is known about the ecology of such events. Animals are thought to optimize behaviours (e.g., feeding [Charnov 1976], or social behaviours such as dominance [Clutton-Brock et al. 1979], or interactions [Macarthur, Geist, & Johnston 1982]). Similarly, optimizing conspecific interactions means a trade-off between the number of interactions individuals share and the duration of interaction to achieve the same social outcome. Social interactions serve to transfer information or genes from one individual to another (e.g., hierarchy reinforcement, mating, etc) and the transmission of pathogens is a by-product (Wilson 1975).

The above can be modelled explicitly. Initially I follow Begon et al. (2002):

$$\frac{dI}{dt} = Scpv \text{ (Begon et al. 2002) [2.1]}$$

where, $\frac{dI}{dt}$, is the change in infectious individuals (*I)* over time (t), which depends on the number of susceptible individuals (S), the contact rate (c), the probability that a contact is with an infectious host (p), and the probability of successful transmission (v) (Begon et al. 2002). However, I suggest that the probability of successful transmission, v, is unlikely to be constant; rather it varies with interaction duration such that successful pathogen transmission is the function of the quantity of interactions and the quality of interactions (Fig. 2.1). Social behaviours in mammals are complex and do not always result in physical contact (Weckerly 1999), and even when physical contact occurs it may not always result in an exchange of bodily fluids that contain the pathogen. Transmission, therefore, can occur because of many interactions of poor quality, or of few interactions of high quality.

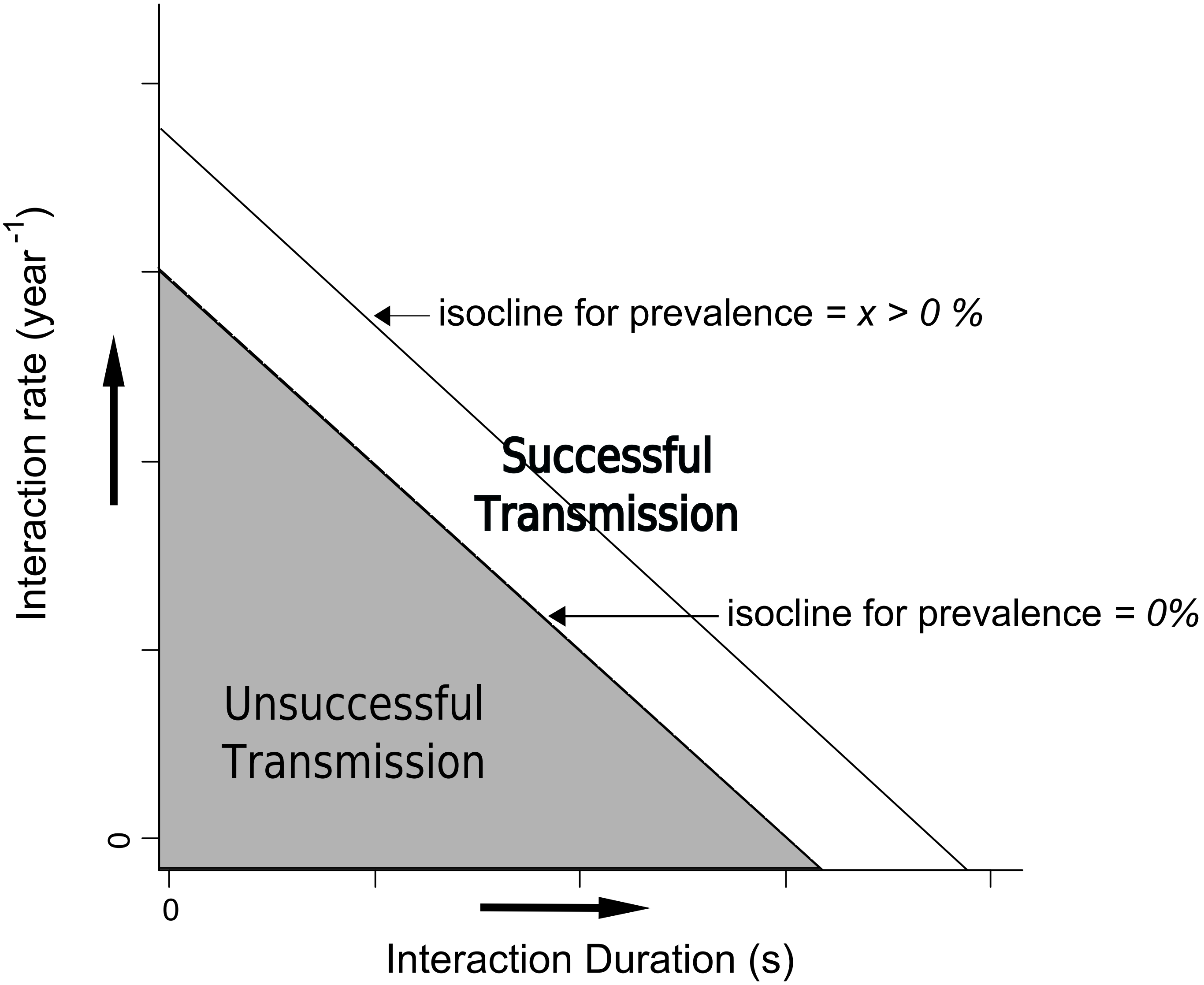

Fig. 2.1 The model predicts a range of possible strategies where transmission can occur which vary according to a function of interaction quantity (i.e., rate) and interaction quality (i.e., duration): e.g., as quantity of interaction increases, interaction duration can decrease while still providing similar probability for transmission to occur; conversely, as the quality of interaction increases less interactions are required for successful transmission of a pathogen. Area (in gray) below the zero prevalence isocline (dashed line) represents combinations of interaction rates by duration where transmission is unlikely, whereas for areas above the zero prevalence isocline transmission is predicted to occur. Above the zero prevalence isocline are a series (i.e., 1–100%) of equal prevalence isoclines, e.g., the $x > 0$ % prevalence isocline (solid line).

Plotting this hypothetical relationship (Fig. 2.1) I have an isocline of equal probability for pathogen transmission or information transfer at a given time scale. As the probability of transmission is difficult to estimate, this isocline may be considered a line of equal disease prevalence within a sampling period.

If risk of contracting transmissible disease is predicted to be disparate according to the biology of seasonally and sexually segregated animals, what explains the similar apparent prevalence of bovine tuberculosis (TB) between sexes in elk of Riding Mountain National Park (RMNP)? Similar apparent prevalence in female (14/428, 3%) and male elk (14/344, 4%) (2002–2008 Parks Canada unpublished data, see 2.3 Methods) suggests that the assumption of homogenous mixing is not unfounded; however, it is not in accordance with basic elk biology, which dictates that interaction rates will vary based on sex and season (Vos et al. 1967; Clutton-Brock et al. 1982). Information on the transmission route for TB among wild cervids is sparse. Due to observed TB lesions in the lungs of RMNP elk (Parks Canada unpublished data) and knowledge from research on cattle (Menzies & Neill 2000), I assume that direct transmission is critical for maintaining TB within the population. This assumption is further reinforced by examining the social structures and apparent prevalence rates of TB in elk compared to sympatric white-tailed deer (*Odecoilieus* v*irginianus*) in the RMNP system. The less social cervid, white-tailed deer, have a lower estimated apparent prevalence than that of elk (1% Nishi et al. 2006).

I examined the role of sexual segregation on interaction rates and durations (as a proxy for pathogen transmission) for elk in RMNP. I submit that environmental contamination with TB (Duffield & Young 1985) is not a primary route of transmission in RMNP, and therefore I focus exclusively on possible instances of direct transmission. Thus, due to similar sex-specific estimates of apparent prevalence, I predict that interactions are more likely to occur within a sex, as a function of sexual segregation. If true, this suggests that within-sex routes of disease transmission are more likely to maintain disease in a population than between-sex transmission. Furthermore, if risk of contracting transmissible disease varies with season, I predict that behaviours that may result in successful pathogen transmission are reduced during periods of high risk (Table 2.2). Such variability in interaction rate (Fig. 2.2a) and interaction duration (Fig. 2.2b) are present in elk of RMNP.

Table 2.2 Seasonal predictions for changes in interaction rates and duration for male and female elk

Sex	Season	Prediction		Rational
		Interaction Rate	Interaction Duration	
Females	Winter	↑	↑	Females group in the winter as an antipredator strategy (Creel & Winnie 2005). Grouping will increase interactions (Molvar & Bowyer 1994) thus increasing the probability of transferring transmissible diseases.
	Summer	↓	↓	Calving and foraging strategies in females result in smaller nursing groups (Altmann 1952; Vos et al. 1967; Geist 1982) and solitary behaviours (Franklin, Mossman, & Dole 1975). Therefore decreasing the interaction rates among adults.
	Autumn	↑	↑	Breeding harems will result in females being in close proximity to one another (Vos et al. 1967; Clutton-Brock et al. 1982). Following breeding females will continue to occupy groups into the winter.
Males	Winter	↓	↓	Small male groups will form post-breeding (Geist 1982). Post-breeding 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 post-breeding hierarchy aided by of antler retention.
	Summer	↓	↓	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 & Coblentz 1990).
	Autumn	↑	↑	Although bachelor groups break apart, breeding activities and establishment of hierarchy will result in the most interactions among males (Geist 1982).

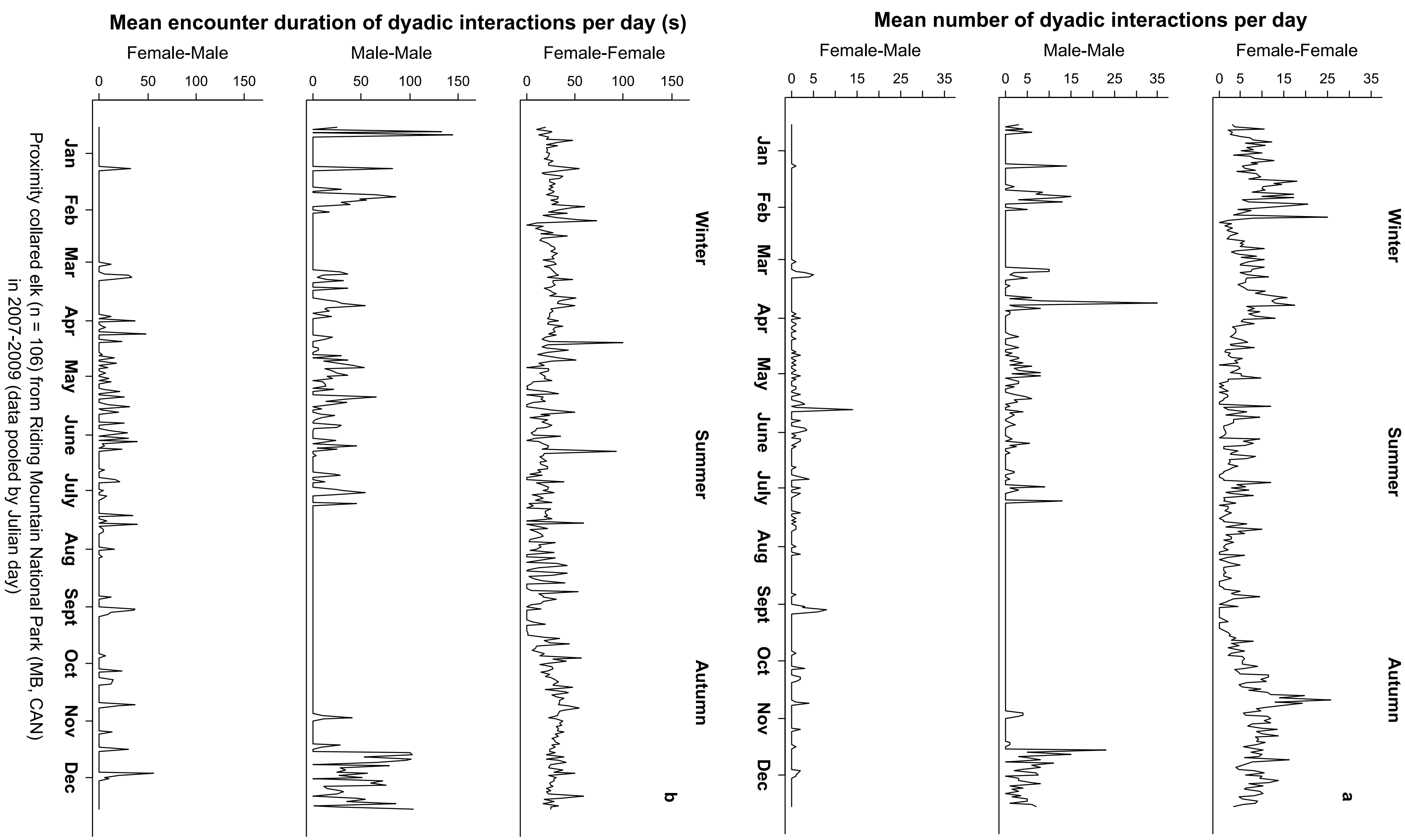

Fig. 2.2 Annual time series trisected by season for mean count of dyadic interactions (a) and mean duration per interaction (b) from proximity collared elk (*n* = 106) from Riding Mountain National Park (MB, CAN) in 2007–2009 (data pooled by Julian day): female-female dyads (*n* = 379 dyads; *n* = 23580 events); male-male (*n* = 41 dyads; *n* = 604 events) and ; female-male (*n* = 35 dyads; *n* = 168 events).

2.3 Methods

2.3.1 Study Area

Riding Mountain National Park (RMNP; 3000 km^2; Fig. 2.3) is in southwestern Manitoba, Canada. Riding Mountain National Park occurs in transition from the prairies to the northern Boreal Plains ecoregion (Bailey 1968). An elevational gradient exists in RMNP: the eastern portions of the park rise 475 m from the Manitoba lowlands up the Manitoba escarpment and declines gradually to the western limit of the park. The vegetation consists of northern boreal forest (at higher elevations), aspen parkland, bur oak (*Quercus macrocarpa*) savannah, grassland, and eastern deciduous forest (Rowe 1972; Caners & Kenkel 2003). RMNP is surrounded by an agricultural matrix resulting in very low exchange of elk in and out of the region (Brook 2008). RMNP has a history with TB extending back before the 1950s when cattle grazed within the Park's boundaries (Copeland 2002; Brook 2009). Prior to 1986, when MB was declared TB free, two confirmed cases of TB were detected in RMNP wolves (*Canis lupus*; in 1978). However, from 1991 to 2009 outbreaks involving elk (n = 35), deer (n = 7) and cattle (n = 12 herds) occurred (Brook & McLachlan 2009).

2.3.2 Elk sampling

In February–March of 2007 and again in 2008 we captured free ranging elk (n = 106) using a net-gun fired from a helicopter (Cattet et al. 2004). Elk were collared for one year, i.e., in 2008 new individuals were collared. We equipped 47 adult females and 59 adult male elk with Sirtrack Proximity Logger radio-collars (Sirtrack Ltd., Havelock North, New Zealand): (see Swain & Bishop-Hurley 2007 for an example).

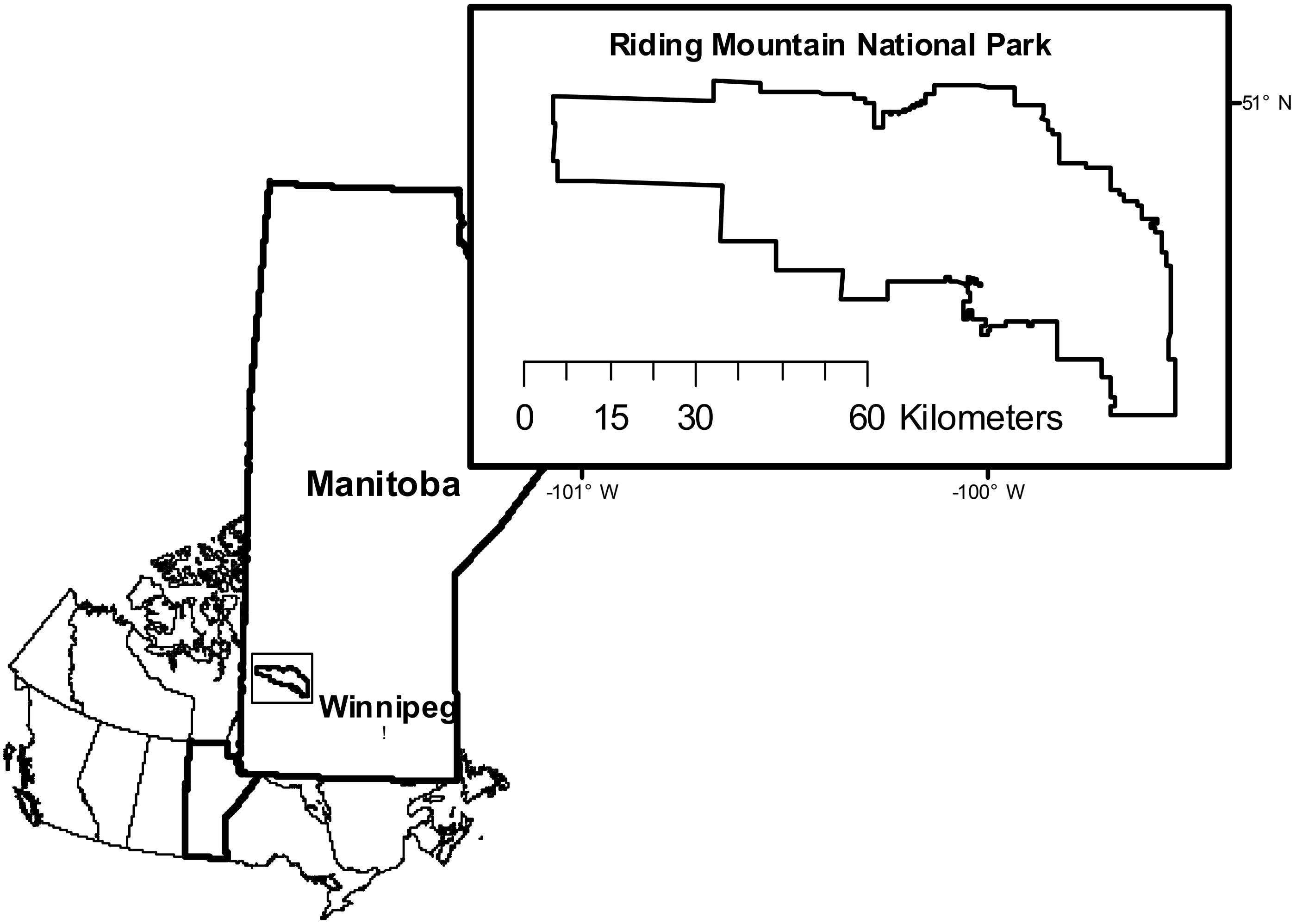

Fig. 2.3 Riding Mountain National Park (3000 km^2) is located in central Canada. Elk (*Cervus elaphus manitobensis*) live primarily within and near the periphery of the preserve which lies predominantly in the prairie parkland and boreal plains transition zone.

My proximity loggers were programmed to activate and collect data whenever a collared elk came within 1.4 m of another collar (initiation distance 1.42 ± 0.20 m [$\bar{x}$ ± 95%CI] [Goodman 2007]). Collars deactivated recording an encounter every time a pair separated from one another for >30 s at a distance of 1.98 ± 0.32 m ($\bar{x}$ ± 95% CI) (Goodman 2007). These collars recorded a count and duration of the number of pairwise interactions (*sensu* Whitehead & Dufault 1999) between animals wearing collars. My research followed Animal Care Protocol #20060067 of the University of Saskatchewan, following guidelines of the Canadian Council on Animal Care.

2.3.3 Estimating Apparent Prevalence

From 2002–2008, 428 female and 344 male elk in RMNP were tested for TB infection By Parks Canada Agency. During elk captures (described above) animals were fit with biotelemetry collars and blood was drawn and subsequently tested with a battery of assays including: Lateral-flow rapid test (CervidTB STAT-PAK Assay, Chembio Diagnostic Systems, Inc), Multi-antigen print immunoassay, Lymphoscyte Stimluation Test, and Florecense Polarization Assay (see Surujballi et al. 2009). If an animal was suspect for TB on any assay they were recaptured, euthanized, and necropsied to recover tissues from their lymph nodes for mycobacterial culture (see Rohonczy et al. 1996 for culture technique) and histopathology (Rousseau & Bergeson 2005). Elk were considered TB positive if tissues were tested positive during mycobacterial culture, were histopathological for TB, or a Polymerase Chain Reaction (PCR) for TB indicated they were positive (see Surujballi et al. 2009 for histopathological and PCR techniques).

2.3.4 Sex-specific dyads

In separate models, I compared number of interactions per dyad and duration of interaction among sex-specific combinations: female-female, female-male, and male-male interactions. I used a generalized linear mixed model (GLMM; Bates & Maechler 2010; R Development Core Team 2010) to analyze my data. Individual was added as a random intercept to control for behavioural bias. In addition, dyad was added as a random intercept to account for non-independence between individuals grouped within a dyad. I performed comparisons of all fixed effects using *P*-adjusted pairwise z-scores (Hothorn, Bretz, & Westfall 2008).

I 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. The transformed data maintained a Poisson distribution, but were no longer zero-truncated and led to better model diagnostics, i.e., normalized residuals and QQ-plots (Zuur et al. 2009). Generalized linear models of number of interaction data used a Poisson distribution and were over-dispersed. Interaction duration data, however, were normalized with the natural logarithm transformation; hence, I employed general linear models with a Gaussian distribution.

2.3.5 Season

Variation in interaction rate (Fig. 2.2a) and duration (Fig. 2.2b) existed for sex-specific dyads. In separate models, I compared the number of interactions per dyad and duration of interaction among three *a priori* selected seasons. Spring–“summer” was designated as being the snow-free period beginning on 1 May, shortly before calving occurred (Brook

2010). “Autumn”–early winter began at the end of 31 August before mating season and ran into late 30 December. Late “winter” began as day length increased until snowmelt and pre-calving (31 April). Sample size of male-male and female-male dyadic interactions precluded further fine-scale divisions of seasonality. I used a combination of GLMMs, similar to interaction rate (above), to model and detect differences among seasons for each sex-specific combination.

2.4 Results

2.4.1 Sex-specific dyads

Female-female dyadic interaction rate varied throughout the year (Fig. 2.4a; [Table 2.3]), occurring significantly more frequently than male-male and female-male dyads (♀-♀ vs. ♀-♂ $P < 0.0001$; ♀-♀ vs. ♂-♂ $P < 0.0001$; $n = 455$; [Table 2.4]). However, I failed to reject the null hypothesis that there was no significant difference between male-male and female-male dyad interactions rates (♂-♂ vs. ♀-♂ $P = 0.181$; $n = 455$) (Fig. 2.4a).

Interaction duration also varied annually (Fig. 2.4b; [Table 2.5]). Male-male dyads had significantly longer interaction durations than female-female or female-male pairs (♀-♀ vs. ♂-♂ $P < 0.0001$; ♂-♂ vs. ♀-♂ $P = 0.001$; $n = 24352$; [Table 2.6]). However, no significant difference in interaction duration existed between female-female dyads and female-male dyads ($P = 0.350$; $n = 24352$) (Fig. 2.4b).

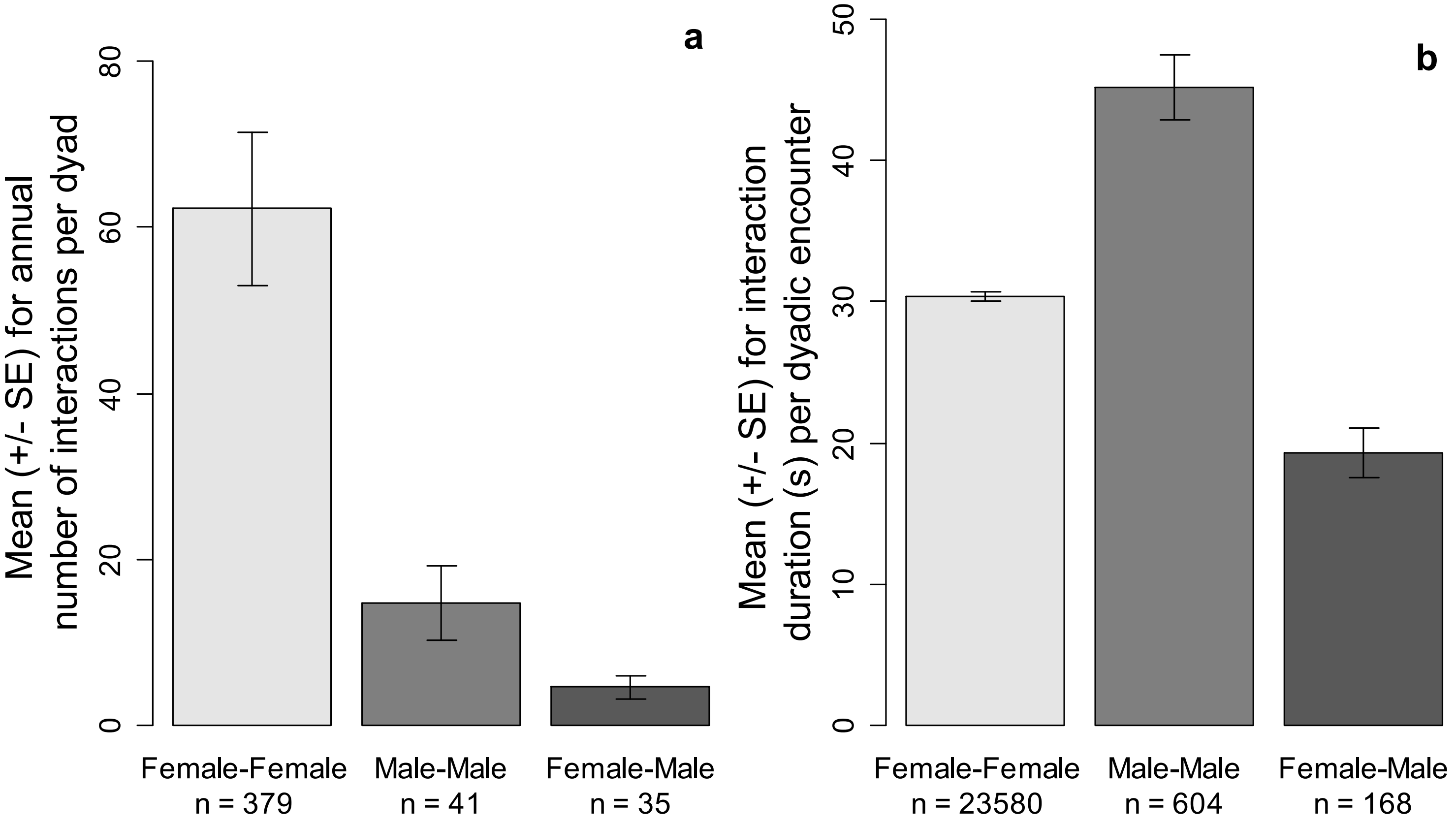

Fig. 2.4 Mean (+/- 1 SE) annual interaction rates (a) and interaction duration (b) among sex-specific dyads from proximity collared elk (*n* = 59 females and 47 males) in Riding Mountain National Park (MB, CAN) in 2007–2009.

Table 2.3 Median (25%–75% quantile) and sample size for count of sex-specific dyadic elk interactions per season (RMNP 2008–2009).

Dyad	Autumn	Summer	Winter	Annual
Female-female	15 (4–64) *n* = 147	4 (2–15.25) *n* = 74	15 (3–59.5) *n* = 158	16.5 (5–73.25) *n* = 224
Female-male	3 (1.25–4.75) *n* = 14	2 (1–4) *n* = 15	1 (1–2.5) *n* = 7	2 (1–4.75) *n* = 30
Male-male	14.5 (4.25–39) *n* = 6	3 (1.5–4.5) *n* = 27	7.5 (1.75–33.75) *n* = 8	1 (3–7) *n* = 36

Table 2.4 Summary of fixed effects from mixed generalized linear model with over-dispersed Poisson distribution predicting differences in number of interactions per year ($\log_{10}$) by sex for *n* = 59 females and 47 male elk (forming 290 dyads) in Riding Mountain National Park, Manitoba Canada, 2007–2009.

Factor (Sex-specific dyad)[*]	Beta	SE	*t*-value	*P* (*df* = 106)
Female-female	0.235	0.029	7.993	<0.001
Female-male	-1.027	0.136	-7.508	<0.001
Male-male	-0.730	0.109	-6.680	<0.001

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[*] *P*-adjusted multiple comparison z-score: ♀-♀ vs. ♀-♂ *P*<0.0001; ♀-♀ vs. ♂-♂ *P*<0.0001; ♂-♂ vs. ♀-♂ *P*=0.181.

Table 2.5 Median (25%–75% quantile) and sample size for interaction duration (s) of sex-specific dyadic elk interactions per season (RMNP 2008–2009).

Dyad	Autumn	Summer	Winter	Annual
Female-female	17 (6–37) *n* = 13089	12 (5–26) *n* = 1157	16 (6–36) *n* = 9334	16 (6–36) *n* = 23580
Female-male	12 (5.75–27.5) *n* = 56	10 (4–22.5) *n* = 83	11 (5–24) *n* = 29	10.5 (5–24) *n* = 168
Male-male	31 (13–75.5) *n* = 199	19 (9–35.5) *n* = 175	27.5 (9 –56.5) *n* = 230	26 (10–53) *n* = 604

Table 2.6 Summary of fixed effects from mixed generalized linear model (ln transformed; Gaussian distribution) predicting differences in encounter length by sex for *n* = 59 females and 47 male elk (48,704 events in 290 dyads) in Riding Mountain National Park, Manitoba Canada, 2007–2009.

Factor (Sex-specific dyad)[2]	Beta	SE	*t*-value	*P* (*df* = 106)
Female-female	2.668	0.022	119.7	<0.001
Female-male	-0.126	0.093	-1.4	0.164
Male-male	0.315	0.077	4.1	<0.001

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[2] *P*-adjusted multiple comparison z-score: ♀-♀ vs. ♀-♂ *P*=0.35; ♀-♀ vs. ♂-♂ *P*<0.001; ♂-♂ vs. ♀-♂ *P*<0.001.

2.4.2 Season

Female-female dyadic interaction rate (Fig. 2.5a) was significantly lower in the summer than winter and autumn; however, winter and autumn did not differ (autumn vs. summer $P < 0.001$; winter vs. summer $P < 0.001$; winter vs. autumn $P = 0.535$; $n = 379$ [Table 2.7]). Mean interaction duration (Fig. 2.5b) was longer in winter and autumn than summer. All groups were significantly different (autumn vs. summer $P < 0.001$; winter vs. autumn $P = 0.001$; winter vs. summer $P < 0.001$; $n = 23580$). Male-male dyadic interaction rate (Fig. 2.5c) was significantly lower in the summer than winter and autumn; rates in winter and autumn did not differ (autumn vs. summer $P < 0.001$; winter vs. summer $P < 0.003$; winter vs. autumn $P = 0.630$ $n = 41$). Mean interaction duration (Fig. 2.5d) was longer in winter and autumn than summer; all groups were significantly different (autumn vs. summer $P < 0.001$; winter vs. autumn $P = 0.016$; winter vs. summer $P < 0.001$; $n = 444$; [Table 2.8]). Female-male dyadic interaction rates (Fig. 2.5e) did not differ among seasons (autumn vs. summer $P = 0.624$; winter vs. autumn $P = 0.247$; winter vs. summer $P = 0.633$; $n = 36$). Mean interaction duration (Fig. 2.5f) was longer in winter and autumn than summer. However, winter and autumn did not differ (autumn vs. summer $P < 0.021$; winter vs. summer $P < 0.022$; winter vs. autumn $P = 0.737$; $n = 168$).

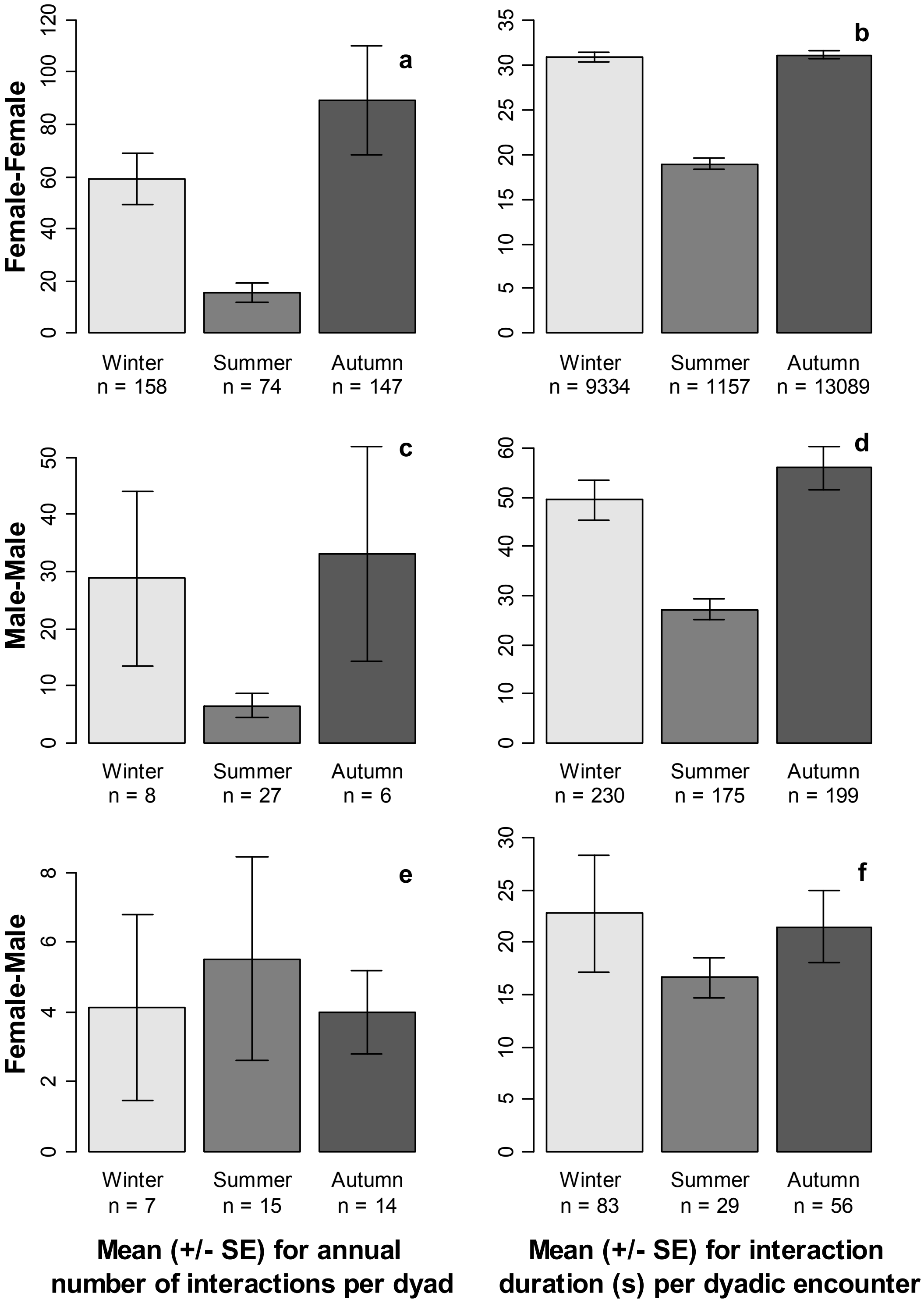

Fig. 2.5 Mean (+/- 1 SE) female-female, male-male, and female-male annual dyadic interaction rate (a, c, and e respectively) and interaction duration (b, d, and f respectively) compared within sex-specific combination among seasons: winter, summer, and autumn.

Table 2.7 Summary of fixed effects from three sex specific mixed generalized linear model predicting differences count of interactions by season for *n* = 58 females and 47 male elk forming 224 female-female, 36 male-male, and 30 female-male dyads in Riding Mountain National Park, Manitoba Canada, 2007–2009.

Factor (Season)	Beta	SE	*t*-value	*P*-value[3]
Female-female[4] (n = 224 dyads)				*P* (*df* = 58)
Autumn	0.107	0.0364	2.955	0.004
Summer	-0.622	0.0695	-8.948	<0.001
Late Winter	-0.049	0.0468	-1.057	0.295
Female-male[5] (n = 30 dyads)				*P* (*df* = 30)
Autumn	-0.825	0.123	-6.698	<0.001
Summer	-0.164	0.178	-0.919	0.365
Late Winter	-0.388	0.244	-1.587	0.123
Male-male[6] (n = 36 dyads)				*P* (*df* = 36)
Autumn	-0.100	0.144	-0.697	0.490
Summer	-0.692	0.169	-4.074	<0.001
Late Winter	-0.167	0.183	-0.915	0.366

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[3] Degrees of freedom estimated by number of unique individuals or dyad in the analysis (random factor = individual elk and dyad)

[4] ♀-♀ *P*-adjusted multiple comparison z-score: autumn vs. summer *P*<0.001; winter vs. autumn *P*=0.535; winter vs. summer *P*<0.001

[5] ♀-♂ *P*-adjusted multiple comparison z-score: autumn vs. summer *P*=0.624; winter vs. autumn *P*=0.247; winter vs. summer *P*=0.633

[6] ♂-♂ *P*-adjusted multiple comparison z-score: autumn vs. summer *P*<0.001; winter vs. autumn *P*=0.630; winter vs. summer *P*=0.003

Table 2.8 Summary of fixed effects from three sex specific mixed generalized linear model (ln transformed; Gaussian distribution) predicting differences in encounter duration (*n* = 48,704 events) by season for n = 58 females and 47 male elk forming 224 female-female, 36 male-male, and 30 female-male dyads in Riding Mountain National Park, Manitoba Canada, 2007–2009.

Factor (Season)	Beta	SE	*t*-value	*P*-value[7]
Female-female[8] (n = 224 dyads)				*P* (*df* = 58)
Autumn	2.668	0.022	118.8	<0.001
Summer	-0.282	0.027	-10.1	<0.001
Late Winter	0.052	0.012	4.1	<0.001
Female-male[9] (n = 30 dyads)				*P* (*df* = 30)
Autumn	2.603	0.158	16.46	<0.001
Summer	-0.525	0.198	-2.65	0.013
Late Winter	0.213	0.288	0.74	0.465
Male-male[10] (n = 36 dyads)				*P* (*df* = 36)
Autumn	3.422	0.149	23.01	<0.001
Summer	-0.827	0.138	-5.99	<0.001
Late Winter	-0.282	0.103	-2.75	0.031

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[7] Degrees of freedom estimated by number of unique individuals or dyad in the analysis (random factor = individual elk and dyad)

[8] ♀-♀ *P*-adjusted multiple comparison z-score: autumn vs. summer *P*<0.001; winter vs. autumn *P*=0.001; winter vs. summer *P*<0.001

[9] ♀-♂ *P*-adjusted multiple comparison z-score: autumn vs. summer *P*=0.021; winter vs. autumn *P*=0.737; winter vs. summer *P*=0.022

[10] ♂-♂ *P*-adjusted multiple comparison z-score: autumn vs. summer *P*<0.001; winter vs. autumn *P*=0.016; winter vs. summer *P*=0.001

2.5 Discussion

My results illustrate two key findings: female-female dyads interact four times more frequently than male-male dyads (mean annual interaction rate: ♀-♀ = 62 vs. ♂-♂ = 14); and male-male interactions are 1.5 times longer in duration than female-female interactions (mean interaction length: ♀-♀ = 30 s vs. ♂-♂ = 45 s). Biologically, higher female-female interaction rates may be related to a need to reassert hierarchy within herds. Female elk form larger groups with mixing matrilineal subgroups (Geist 1982). Female herd composition is generally more stable than male herds (Franklin et al. 1975) and females exhibit high philopatry (Franklin & Lieb 1979). Millspaugh et al. (2004), however, did not find "sub-herd", i.e., local stable group associations. Rather, at the local scale groups freely mixed. Within-group dyads that frequently associate are known to have distinct interactions, using behaviours that include social bonding and aggression to reassert their hierarchy within the herd (Weckerly 1999).

Furthermore, females lack obvious visual cues such as antlers. Upon shedding their antlers males are known to become aggressive, disperse, or create discord within the group (Knight 1970; Geist 1982). This spike is apparent in my time-series data (Fig. 2.2a), but is not an obvious driver at longer time scales (Fig. 2.5c). Similar to other non-migratory elk populations (e.g., Bender & Haufler 1999), females tend to live in larger groups than males (Geist 1982), creating more mixing and more hierarchical interactions and opportunity for aggression. On the contrary, the smaller groups of males (Appendix B) and clear visual queue of antler size might result in fewer interactions. It is important to note that interactions as I measured them occurred whenever two individuals wearing collars came within 1.4 m of each other. Males could co-occur in a group without logging interactions because they remained greater than 1.4 m from one another. However, when interactions between males do occur, they last for longer times than all-female interactions.

Seasonal differences in interaction rate and duration are apparent (Figs. 2.2 and 2.5). Results for seasonal female-female interaction did not vary from my predictions (Table 2.2). These results are in accord with predictions based on group sizes, forage rates, and the behavioural changes of having a calf at heel. Conversely, results for male-male interactions varied from predictions (Table 2.2). Summer was clearly a time of reduced interaction rates and durations for females and males. Male-male dyads interacted with similar frequency in winter and autumn rather than with reduced frequency in winter. Closer inspection of daily male-male dyadic interaction rates (Fig. 2.2a) reveals a peak in dyadic male interactions following shedding of antlers and an absence of dyadic interactions during the breeding season. Late in the breeding season (i.e., November) interactions among dyadic males are again detected. Both seasons have dyadic interactions that are clearly more frequent than during the summer. My results indicate that three coarse seasons are probably unwarranted. At my scale of analysis two seasons exist. Summer, when feeding for females is constrained by caring for calves and males employ a forage maximizing strategy. The second season is autumn–winter, including mating behaviours for both sexes and when females are gestating and predation risk on males is highest due to post-rut recovery. More local scale variation seems apparent (Fig. 2.2), but is beyond the scope of my analysis.

The absence of male-male interactions during the rut (Fig. 2.2a) could be a function of pre-rut group hierarchies. This hypothesis, however, has since been rejected as pre-rut hierarchies have been shown to differ from rutting hierarchies (Clutton-Brock et al. 1982). A likely criticism is that male samples sizes were too low to detect rutting behaviours. I would then question why sample sizes were not too low to detect dyadic interactions outside of the breeding season. I selected adult males that would likely compete for breeding opportunities. All males collared in winter were adults that I predicted would have a minimum of 10–12 tines per rack the following breeding season.

The dichotomy between interaction rate and duration in females and males highlights two important aspects of information transfer and subsequent communicable disease transmission. Successful pathogen transmission or communication results from both quantity and quality of interactions. In my case, females interacted more frequently with each other (i.e., high quantity) but males interacted for longer periods (i.e., high quality, where interaction duration acts as a proximate measure for quality). I recorded female-male dyadic interactions; however, these interactions had quantity indistinguishable from male-male interactions (i.e., low) and quality indistinguishable from female-female interactions (i.e., low). I cannot rule out that transmission might occur from female to male or vice versa. However, if TB in females is a function of quantity of interaction and transmission in males is a function of interaction duration, then transmission is most likely to occur within, rather than between sexes. Following the model of Fig. 2.1, Fig. 2.6a depicts the isocline of behaviour (i.e., a continuum of interaction rates and durations) that may result in equal apparent prevalence of TB in RMNP elk.

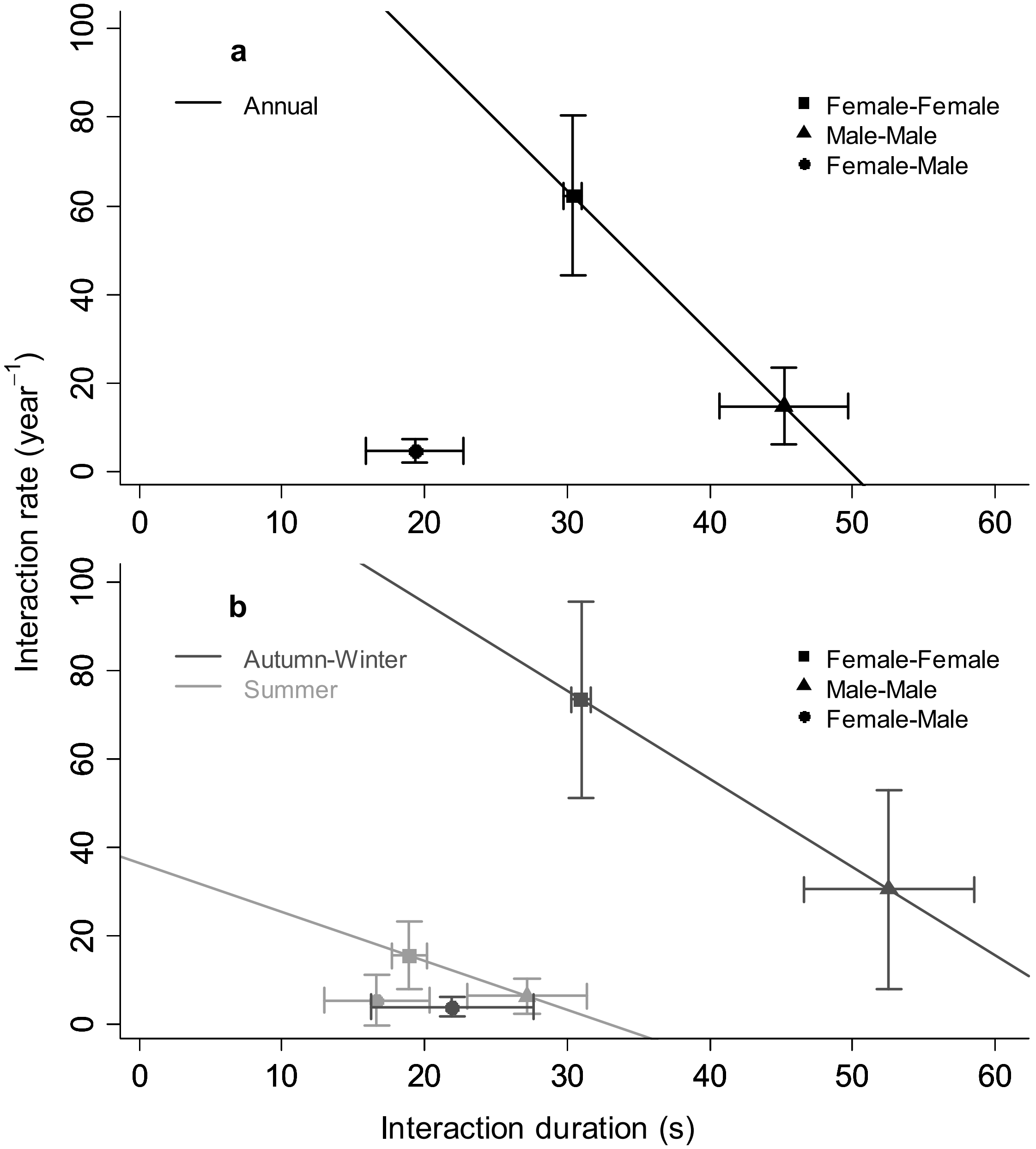

Fig. 2.6. Following Fig. 2.1, I depict the relationship between sex-specific (female-female [■], male-male [▲], and female-male [●] dyads) interaction quantity and quality for elk (*n* = 106) in Riding Mountain National Park (MB,CAN; 2007–2009 [RMNP]). Further I described the prevalence-specific isocline derived from annual (a) and seasonal (b) dyadic interaction rates and interaction durations. The annual model (a) illustrates that quantity and quality of dyadic interactions between female-male dyads fall below a threshold derived from the prevalence-specific isocline for female-female and male-male dyads, suggesting that transmission within sexes is more critical than between the sexes. This relationship is exacerbated in the seasonal models (b) where female-female, male-male, and female-male summer interaction rates and durations fall below the autumn-winter prevalence-specific isocline limited by female-female interaction rates and male-male interaction durations. Thus I argue that between sex routes of transmission do not play a critical role in maintaining TB in the RMNP elk population and transmission will occur predominately during the autumn-winter season.

The isocline:

$$6.29\times10^{-3}R+2.00\times10^{-2}D=Apr \qquad [2.2]$$

where R is the interaction rate, D the interaction duration, and Apr is the observed apparent prevalence of elk in RMNP. Input values for R and D equalling a value greater than 1 will result in higher apparent prevalence than is currently observed. Thus, female-male interaction rate and duration (Fig. 2.6a) falls below the critical value. Furthermore, the model (i.e., equation [2.1]) suggests that interaction duration is three times more important than interaction rate for maintaining equal prevalence.

Seasonally, however, the autumn-winter-specific isocline is greater than the summer-specific isocline (Fig. 2.6b):

$$7.00\times10^{-3}R_{aw}+1.48\times10^{-2}D_{aw}>2.77\times10^{-2}R_{s}+3.05\times10^{-2}D_{s} \qquad [2.3]$$

where R_{aw} and R_s are the interaction rates for autumn-winter and summer respectively, and D_{aw} and D_s are the interaction durations for autumn-winter and summer respectively. Given that all summer-specific rate-by-duration combinations fall below the autumn-winter (Fig. 2.6b) and annual (Fig. 2.6a) isocline of transmission, I contend that autumn-winter is more critical for transmission. Furthermore, female-male interactions in autumn-winter also occur below the summer-specific isocline, reinforcing the importance of sex-specific routes of transmission.

My choice of a linear isocline (Fig. 2.6) is for simplicity. Other factors, such as pathogen virulence (Rigaud, Perrot-Minnot, & Brown 2010), or host susceptibility (Seppälä et al. 2010) may modify the shape of the transmission relationship. My model (Figs. 2.1 and 2.6) has further limitations, for example, the probability of crossover from one intra-sex route of transmission to the other, though smaller than intra-sex, is not absent. Similarly, I argue that autumn-winter is a more critical period for transmission.

However, as interactions do occur during the summer, so too does the possibility for pathogen transmission, albeit significantly less than autumn-winter. Additionally apparent prevalence of TB in RMNP elk is low and tests to detect TB are imperfect. However, low apparent prevalence provides the opportunity for subtle management of disease. If more power was available to detect differences between sex specific prevalence, I would likely still be working with similar values (i.e., values < 5%). Apparent prevalence measures the number of individuals in the population that are infected/infectious; this measure is inclusive of whether animals haves succumbed to infection. Similarly, I do not account for seasonal variation in susceptibility, such as poor male body condition following the rut or late-winter body condition. Finally, intra-sex routes do not preclude inter-sex routes of transmission, however, female condition is high during the rut, and thus susceptibility is likely to be low.

Although an imperfect model, the theoretical ecology of disease transmission at the scale of behavioural interaction and possible contact has not been empirically investigated or synthesized for many species, let alone one that exhibits sexual segregation. If routes of transmission (Fellous & Koella 2009) and susceptibility to disease (Lindsey & Altizer 2009) can be sex-specific then a pathogen that affects reproduction or survival (i.e., individual fitness) will have sex-specific consequences on behaviour. Ultimately, behaviours that minimize transmission should be selected for. Sexual segregation may evolve to maintain specific strategies of pathogen transmission if the mechanics of transmission differ between the sexes, e.g., short interaction duration is an evolved response in females to minimize transmission, whereas males have evolved to minimize pathogen transmission via limited interaction rate. Conversely, sexual segregation may be the prerequisite for different strategies of minimized pathogen transmission. Ultimately, the effect pathogen transmission has on the evolution of sexual segregation is unclear and would require modelling whether intra-specific routes of pathogen transmission result in lower prevalence and increased survival than a homogenous mixing model. This is beyond the scope of my study. However, I present evidence that supports one model to reconcile how different pathways for information flow and pathogen transmission predicated on disparate subsets of behaviour can result in similar apparent prevalence within a sexually segregated cervid.

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Chapter 3: Sex-based differences in density effects on sociality: an experiment with a gregarious ungulate

3.1 Abstract

For animals living in natural or semi-natural settings, empirical data on how sociality changes in response to increasing population density are few, especially concerning responses to true conspecific density and not group size. Insight into this line of research may be far-reaching, however, from understanding density-dependence in sexual selection to improving models of disease transmission. Using elk held in enclosures, I conducted sex-stratified experiments to test how the frequency of dyadic pairings (interaction rate) and their quality (duration) responded to manipulations in exposure to density. Using proximity-logging radio-collars I recorded when and for how long individuals shared a space within 1.4 m of each other. As predicted, males increased their interaction rate as density increased. Female interaction rates, however, increased initially as density increased, but soon declined to become indistinguishable from rates at low density. Females interacted for longer periods at medium densities, whereas male interaction length clearly decreased as density increased. I highlight a sexually dichotomous, density-dependent response in sociality that has yet to be reported. In addition to furthering my understanding of sociobiology (e.g., implications of time constraints presented by density on duration of interactions), my results have implications for managing communicable disease in gregarious species of livestock and wildlife.

3.2 Introduction

Understanding effects of population density on important ecological processes like predation, competition, and disease is fundamental to ecology. Mechanisms that underlie density-dependent phenomena are best tested, however, at the level of the individual (Sutherland 1996). For example, understanding effects of density on productivity may need information on individual trade-offs in time spent in conflict vs. foraging (e.g., Blanc and Thériez 1998), and effects of density on contact rates for disease modelling requires information on the frequency of animal interactions (Lloyd-Smith et al. 2005).

How animals modify their social interactions in response to changes in conspecific density is best understood through experimentation or intensive observation. This limits the types of species for which questions can be asked, and most of my work on this topic has been restricted to invertebrates and fish (e.g., Kaiser et al. 1995, Moyle et al. 2009, Casalini et al. 2010), rodents (e.g., Calhoun 1962, Brashares et al. 2010), birds (e.g., Pettit-Riley et al. 2002), and livestock (reviews in Keeling and Gonyou 2001, Broom and Frazer 2007); non-human primates (e.g., Alexander and Roth 1971, Elton and Anderson 1977, Eaton et al. 1981, Sannen et al. 2004); and humans (e.g., Loo 1972, Huckfeldt 2009). For animals living in natural or semi-natural settings, research remains limited, especially concerning social responses to true conspecific density and not only group size. The applications of such knowledge, however, may be far-reaching, from understanding density-dependence in sexual selection (Kokko & Rankin 2006) to improving models of pathogen transmission and management (Ferrari et al. 2004; Dobson 2005; Lloyd-Smith et al. 2005; Matthews 2009; Kirkpatrick & Altizer 2010; Tompkins et al. 2010).

Using a gregarious, large herbivore as a model (captive elk [*Cervus elaphus* Linnaeus] feeding on naturally available forage in 7–20 ha enclosures), I conducted a series of sex-stratified experiments to test how the frequency of dyadic pairings (interaction rate) and their quality (duration) responded to manipulations in population density. The latter relationship has received very little attention before in a wild ungulate; however, measuring duration of interaction may be as important as quantifying the number of interactions over time when I consider, e.g., implications of density-dependent sociality to the spread of disease. I quantified interaction rates and their duration using novel proximity-logging radio-collars (see Swain & Bishop-Hurley 2007), which recorded when and for how long individuals of an experiment shared a space within 1.4 m of each other; hence, I defined interactions *sensu* Whitehead & Dufault 1999). Based on predictions drawn from previous laboratory studies (e.g., Blanc and Thériez 1998, Gaskin et al. 2002), I hypothesized that interaction frequency would increase with density due to increased opportunities for competitive interactions. Following the first prediction I reasoned that interaction duration would decrease as density increased due to less time in which dyadic pairings could occur in isolation; it was also possible that if agonistic interactions were involved, which are often short occurrences for social ungulates (e.g., Weckerly 1999), could lead to reduced lengths of interactions than at lower density. I highlight a sexually dichotomous, density-dependent response in sociality that has yet to be reported. My results have implications for managing communicable diseases in gregarious species of livestock and wildlife.

3.3 Methods

3.3.1 Data collection

I based my analysis on data collected outside the breeding season in summer 2007 for two captive herds of adult elk (14 females and 10 males) located at the Specialized Research Centre field plots of the Western College of Veterinary Medicine in southeast Saskatchewan, Canada. My research followed Animal Care Protocol #20060067 of the University of Saskatchewan, following guidelines of the Canadian Council on Animal Care. All animals used in my experiments were adults. Males were polled to prevent injuring one another. Females were without calves at heel. Elk were infrequently handled, and maintained their natural avoidance responses to humans. Thompson and Henderson (1998) note that in environments close to human occupancy, the study of wild elk has been confounded due to elk habituating to human activity. Although my experiment was located in rural Saskatchewan, the merits of avoiding habituation remain. To avoid potential complications, I handled animals only twice throughout the entire experiment: to apply and remove Sirtrack Proximity Logger radio-collars (Sirtrack Ltd., Havelock North, New Zealand). All elk were handled for collar fitting by corralling and immobilization in a livestock processing chute and squeeze facility.

As in Chapter 2, I programmed each Sirtrack proximity collar (Goodman 2007) to activate and collect data whenever one collar came within 1.4 m of another collar (1.42 ± 1.00 m SD, 0.20 m SE) Collars deactivated recording an encounter each time a pair separated for >30 s and a distance of 1.98 ± 1.60 m SD, 0.32 m SE. These collars allowed for both a count of the number of interactions between animals wearing collars, but also recorded interaction length in seconds.

Elk tend to spend most of their time in single-sex groups (Altmann 1952; Clutton-Brock, Guinness, & Albon 1982); hence, I created two separate experiments (one for each sex), each with three possible density treatments (low, medium, and high), which I replicated twice. Density treatments for females and males were similar, but not identical. A 14-member herd of females was moved among enclosures of 19.6, 13.4, and 9.8 ha (0.71 elk/ha, 1.05 elk/ha, and 1.43 elk/ha, respectively). The male herd had 10 individuals and was moved among enclosures of 13.4, 9.8, and 6.7 ha (0.75 elk/ha, 0, 1.02 elk/ha, and 1.49 elk/ha, respectively). My high density constructs were not unrealistic for elk under natural conditions (e.g., 2.15 elk/ha in Beneke Creek Wildlife Management Area, Oregon [Mereszczak et al. 1981]). Foraging competition in elk is expected to be through scramble competition rather than interference competition, as food resources are not concentrated in their natural meadow or forest habitat (Boyce et al. 2003). My experiment mimicked these natural conditions by allowing elk to feed only on naturally available forage without supplementation.

I herded elk between treatments without direct handling. Each treatment ran for seven days. I randomized treatment and replicate schedules to minimize any bias that may have been related to day length or food conditions over the course of the experiment. Days where the animals were moved between treatments and collaring days were removed from the dataset to ensure that any confounding data from the herding event was not included.

3.3.2 Statistical Analyses

I analyzed my data in the R environment for statistical programming (R Development Core Team 2010). Replicates were pooled and I tested for differences in treatments using mixed-effects generalized linear models (GLMM). I added random intercepts to the GLMM for individual (to control for unknown behavioural proclivities, e.g., social status) and dyad (to account for the non-independence of pairwise interactions). Interaction rate (count of interactions per treatment period) conformed to an over-dispersed Poisson distribution. I was able to normalize interaction duration, however, with a natural logarithm transformation. I based my models on these distributions, respectively.

3.4 Results

The frequencies at which male interactions occurred between low- and medium-density treatments were not significantly different (Fig. 3.1A); however, both treatments produced significantly lower interaction rates than did the high density treatment (P-adjusted multiple comparison z-score of a generalized linear model: Low-Medium $P = 0.10$; Low-High $P < 0.001$; Medium-High $P < 0.001$). Interaction duration for males was longest at low density (Fig. 3.2A). All treatments were significantly different with respect to interaction duration (Fig. 3.2A; P-adjusted multiple comparison z-score of a generalized linear model: Low-Medium $P < 0.001$; Low-High $P < 0.001$; Medium-High $P = 0.027$).

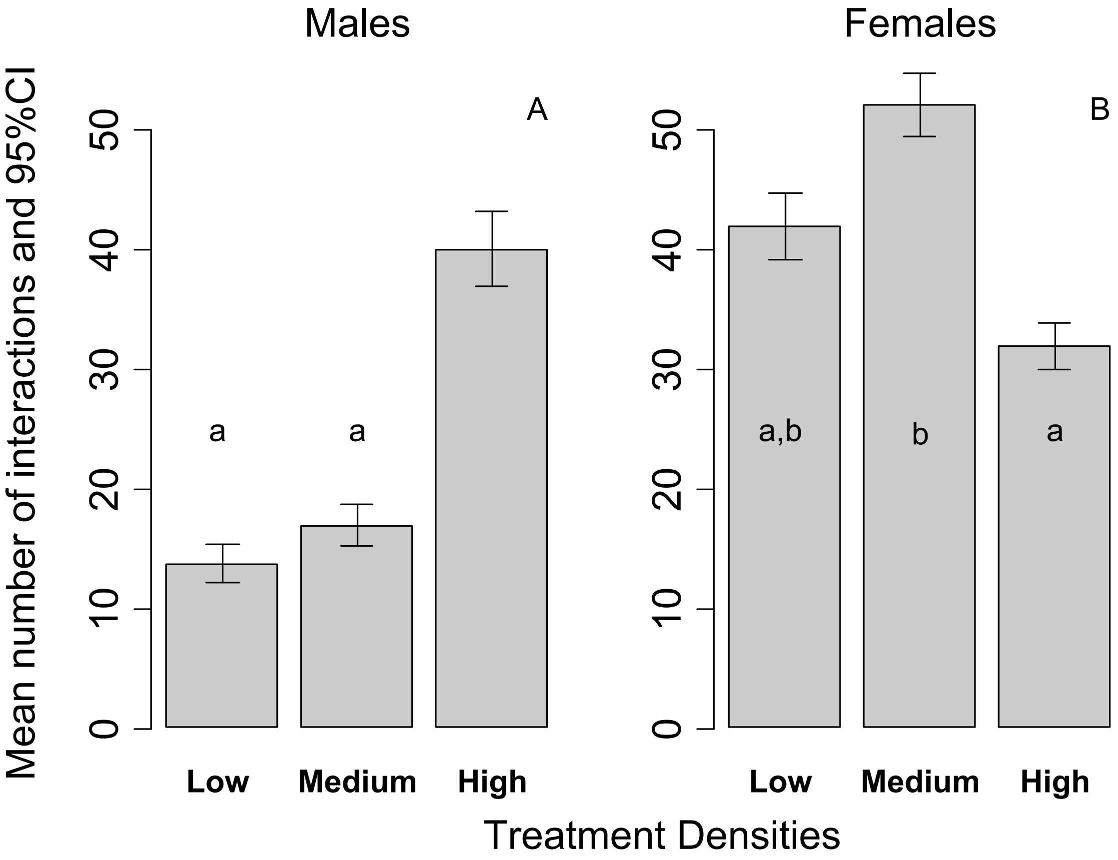

Fig. 3.1. Mean and 95% CI of frequency of interactions for proximity-collared captive elk at low, medium, and high experimental densities in Saskatchewan, Canada, 2007. A. Male elk (*n* = 10). B. Female elk (*n* = 14).

Interaction rates of females was highest at medium density and significantly greater than at high density, although interaction rate at low density, with fewer interactions, was not significantly different compared to the medium density treatment (Fig. 3.1B; *P*-adjusted multiple comparison *z*-score of a generalized linear model: Low-Medium P = 0.333; Low-High P = 0.264; Medium-High P = 0.009). Interaction duration in the medium-density treatment was significantly longer than in the other treatments, but duration did not significantly differ between the low- and high-density treatments (*P*-adjusted multiple comparison *z*-score of a generalized linear model: Low-Medium $P <$ 0.001; Low-High P = 0.648; Medium-High $P <$ 0.001).

3.5 Discussion

My results suggest that social ungulates will modify their sociality based on changes in local density under constant group size; however, this response is sex-specific. Interaction rates for males increased as I had predicted, but for females I noted the greatest number of interactions occurring at an intermediate density. These trends were clearly evident in my replicated study, and I suggest they are biologically meaningful.

I submit that observed differences in how sexes responded to changes in population density are related to differences in perceived costs and benefits of living in a group. Animals that form social groups are subject to a number of costs and benefits that affect survival and reproduction (Estevez, Andersen, & Nævdal 2007). Benefits include reduced predation risk and associated reductions in vigilance, allowing for more time feeding or resting (Lima 1987; Roberts 1996).

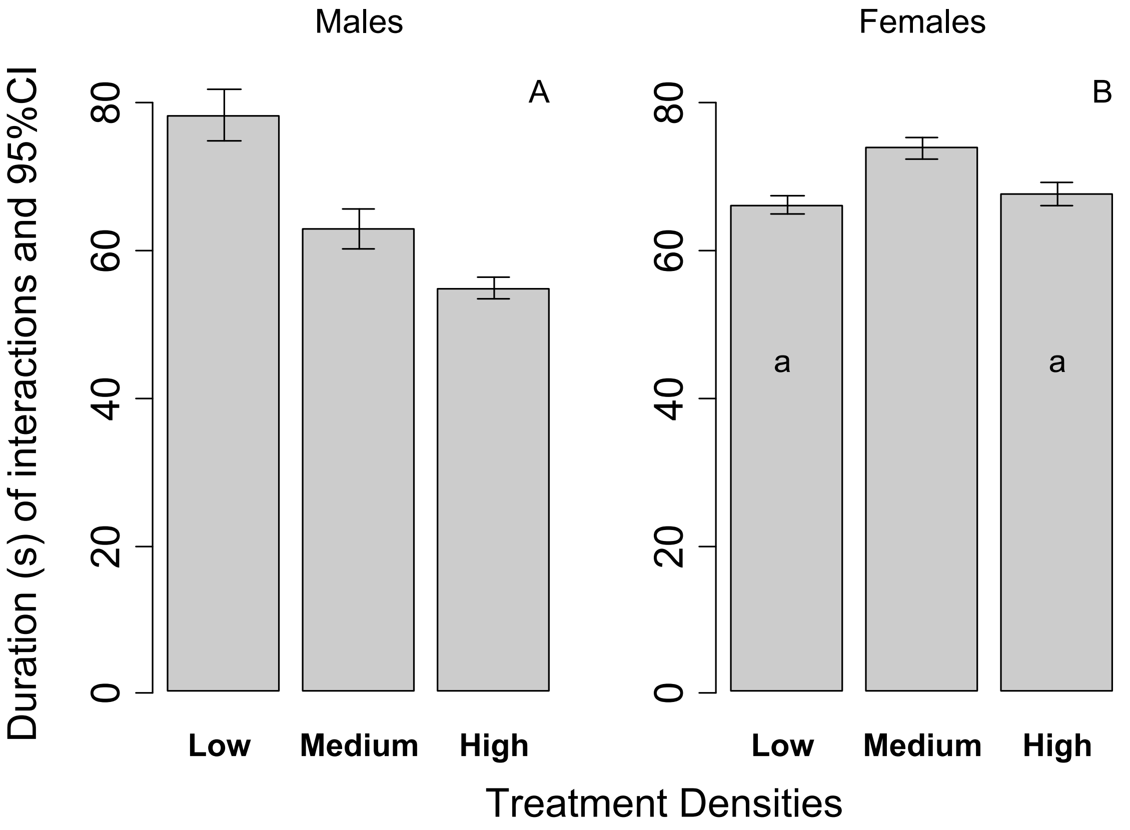

Fig. 3.2. Mean and 95% CI of interaction duration (s) for proximity collared captive elk at low, medium, and high experimental densities in Saskatchewan, Canada, 2007. A. Male elk (*n* = 10). B. Female elk (*n* = 14).

Some costs include decreased access to resources, and increased levels of stress and competition because of this lack of resources (Lung & Childress 2007). In natural situations, if the costs exceed the benefits an animal may leave the group (Weckerly, Ricca, & Meyer 2001; Krause & Ruxton 2002); however, in my experiment, leaving the group was not an option.

Why males increased the number of interactions as density increased, in contrast to females, may be related to lower perceived benefits derived from group-size mediated defences against predation. Childress & Lung (2003) show that male elk are primarily vigilant for monitoring conspecifics, and predators are of secondary concern. The opposite is true for females, whose vigilance behaviour is mainly anti-predator. This supports the hypothesis that males will invest more of their energy in being competitive, and so, under situations of higher population density, relatively more effort will be invested in agonistic behaviours than females. Females are undoubtedly affected in a similar fashion to male elk in that increased density and competition typically leads to lower body weight and reduced performance (e.g., Mysterud et al. 2001, Stewart et al. 2005); however, females likely place less a cost on high group size than males (Appendix B). Females, which are smaller and may move with offspring, are more vulnerable to predation and hence likely more comfortable in larger group sizes than are males. This observation is supported by Richardson and Weckerly (2007), who observed that, in white-tailed deer, male groups were spaced farther apart and were more aggressive to each other than were female groups.

Females existing in dominance hierarchies are less likely to be aggressive to each other when individuals are known or related to each other (e.g., primates [Perry et al.

2008], red deer [Thouless and Guinness 1986], sheep [Guilhem et al. 2000]). In my experiment, it is likely that the females I used were in some cases related, and that an established dominance hierarchy already existed. Female philopatric groupings are the natural condition for wild elk and red deer (Clutton-Brock et al. 1982). Weckerly (1999) found that aggressive interactions in female elk in the same social group were very short (<5 s), were decisive, and involved relatively little physical contact. Weckerly (1999) is the only study recording similar interactions, however. My techniques for measuring interaction duration differed making direct comparison difficult. Notwithstanding this caveat, I observed much longer interactions for females than expected for conflict (Fig. 2B) predicated on Weckerly's (1999) observations; suggesting the possibility that I had few aggressive interactions among females. That interaction duration did not decline with density from low to high density suggests that the types of interactions performed also did not vary substantially with density.

Interaction duration for males declined significantly as density increased and number of interactions increased in the male herd. This suggests the opposite compared to females: that aggressive interactions increased for males with population density. My results also suggest a potential trade-off in the number and duration of interactions that may occur in social situations for male elk. This invites further research, as the implications to density-dependent theory on sexual selection (Kokko & Rankin 2006) may be important. With increasing density, average male mating success is expected to decrease (Gaskin et al. 2002; Zhang & Zhang 2003; Härdling & Kaitala 2005; Kokko & Rankin 2006) possibly because when local population density increases, male–male interference and competition increase (Zhang & Zhang 2003; Kokko & Rankin 2006;

Wang et al. 2009)females become choosier (Shelly & Bailey 1992; Kokko & Rankin 2006; Wang et al. 2009), or some males become more likely to be engaged in courtships to other males (Gaskin et al. 2002). My data suggest that for elk under high density situations, because of time constraints, social behaviours may also become shorter in length, which has the possibility to influence strength of selection. This idea is supported by Clutton-Brock et al. (1997), who observed that for red deer at high densities sexual selection was relaxed, males held harems for shorter periods, and a higher proportion of males fathered offspring. The potential importance of time constraints on performing reproductively important social displays as density increases has yet to be fully considered in ecology.

My results may also have implications for the management of wildlife disease. Social interaction is often necessary for the transmission of communicable wildlife diseases, such as rabies (*Lyssavirus* spp.), distemper (*Morbilliviris* spp.), and tuberculosis (*Mycobacterium* spp.); and transmission is generally assumed to be directly density-(McCallum, Barlow, & Hone 2001) or in some cases ratio-dependent (Begon et al. 1999). Functionally, the mechanisms for successful transmission of communicable disease break down into two categories that occur and vary at the level of the individual: how host density relates to the quantity (e.g., interaction frequency) and quality (e.g., length of encounter) of social interactions. The shape of these relationships, and how they might vary among different components of a population (age, sex), are largely unknown, presenting an important gap in my understanding of disease transmission. Furthermore, classic disease models predominantly assume increased transmission with increased contact between animals (see Hethcote 1976; Hethcote 1989). These models predict that even the most virulent pathogens do not have a 100% transmission rate between hosts, and increasing the duration or frequency of contact between animals will serve to increase the infection rate. However, it is infrequent that variations in social behaviours are interpreted in the context of pathogen transmission. Understanding relationships between density and the quantity and quality of individual interactions may be important for managing and eradicating communicable disease.

My observations differed from my predictions reinforcing the notion that managing elk or other social ungulates with regards to pathogen transmission can be confounded by individual behavioral responses (Matthews 2009; Kirkpatrick & Altizer 2010; Tompkins et al. 2010). For males, higher density is clearly a cause for increased interaction rates, albeit with reduced duration of interactions (although average length of interactions was still substantial, e.g., >50 s; Fig. 3.2A). These results have some practical management implications. For example, I may be able to decrease contact rates among male social ungulates by reducing population density, and fencing a diseased population to prevent movements of dispersing males may be a poor idea if reducing the overall prevalence of a disease is a goal. My results for females suggest that reducing density in sexually-segregated, female philopatric ungulates may have no effect or actually serve to increase the number of interactions within a herd, thus increasing the infection rate. All together, my results suggest there may be opportunities to control the spread of communicable disease in gregarious species of ungulates by targeting population control toward males while maintaining female numbers.

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Chapter 4: A comparison of density- and frequency-dependent social behaviours reveals mechanisms for an intermediate strategy: implications for pathogen transmission

4.1 Abstract

Few empirical studies have tested the assumptions of frequency- vs. density-dependent pathogen transmission. Even fewer studies have tested how conspecific density affects behavioural mechanisms upon which pathogen transmission is based, i.e., interaction rates and intraspecific relationships. I tested whether interaction rates (i.e., when focal animals came within 1.4 m using SirTrack Proximity Collars) and degree of social familiarity among conspecifics were frequency- or density-dependent using two spatially isolated subpopulations of elk. One subpopulation had high conspecific density and elk infected with bovine tuberculosis (TB); and the other, low conspecific density and no elk infectious with TB. The frequency of dyadic interactions was significantly greater at high conspecific density ($P = 0.03$) and the number of animals a focal individual is familiar with was not significantly different between subpopulations assuming weak relationships (i.e., ≤3 interactions/year, $P > 0.05$). However, as dyads interact more frequently, conspecific familiarity changes from being frequency- to density-dependent ($P < 0.05$). I argue that interaction rate is density-dependent and the number of individuals a given animal is familiar with is both a function of the proportion of animals in the subpopulation, i.e., frequency-dependent, and density-dependent contingent on the strength of the dyadic relationship.

4.2 Introduction

Density-dependence in processes such as predation (Holling 1966; Bassar et al. 2010), competition (Morris 2003; Stewart et al. 2005; McLoughlin et al. 2006), sociality (Albon et al. 1992; L'heureux et al. 1995), and pathogen transmission (Anderson & May 1979; May & Anderson 1979; Lloyd-Smith et al. 2005) is fundamental to the ecology and evolution of species. Each of these processes is predicated on specific animal behaviours occurring at the individual scale (e.g., escape responses, interference strategies, consumption patterns, interaction rates). How individual-level processes are influenced by population-level phenomena such as density-dependence is one of the great problems in population ecology (Sutherland 1996).

In social species, other-oriented behaviours are conducted to assert dominance over conspecifics (e.g., red deer, *Cervus elaphus*, [Appleby 1980; Clutton-Brock et al. 1982] bighorn sheep, *Ovis canadensis* [Festa-Bianchet 1991; Pelletier & Festa-Bianchet 2004]), for group cohesion necessary for survival (eg., red wolf, *Canis rufus*, [Sparkman et al. 2011], mutual grooming (e.g., meerkats, *Suricatta suricatta*, [Kutsukake & Clutton-Brock 2010; Drewe 2010]), or for mating (e.g., feral horses, *Equus callabus*, [Berger 1977; Heitor et al. 2006]). Such behaviours accord some advantage to one or all interacting participants. However, other-oriented behaviours can also be disadvantageous. For example, in hierarchical interactions, the loser must subordinate to the winner losing mating opportunities or access for foods (e.g., red deer [Appleby 1982]). Furthermore, whenever one behaviour is chosen over an alternate behaviour, trade-offs exist, e.g, feeding may occur at the expense of vigilance (Cowlishaw et al. 2004; Beauchamp 2009). However, in social foragers this may be modified by degree of familiarity (Griffiths et al.

2004), which itself is contingent on a time-consuming behaviour. I define familiarity as when two animals are known to one another. As animals can only conduct a given number of behaviours simultaneously (e.g., it is uncommon for vigilance and feeding to occur concordantly [McNamara & Houston 1992]), and as extrinsic pressures such as conspecific density increases, so do the costs associated with social behaviours as they need be focussed on more individuals. How individual social behaviours change at different conspecific densities is not well known. For pathogen transmission, however, theoretical and empirical studies have been conducted to investigate how contact rate, which is a social behaviour, might change with increasing population density (see Altizer et al. 2003 and Cross et al. 2009 for review), resulting in higher disease prevalence (McCallum, Barlow, & Hone 2001).

Pathogen transmission is typically modelled in one of two ways: as density-dependent or frequency-dependent (McCallum et al. 2001; Begon et al. 2002). Density-dependent transmission implies that contact rate (*sensu* McCallum et al. 2001, i.e., the number of potentially infectious contacts made per infected host per unit time) varies in a curvilinear fashion with density (e.g., for directly transmitted diseases [Anderson & May 1979]). Conversely, contact rate is constant for frequency-dependent transmission (e.g., sexually transmitted diseases Lockhart et al. 1996; Lloyd-Smith et al. 2004). Studies of pathogen transmission predominantly focus on population-level phenomena (e.g., changes in host density) or rates of pathogen transmission. Tompkins et al. (2010) indicate that although population level patterns can be indicative of individual-level phenomena it is difficult to effectively address the mechanisms behind such phenomena. Despite this challenge, studies of contact-rate and contact networks have recently focussed on individual-level mechanisms for pathogen transmission (see Cross et al. 2009; Matthews 2009 and Tompkins et al. 2010 for reviews).

Easily transmissible pathogens are thought to exhibit classical density-dependent transmission among conspecifics. Conversely, frequency-dependent (i.e., proportional to the number of conspecifics) transmission is typically reserved for chronic-less transmissible pathogens (Lloyd-Smith et al. 2005). However, recent theoretical studies of transmission functions for chronic wasting disease in cervids (Schauber & Woolf 2003), cowpox virus models (Smith et al. 2009), and for brucellosis transmission in elk (Cross et al. 2010), have suggested that some intermediate function of transmission may exist. Transmission, as described by (Begon et al. 2002), is a function predicated on a) the occurrence of a contact event, and b) the probability that said event results in successful transmission of the pathogen. My study focuses primarily on the former using dyadic interactions (*sensu* Whitehead & Dufault 1999) as a proxy for contacts and a foundation for networks of familiarity. However, I also investigate interaction duration, as I predict that probability of successful transmission increases with increased contact time. Few empirical studies ever test the assumptions of frequency- vs. density-dependent transmission, even fewer studies have investigated the behavioural mechanisms upon which pathogen transmission is purportedly based, i.e., contact or interaction rates and intraspecific relationships, or how said mechanisms are affected by changes in conspecific density (but see Caley et al. 1998; Ramsey et al. 2002).

In gregarious mammals, dyadic interactions are not only the basis for social structure and information transfer within a population, but are also routes of pathogen transmission (Wilson 1975; Cross et al. 2009). Elk are among the most social ungulates

(Vos, Brokx, & Geist 1967; Geist 1974). As social ungulates, elk interact to maintain dominance hierarchies and often exhibit aggressive behaviours toward conspecifics (Weckerly 1999; Weckerly 2001). I used female elk in Riding Mountain National Park (RMNP), as my model system to apply both a dyadic and higher-order (i.e., social network) approach to test whether subpopulation density affects social behaviours that may influence pathogen transmission. Spatial variation in apparent disease prevalence of TB in RMNP elk suggests that TB can only persist in the subpopulation within the Park that has highest conspecific density. Hence, my overarching prediction regarding pathogen transmission is that social behaviours in the low density subpopulation differ from those in the high density subpopulation. I predict that a threshold for TB transmission exists between the two subpopulations, i.e., transmission of TB is density-dependent. However, my specific predictions look not at pathogen transmission per se, but rather at how density affects animal behaviour; behaviours not only with implications for pathogen transmission, but also for information flow between individuals in dyads and through the population. I predict that elk in the low density landscape will have fewer dyadic interaction with conspecifics than elk in the high density landscape (i.e., dyadic interact rate is density-dependent). Furthermore I predict a non-linear (i.e., density-dependent) relationship between conspecifc density and the number of conspecifics with whom a focal individual is familiar.

4.3 Methods

4.3.1 Study Area

Riding Mountain National Park (RMNP, Fig. 4.1) occurred in a transition zone between the prairies to the northern Boreal Plains ecoregion (Bailey 1968). The eastern portions of the park rise 475 m from the Manitoba lowlands up the Manitoba escarpment and declines gradually to the western limit of the Park. The dominant forest types were northern boreal, aspen (*Populus* spp.) parkland, bur oak (*Quercus macrocarpa*) savannah, fescue (*Festuca* spp.) grassland, and eastern deciduous (Rowe 1972; Caners & Kenkel 2003). RMNP was surrounded by an agricultural matrix resulting in very low exchange of elk in and out of the region (Brook 2008). The area that RMNP now occupies has a history with TB extending back prior to 1950s and 1960s when cattle grazed within the Park's boundaries (Copeland 2002; Brook 2009). In 1986, MB was declared TB free; however, from 1991 to 2009 outbreaks involving elk (*n* = 35), white-tailed deer (*n* = 7) and cattle (*n* = 12 herds) occurred (Brook & McLachlan 2009) resulting in negative economic repercussions (Nishi, Shury, & Elkin 2006).

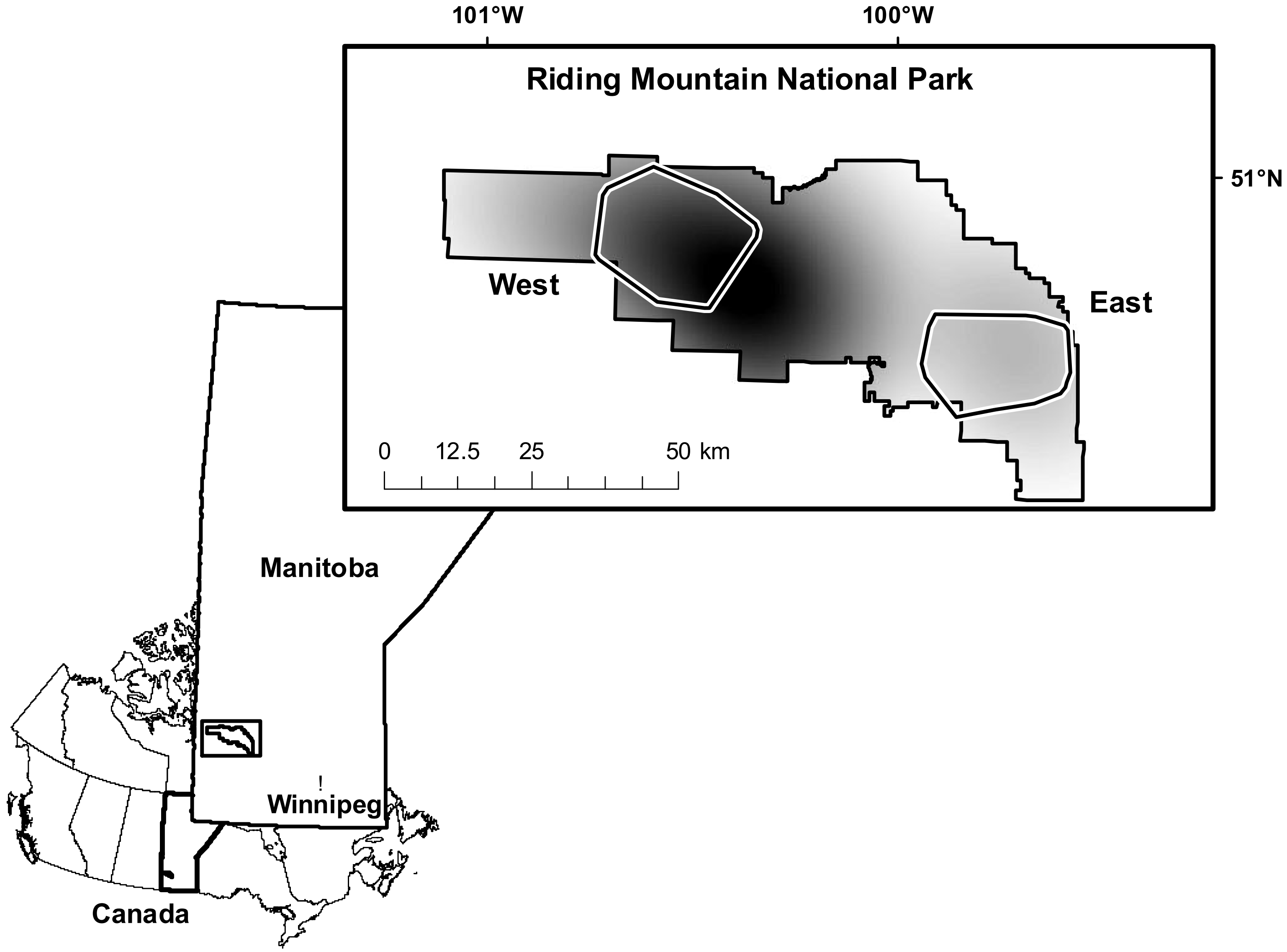


Fig. 4.1 Riding Mountain National Park (RMNP; 2674 km^2) is located in central Canada in the prairie parkland transition ecoregion. Individual elk (*Cervus elaphus*) were sampled in two sub-populations of RMNP denoted with white borders by 95% minimum convex polygons (west n = 792 and east n = 1082 elk relocations 2008-2009). Grey scale (i.e., white = 0 through black = 4 elk/km^2) within each area depicts a three year average (2007–2009) density of elk from RMNP annual 25% aerial survey (Parks Canada unpublished data). Approximate density of elk is: west 0.42/km^2, east 0.22 km^2 (Parks Canada unpublished data).

4.3.2 Study Design

I assumed that randomly sampled focal individuals had the same relationships (e.g., interactions, familiarity) to unsampled individuals as they had to other sampled focal individuals. Therefore,

$$F = v \times d \quad [4.1]$$

where total frequency of a behaviour (*F*) is a function of *v*, the observed frequency of the behaviour, and *d*, conspecific density. However, *v*

$$v = \frac{\overline{v}}{n} \quad [4.2]$$

was contingent on the estimate of the frequency of the behaviour ($\overline{v}$) and the number of focal individuals (*n*) observed. Hence if:

$$v_{d_1} = v_{d_2} \quad [4.3],$$

where v_{d_1} and v_{d_2} were the observed behaviours at density 1 and 2, this would indicate a frequency-dependent behaviour. Conversely if:

$$v_{d_1} \neq v_{d_2} \quad [4.4]$$

behaviours were density-dependent (Fig. 4.2). Thus, by sampling animals in multiple landscapes with different conspecific densities, non-significant differences in behaviour do not reflect similar frequencies of behaviour; rather, they imply that the frequency of a behaviour is proportional to the number of conspecifics present (i.e., frequency dependence).

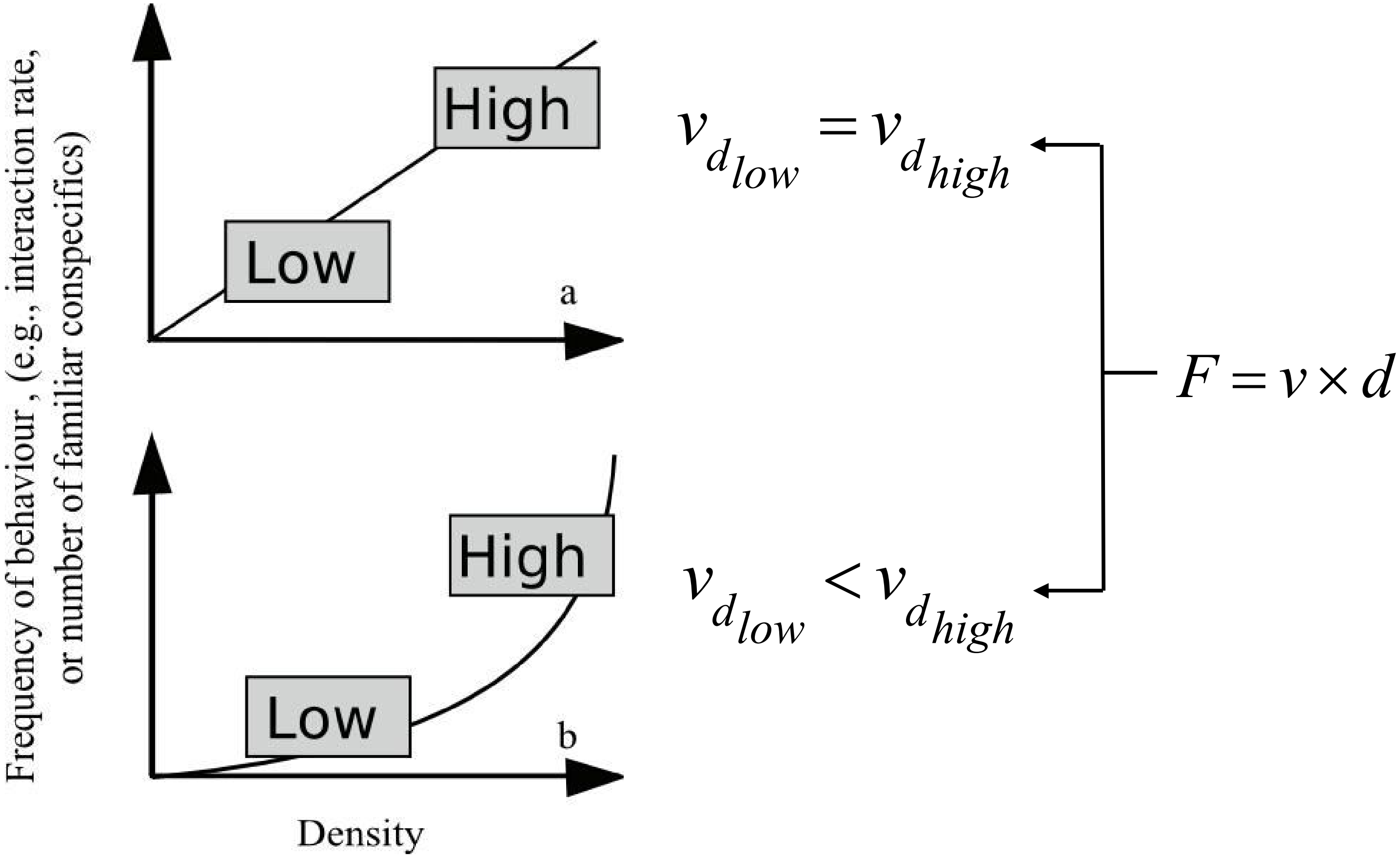


Fig. 4.2 Similar-sized samples of focal individuals are made in the low and high density landscapes (grey boxes). Total frequency of a behaviour (*F*) is equal to the observed frequency of the behaviour (*v*) and the conspecific density (*d*). a) Represents non-significant differences in frequency of behaviour (i.e., $v = v$, [e.g., frequency-dependent]) and (b) where frequency of behaviour is significantly different between treatments (i.e., frequency of behaviour is affected by conspecific density, $v \neq v$ [e.g., density-dependent]). If pathogen transmission is predicated on the behaviour described (e.g., contact rate) and disease exists in the high density landscape but not the low density landscape, then a threshold for disease fade out (i.e., critical community size) in transmission exists between the two densities sampled in (b); however, no such threshold exists in (a).

Conversely, when a significant difference is detected it implies that the change in behaviour frequency is non-linear (i.e., density dependence). Thus, if similar sized samples of focal individuals are made in the low and high density landscapes (i.e., east and west RMNP, respectively), non-significant differences in frequency of behaviour would be represent frequency-dependent behaviour and if frequency of behaviour was significantly different between treatments, I would conclude that there was a density-dependent effect. The critical point to this chapter is this: if pathogen transmission is predicated on the behaviour described (e.g., contact or interaction rate) and disease is predominantly in the high density landscape but not the low density landscape (as is the case in RMNP), then a threshold for disease fade out (i.e., critical community size [Bartlett 1957]) in transmission may exist between the two densities sampled; however, no such threshold exists for behaviours that are frequency-dependent (Fig. 4.2)(Lloyd-Smith et al. 2005).

4.3.3 Elk sampling

In February through March of 2008 we captured free ranging adult female elk (*n* = 35) using a net-gun fired from a helicopter (Cattet et al. 2004). Elk were collared for one year. We equipped all elk with Sirtrack Proximity Logger radio-collars (Sirtrack Ltd., Havelock North, New Zealand; Swain & Bishop-Hurley 2007). See Chapter 2.3.2 for proximity collar programming details and Animal Care Protocol.

4.3.4 Treatment area and density estimate

Treatment areas were designated at the subpopulation scale with 95% minimum convex polygons (Fig. 4.1). Weekly–biweekly aerial telemetry relocations (west *n* = 792 and east *n* = 1082) were conducted in a Cessna 172 (Wichita, KS). Once animals were located a global positioning system was used to record the spatial location.

Western RMNP supports higher densities of elk than eastern RMNP (Fig. 4.1). Approximate densities of elk were 0.42/km^2 (west) and 0.22/km^2 (east) (Fig. 1). Density estimates were derived from a three-year average (2007–2009) of a 25% coverage aerial survey of visible elk (Parks Canada unpublished data). Transects were 200 m wide conducted in January of each year at and altitude of 120 m at 120 km/hr by two trained observers in a Cessna 172 (Wichita, KS). The same flight lines were repeated each year.

4.3.5 Interaction rate and duration analysis

All statistical analyses were preformed in the R environment for statistical computing (R Development Core Team 2010). Interaction rate and duration data were non-normal and non-independent. Transforming interaction data helped normalize the data; however, it failed all omnibus tests of normality (e.g., Lillifors $P > 0.05$). I therefore used a Mann-Whitney U test to compare interaction rate and duration between the two treatment areas.

4.3.6 Network or graph analysis

I constructed social networks or graphs (Table 4.1 for basic network terms) and obtained metrics using the R package iGraph (Csardi & Nepusz 2006). I compared two networks of elk (*n* = 16 and 19, west and east RMNP respectively).

Table 4.1 Some social network terms

Term	Definition
Interaction	Interactions (*sensu* Whitehead & Dufault 1999) occurred when two individuals were within 1.4 m.
Dyad	A dyad is two interacting individuals.
Node	A node is an individual, e.g., each individual elk in my study are nodes
Edge	An edge represents the interaction between two individuals, e.g., in my study the edge represents whether two elk interacted. An edge can represent a single event or multiple events and can be used to show the strength of the bond between two individuals
Network	A network consists of nodes and edges

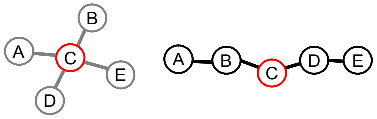
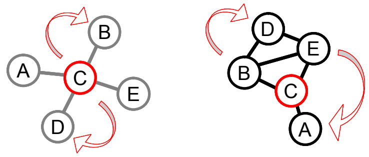
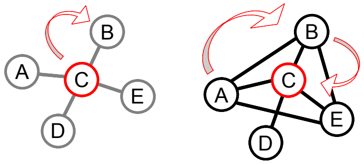
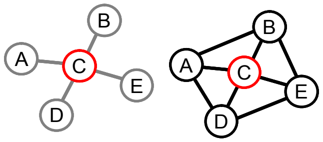
Non-indexed metrics pertaining to focal individuals (e.g., degree and betweenness) were obtained from networks that were resampled at $n = 15$ to control for network size and to generate confidence intervals. Otherwise, the remaining metrics (e.g., graph density and transitivity), were obtained from networks that were $n - 1$ jackknifed to generate confidence intervals. Each network was subsequently resampled for 10,000 iterations (Manly 1998). Network metrics were calculated for each node in each resampled network (for degree, betweenness, and transitivity) or each jack-knifed network (for graph density) (see Table 4.2 for tabular and graphical descriptions of network metrics). I constructed networks for all edge values from one through the maximum number of interactions per dyad (range 1–380). Mean values for node-based metrics were calculated for each resampled or jackknifed network. From this resampled distribution of metric means I calculated 95% CI to compare between treatment areas.

4.4 Results

4.4.1 Dyads and Interaction Rates and Durations

Proportions of dyads formed varied between treatments. Nineteen females collared on the east side of the Park (i.e., low density treatment) formed 27% of possible dyads. In the western high-density treatment, 16 females formed 37% of possible dyads where edges were ≥ 1 (Fig. 4.3). Within those dyads, annual interaction rate (Fig. 4.4a) was significantly different between treatments. In the west (median = 18 and range = 1–330) than the east (median = 6 and range = 1–194) treatments of RMNP (Mann-Whitney U, $P = 0.03$ $df = 1$, $n = 93$). Interaction duration (Fig. 4.5), however, did not differ between treatments (Mann-Whitney U, $P = 0.19$ $df = 1$, $n = 4339$).

Table 4.2 Definitions of social network metrics

Measure	Definition	Graphic	Example and Importance for Pathogen Transmission
Degree	Degree, or degree centrality, is a measure of how many edges a node shares other nodes and indicates a nodes prominence in the network.		Degree is a measure of familiarity. The higher the degree the more individuals with whom an animal is familiar (e.g., C in the the grey network, i.e., Deg = 4 vs. C in the black network, i.e., Deg = 2). More familiarity can result in more pathogen transmission. Animals with very high degree are often termed “superspreaders”.
Betweenness	Betweenness measures how frequently a focal node falls on the shortest path between two other nodes.		For instance, in the grey network C falls on the shortest path from D to B and from A to E. This is contrary to the black network where C only falls on the shortest path from A to E. High Bet measures identify individuals who are likely to be on the path for pathogen transmission.
Transitivity	Transitivity describes how ‘cliquish’ a network is and measures to what extent two neighbours in a group are themselves neighbours.		For instance, in the grey network C is neighbours with A and B, but B is not neighbours with A. The black network is more cliquish because C is neighbours with A and B, who are themselves neighbours. Cliquishness creates redundant routes for pathogen transmission.
Graph density	Graph density is a measure of network compactness based on the number of edges present versus the number of possible edges		The grey graph exhibits four of a possible eight edges (i.e., graph density = 0.5), compared to the black graph which exhibits all eight (i.e., graph density = 1).

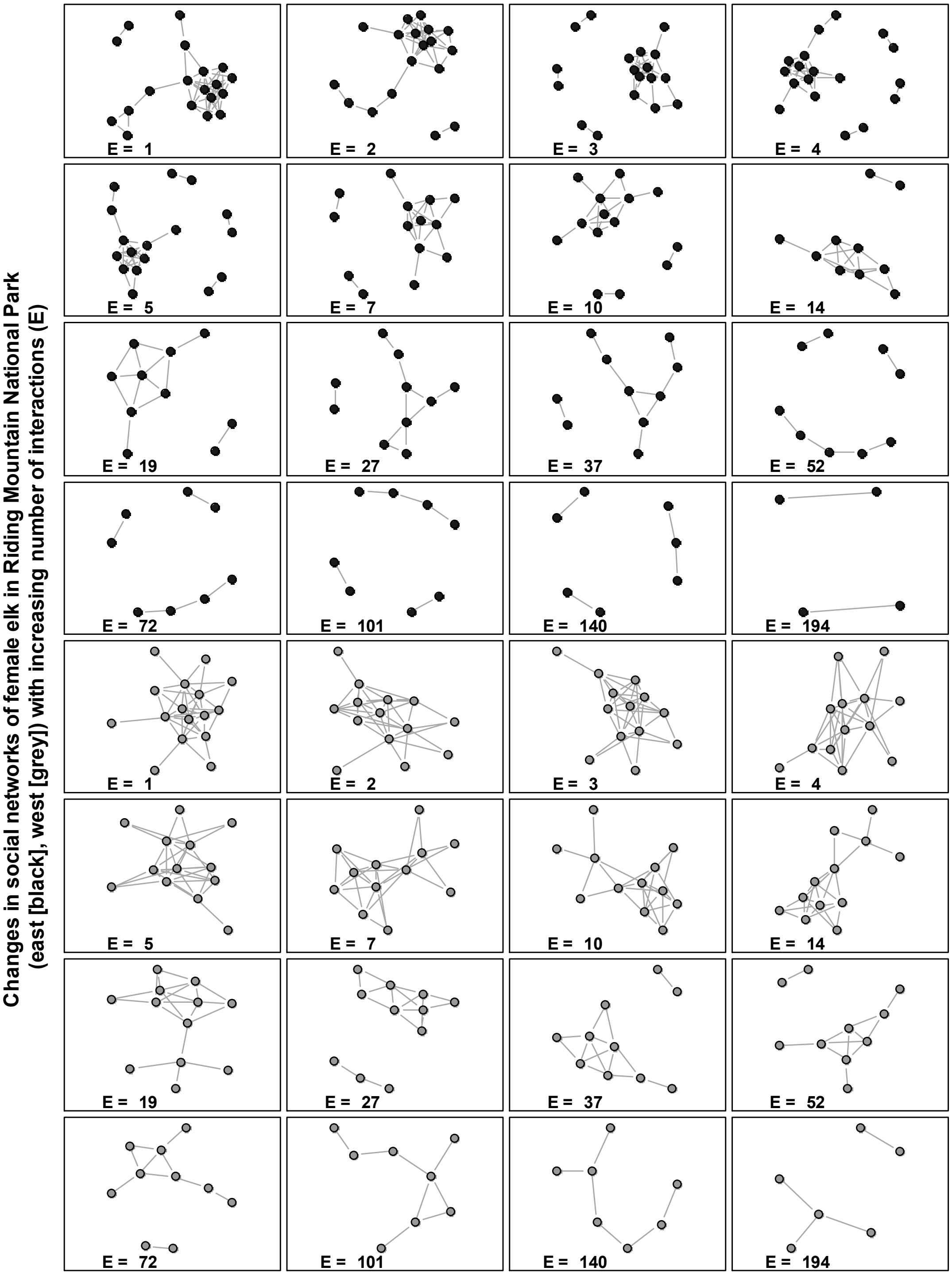


Fig. 4.3 Social networks of proximity collared female elk (n = 19 east [black], n = 16 west [grey]) from Riding Mountain National Park (RMNP), MB, 2008–2009 that are bound by edges (E) whose criterion for connecting two nodes changes by increasing number of interactions (e.g, for E = 1 all edges represent >= one interaction between members of the dyad, whereas E = 194 only includes dyads whom interacted >= 194 times) in each iteration of the network. Animals that do not meet the threshold for minimum number of pairwise interactions in each network are removed from subsequent sub-figures.).

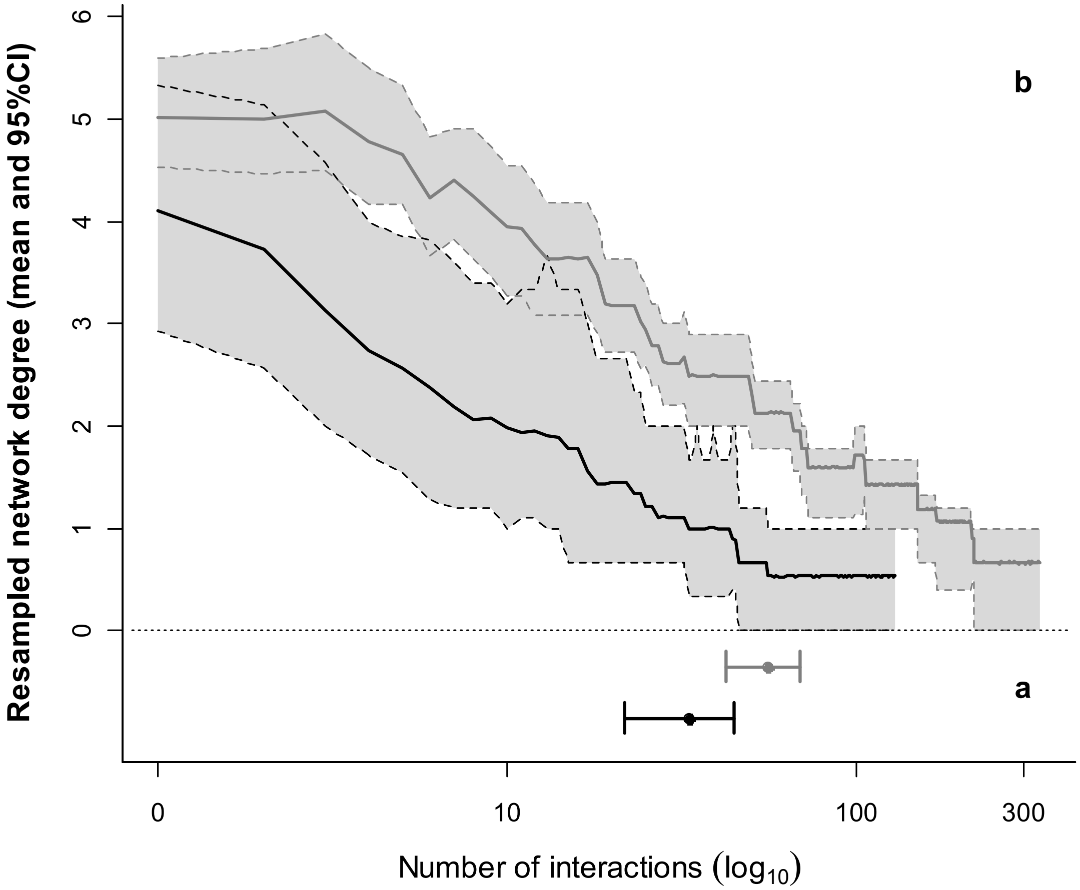


Fig. 4.4 Annual interaction data from proximity collared female elk (*n* = 19 east [black], *n* = 16 west [grey]) from Riding Mountain National Park (RMNP), MB, 2008–2009. Significantly different 95% CIs, 4a, contrast the number of dyadic interaction between elk in two landscapes with varying conspecific density. One landscape is subject to low density (east RMNP: ≈ 0.17 elk/km^2) and the other high density (west RMNP: ≈ 0.42 elk/km^2). Interaction rate from 4a forms the criterion for adjoining individuals in a social network (see Fig. 3). This criterion iteratively changes from one through 120 (east treatment) and one through 337 (west treatment) in 4b. Each iteration, i.e., value on the abscissa, results in a social network of female from which degree of connectedness (i.e., number of familiar conspecifics) among individuals is calculated. Each iterated network is resampled at *n* = 15 to calculate the mean (solid line) and 95% CI (fill bound by dotted lines) for female in east RMNP (black) and west RMNP (grey). Due to unequal density in each landscape, and therefore unequal sampling effort, where confidence intervals overlap indicates that degree of connectedness is frequency-dependent (i.e., the number of familiar conspecifics an individual has is proportional to the number of individuals present). Conversely, where confidence intervals do not overlap, degree of connectedness is density-dependent (i.e., the number of familiar conspecifics an individual has increases non-linearly with density of individuals present).

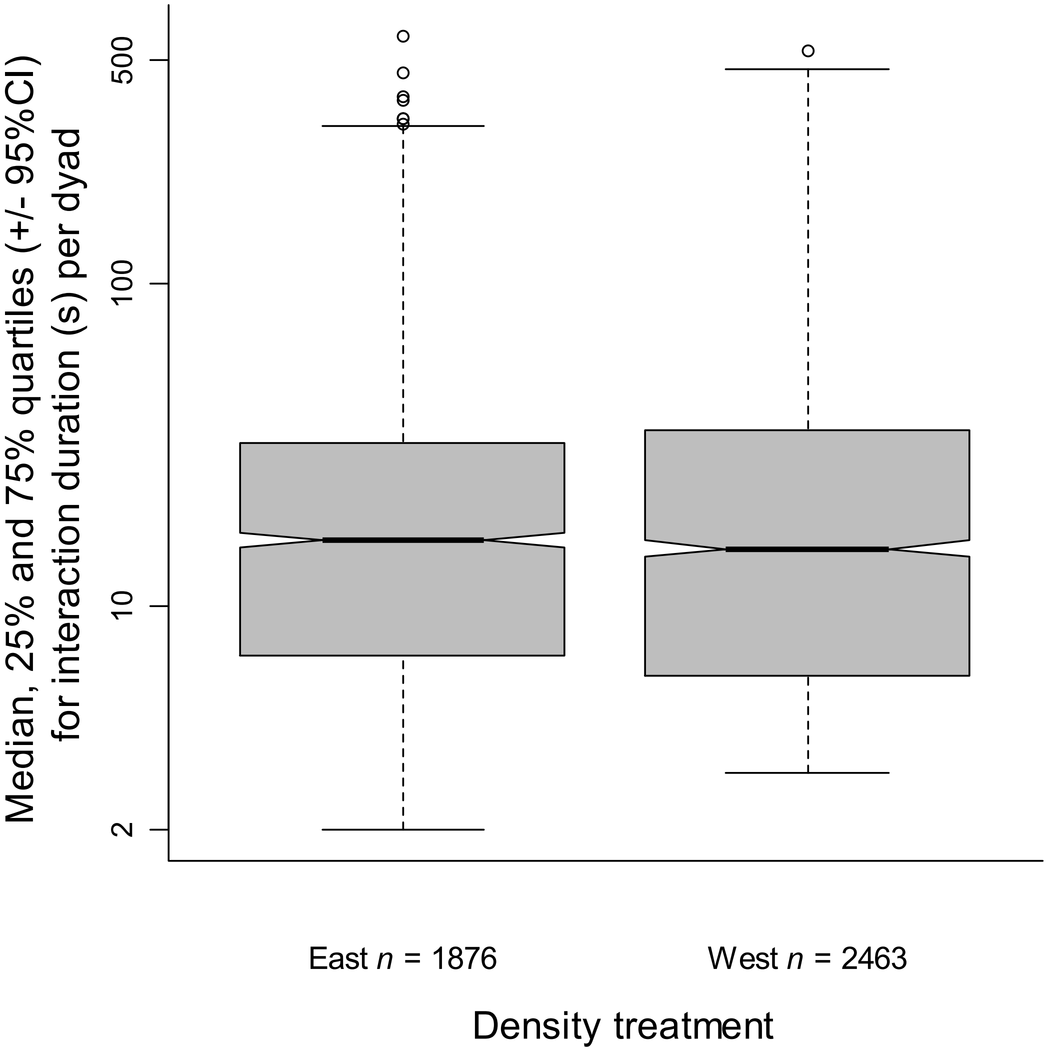


Fig. 4.5 Median, 25% and 75% quartiles, and 95%CI for interaction duration among female-female elk dyads fit with proximity collars in Riding Mountain National Park (RMNP), MB, 2008–2009, where one landscape is subject to low conspecific elk density (east RMNP: ≈ 0.17 elk/km^2) and the other high density (west RMNP: ≈ 0.42 elk/km^2). Overlappling notches in the sides of the boxes indicate no significant difference between groups (Chambers et al. 1983) and therefore no density-dependent effect.).

4.4.2 Social Network Metrics

Where nodes were connected by edges consisting of ≥1 interaction (Fig. 4.3), degree of familiarity was not significantly different among elk in the east $\bar{x}$ = 4.1 (95% CI [Confidence Interval] 2.9–5.5) and west $\bar{x}$ = 5.0 (95% CI 4.5–5.6) (Fig. 4.4b). However, when dyads have ≥4 interactions, degree of familiarity first became significantly different: east was $\bar{x}$ = 2.7 (95% CI 1.6–4.0) and west $\bar{x}$ = 4.8 (95% CI 4.2–5.5) (Fig. 4b). Some ambiguity exists until there are ≥17 interactions/dyad/year when degree of familiarity remains predominantly significantly different between treatments, where east was $\bar{x}$ = 1.6 (95% CI 0.7–3) and west $\bar{x}$ = 3.6 (95% CI 3.1–4.2) (Fig. 4.4b) until sample sizes and resampling preclude comparison.

Network density was significantly different between treatments for edges including 1–12 interactions (east $\bar{x}$ = 0.29–0.24 [95% CI, lower = 0.26–0.19, upper = 0.32–0.27]) (Fig. 6). Network density fluctuated between significance to non-significance between edges = 13–273, where edges ≥273 were predominantly not significantly different between east and west treatments (Fig. 4.6).

Differences in betweenness across treatments were predominantly insignificant. (Fig. 4.7). I found significant differences in only two different network iterations as edges 56–72 represent iterations of the same network (Fig. 4.3). No statistical difference was detected between treatments for transitivity (Fig. 4.8). At edge ≥12 both treatments had precipitous drops in transitivity (Fig. 4.8).

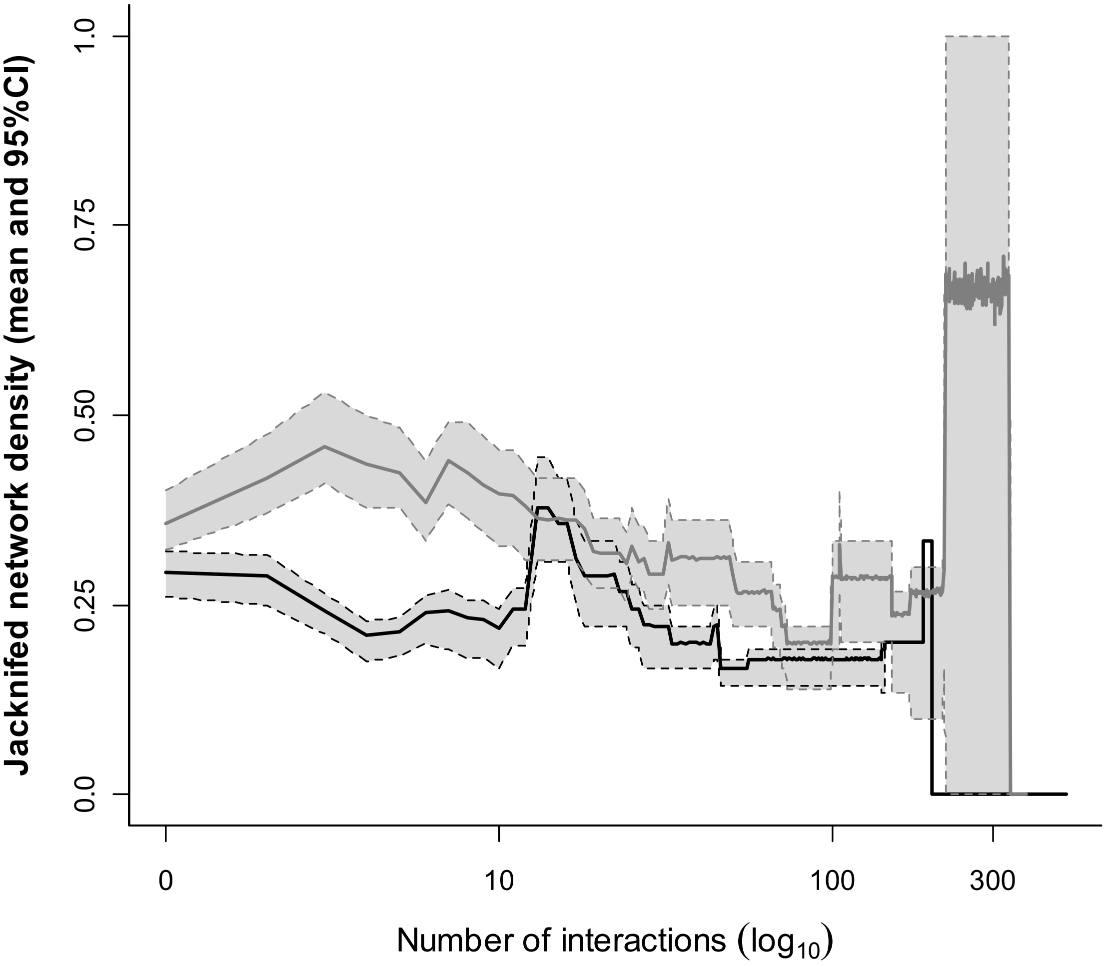


Fig. 4.6 Mean and $n - 1$ jackknifed network CIs of network density for data from proximity collared female elk ($n = 19$ east [black], $n = 16$ west [grey]) from Riding Mountain National Park (RMNP), MB, 2008–2009, where one landscape is subject to low conspecific elk density (east RMNP: ≈ 0.17 elk/km^2) and the other high density (west RMNP: ≈ 0.42 elk/km^2). Non-overlapping confidence intervals indicate a density-dependent effect.).

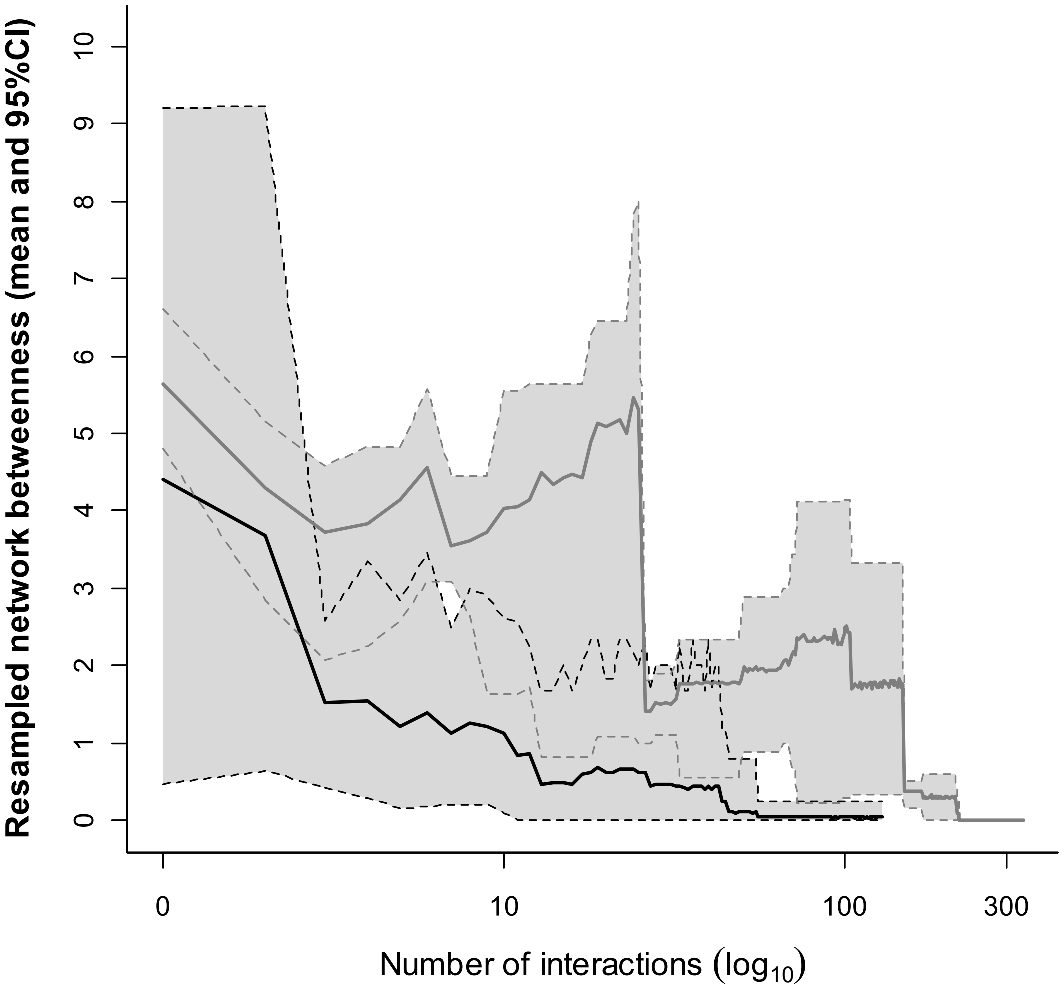


Fig. 4.7 Mean network betweenness and 95%CIs for data from proximity collared female elk (resampled at *n* = 15 east [black], *n* = 15 west [grey]) from Riding Mountain National Park (RMNP), MB, 2008–2009, where one landscape is subject to low conspecific elk density (east RMNP: ≈ 0.17 elk/km^2) and the other high density (west RMNP: ≈ 0.42 elk/km^2). Non-overlapping confidence intervals indicate a density-dependent effect.

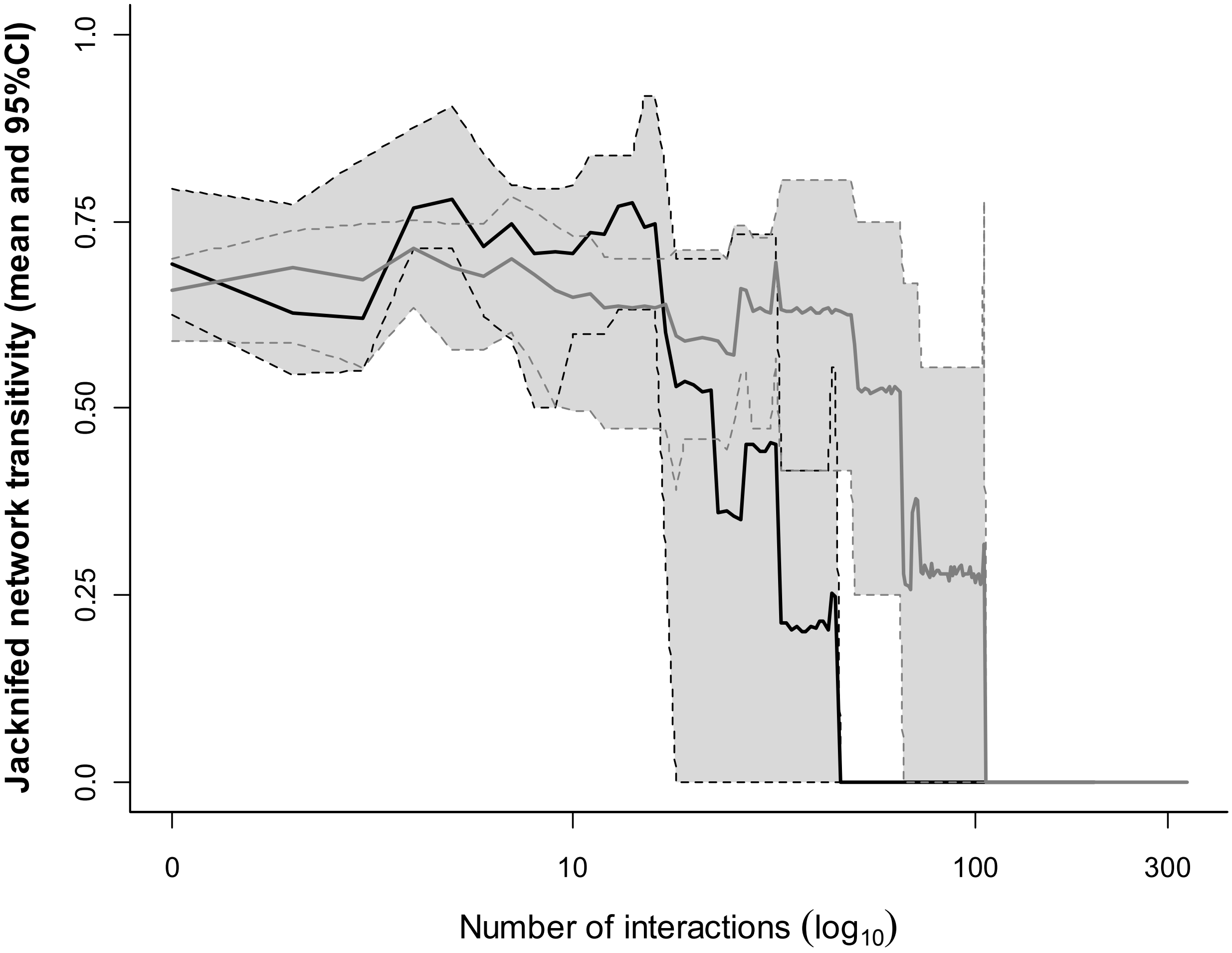


Fig. 4.8 Mean and *n* – 1 jackknifed network CIs of network transitivity for data from proximity collared female elk (*n* = 19 east [black], *n* = 16 west [grey]) from Riding Mountain National Park (RMNP), MB, 2008–2009, where one landscape is subject to low conspecific elk density (east RMNP: ≈ 0.17 elk/km^2) and the other high density (west RMNP: ≈ 0.42 elk/km^2). Non-overlapping confidence intervals indicate a density-dependent effect.

4.5 Discussion

As I predicted, conspecific density resulted in significant differences in behaviours and social network measures (Fig. 4.4). In particular, dyadic interaction rate varied non-linearly with conspecific density. Although the quantity of interactions changed with density, the nature or quality of those interactions (i.e., interaction duration) was not significantly different between subpopulations or treatments (Fig. 4.5). However, even if duration per dyadic interaction remains the same as interaction rate increases, the total time an animal dedicates to other oriented behaviours (e.g., interacting with conspecifics) increases. As my study design was dichotomous I cannot comment on where the upper threshold may exist where animals can no longer accommodate more conspecific interactions.

Dyadic interactions form the base of any social relationship among individuals. However, how these relationships respond to density as strength of the relationship changes is less intuitive. Variation existed among individuals, with some individuals forming few strong pair bonds (e.g., ≥ 100 interactions/year), and some exhibit weak familiarity (e.g., ≥ 5 interactions/year). Relationships predicated on weak familiarity responded differently to conspecific density than did relationships predicated on strong pair bonds, i.e., weak relationships appear to be invariant to density, whereas strong pair bonds do vary with density. Subpopulation density had a linear effect (e.g., Fig. 4.2a) on the number of familiar conspecifics where relationships are defined as having ≥1 pairwise interaction (Fig. 4.4b). Where relationships are predicated on repeated interactions within dyad, i.e., ≥5 interactions, conspecific density did have a non-linear effect (e.g., Fig. 4.2b) on the number of familiar conspecifics (Fig. 4.4b). This suggests that ephemeral relationships, where degree of familiarity is more important than interaction rate, resulted in a behaviour that was frequency-dependent (i.e., proportional to the number of conspecifics present). On the contrary, re-affirmed pairwise bonds (e.g., 5–200 interactions/year) varied largely non-linearly with subpopulation density, i.e., were density-dependent and a threshold in degree of familiarity likely existed between the low and high density subpopulations.

Network density also varied non-linearly between landscapes (Fig. 4.6). Higher conspecific density resulted in more dense networks. Higher network density, or saturated networks, may represent weaker social structure, more egalitarian groups, or social structure in flux (Drewe, Madden, & Pearce 2009). Higher network density should also result in more redundant routes for pathogen transmission, although this is not reflected in network transitivity (Fig. 4.8). Network density does not scale linearly with subpopulation density which suggests that a threshold in network density likely exists between my low and high density subpopulations. As conspecific density increases so too does the absolute number of individuals with which any given elk interacts. The more relationships an animal has to maintain the higher likelihood for social disorder, or social structure in flux. Additionally, given a finite amount of time to commit to other oriented behaviours which reaffirm social structure, an increasing number of individuals may result in weakened social structure.

If a difference in betweenness had existed between treatments, it would sugget that more focal individuals (i.e., superspreaders [Lloyd-Smith et al. 2005], or individuals that are central to the network and are more likely to contract and transmit diseases) exist at one density (presumably the high density treatment) than at the alternate density.

Specifically, that I detected no difference in betweenness between density treatment suggests that there are not proportionally more individuals in either network that fall on the shortest path between all nodes (Fig. 4.7). This suggests no difference in the role focal animals play in information flow or pathogen transmission can be attributed to subpopulation density, i.e., increased conspecific density does not increase the proportion of focal animals.

The dichotomy between frequency- and density-dependent effects has important implications for pathogen transmission. Successful pathogen transmission (i.e., conversion of susceptible [*S*] individuals to infectious [*I*]), however, is predicated on a number of factors:

$$\frac{dI}{dt} = Scpv \text{ (Begon et al. 2002) [4.5]}$$

where $\frac{dI}{dt}$, is the change in infectious individuals (I) over time (t), which depends on the number of susceptible individuals (S), the contact rate (c), the probability that a contact is with an infectious host (p), and the probability of successful transmission (v) (Begon et al. 2002). I predicted that or probability of successful transmission (v) would increase with interaction duration; however, there appeared to be no difference between interaction duration between subpopulations (Fig. 4.5). Furthermore, I also anticipated increased familiarity, i.e., c, would increase the probability for successful transmission among conspecifics. For easily transmissible pathogens, i.e., pathogens which transmit with few contacts, transmission may be frequency-dependent. Frequency-dependent transmission is typically reserved for chronic-less transmissible pathogens (Lloyd-Smith et al. 2004). However, my results suggest that the behavioural component of transmission may be density-dependent for pathogens where a susceptible host requires repeated exposure before becoming infected.

Furthermore, the dichotomy between frequency and density-dependent degree of familiarity highlights two relationships that likely differ for within-group and between-group transmissions. Cross et al. (2005) emphasized between-group transmissions as more critical than within group. If between-group interactions are less common than within-group interactions, then my results suggest that between-group transmission may be frequency-dependent, whereas within-group transmission may be density-dependent. The debate over density and frequency-dependent transmission is unresolved. Discussions for transmission functions of chronic wasting disease in cervids (Schauber & Woolf 2003), recent cowpox virus models (Smith et al. 2009), and for models for brucellosis transmission on elk (Cross et al. 2010), have suggested that some intermediate function of transmission may exist. Here I have presented some empirical data that suggests an intermediate strategy does exist and is an intrinsic function of animal relationships.

It is increasingly becoming clear that traditional epidemiological approaches to pathogen control—specifically culling—in ecological settings is ineffectual (Blancou, Aubert, & Artois 1991; Donnelly et al. 2006) and that understanding the natural history of hosts and their pathogens (Matthews 2009; Tompkins et al. 2011) and factors that lead to outbreaks (Dobson 2005) will lead to better solutions. This includes understanding how traditional factors known to affect pathogen transmission (like density) influences behavioural mechanisms for transmission (such as contact rate). My results suggest how understanding host behaviour and pathogen transmissibility is likely crucial for managing communicable disease in a population, and traditional epidemiological tools, such as population reduction may not be effective in disease control. If transmission within groups is density-dependent it may appear that thresholds exist, but as the probability of interaction among animals is reduced the likelihood of transmission becoming frequency-dependent without a threshold for disease fade-out increases.

My study, based in social ecology of elk, specifically specifically examined frequencies of behaviours and the nature of relationships. Interaction rate is not contact rate (Whitehead & Dufault 1999), although my measure of an interaction was specifically chosen to best approximate contact. Mine is a general model that can only comment on the rate at which elk interact. Here I have presented some empirical data that suggests an intermediate strategy likely does exist and is an intrinsic function of animal relationships. As the nature of relationships change, e.g., dyads interact more frequently, the number of individuals that a focal animal is familiar with changes from being frequency-dependent to density-dependent. I argue that my sampling design permits us to suggest that interaction rate is density-dependent. My results further suggest the number of individuals a given animal is familiar with is both a function of the proportion of animals in the subpopulation, i.e., frequency-dependent, and density-dependent depending on the strength of the dyadic relationship, i.e., interaction rate. Depending of the probability of transmission, different behaviours may have an impact on whether the pathogen transmission is frequency or density-dependent. Furthermore, within a single population, between-group interactions (i.e., relationships with few interactions) may be frequency-dependent while within-group interactions may be frequency-dependent. My results are among the first to quantify empirically how conspecific density affects social behaviours and to propose behavioural mechanisms for pathogen transmission models which are confounded by ecological realities imposed by animal behaviour and spatial relationships.

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Chapter 5: Habitat-mediated sociality and pathogen transmission in a large herbivore

5.1 Abstract

Ecological processes are oftentimes habitat-dependent, but least studied are effects of habitat on sociality and the transmission of communicable pathogens and parasites. I used a population of elk infected with bovine tuberculosis (TB) as a model system to test the interaction between habitat and local conspecific density on a social behaviour relevant to horizontal pathogen transmission, i.e., close-contact dyadic interactions (when two focal individuals were within 1.4 m). I compared the likelihood of dyadic interactions as it related to a suite of covariates that were *a priori* determined to influence social behaviours against the same covariates and their role in resource selection by elk. Conspecific density was positively related to likelihood of dyadic interaction and was significantly more likely to affect dyadic interactions than selection for conspecifics alone. Local conspecific density positively influenced selection. No difference existed between the equivocally positive effect of open vegetation associations on either likelihood of dyadic interactions or likelihood of selection. Deciduous forest was negatively associated with likelihood of dyadic interactions and selection; however, dyadic interactions were significantly less likely to have occurred than expected from selection alone. The interaction between density and open vegetation associations had a negative effect on likelihood of dyadic interaction and selection creating a negative feedback. This suggests that locally high densities of conspecifics in open vegetation associations may result in an inhibited attraction for conspecifics and open vegetation associations, with a similar effect on likelihood of dyadic interactions. Social behaviours in elk are modified by local resources, including proximity to conspecifics, and in some instances resource use associated with specific social behaviours that differs from

generalised selection patterns. I provide some insight into resource-specific partitioning of behaviours. Furthermore, I present an opportunity to manage disease in wildlife via habitat modification rather than depopulation.

5.2 Introduction

Understanding how relationships between habitat and population density affects ecological interactions is fundamental to our understanding of ecology. Ultimately animals are thought to occupy habitats that maximize individual fitness (Fretwell & Lucas 1969; Rosenzweig 1981) via survival and reproduction, which may be positively related to an animal's use of a particular habitat resource; however, the strength of this relationship should deteriorate with increasing population density (McLoughlin et al. 2006). Resources that comprise habitat are a function of individual behavioural responses to a suite of factors and are selected at a proximal scale and use of specific resources can affect predation and survival (Darimont, Paquet, & Reimchen 2007; Gaillard et al. 2010). Thus, how individual's use available resources can represent a trade-offs between foraging and anti-predator behaviours.

For social species, conspecific behaviours based on social information (e.g., local enhancement or assessment), which result in gregarity or dyadic interactions, are important modifiers of resource use (Beauchamp, Belisle, & Giraldeau 1997; Fletcher 2006). Furthermore, resources that attract higher densities of animals may increase the risk of contracting communicable diseases or parasites (Altizer et al. 2003) despite the benefits to be gained from using preferred resources. This latter problem—what I call habitat-mediated pathogen transmission—is known to exist but has thus far received little attention (see Kjær, Schauber, & Nielsen 2008; Monello & Gompper 2011; Silbernagel et al. 2011), especially in the context of pathogen transmission among a social species where dyadic interactions may underlie contact rates between host individuals.

What makes habitat-mediated pathogen transmission so interesting for social species is the manner in which this might occur, and how it might affect the cost-benefit imbalance that underlies sociality. Social animals that aggregate may assume higher intraspecific competition costs (Skogland 1985; Fortin & Fortin 2009) to offset decreased predation risk (Hamilton 1971; Fortin et al. 2009), but aggregation may also confer other costs due to parasitism or disease (Hochberg 1991; Möller, Dufva, & Allander 1993; but see Wilson et al. [2003]; Elliot & Hart [2010] for benefits due to group immunity). In all cases costs are likely to be modified by habitat-resource distribution. For pathogen transmission (Gompper & Wright 2005; Wright & Gompper 2005; Monello & Gompper 2010), this is likely through increased social interactions and, in some instances, increased environmental contamination by pathogens (i.e., fomites).

Resources can influence prevalence of disease (Farnsworth et al. 2005) and associations among conspecifics (e.g., white-tailed deer, [Kjær et al. 2008]; and mule deer, *Odocoileus hemionus,* [Silbernagel et al. 2011]). However, for gregarious species I also predict that habitat structure will influence degree of sociality. For species that tend to aggregate into groups, individuals require knowledge of the existence of other members of a population to come together, and so I predict that some aspects of habitat will encourage aggregation more than would others, regardless of its value as a resource for other purposes, e.g., food or predator avoidance. For example, use of relatively open vegetation associations may favour aggregation compared to vegetation associations offering greater cover or concealment. This relationship has been observed with several ungulates (e.g., group size, Jarman 1974; Isvaran 2007; Fortin et al. 2009). However, it is critical not to interpret habitat-mediated sociality (i.e., behavioural mechanisms for transmission of communicable diseases) in isolation of density, as density will affect resource selection (McLoughlin et al. 2010) and animal health (Stewart et al. 2005)

I use elk as a model system to test the habitat-mediated pathogen transmission hypothesis. I dissect the interaction between density and habitat (i.e., multi-variable resource selection) on a social behaviour critical for direct transmission of communicable disease (e.g., dyadic interactions). Elk are gregarious cervids which are infected with several diseases of economic concern in North America (e.g., bovine tuberculosis,TB, [Nishi, Shury, & Elkin 2006; Brook & McLachlan 2006], chronic wasting disease, CWD, [Williams & Miller 2002], and brucellosis [Cross et al. 2010]). Often epizootics of such disease are associated with protected areas, such as National Parks (e.g., Riding Mountain National Park, Canada [RMNP] and Yellowstone National Park, USA).

As greater density can increase interaction rate (Chapter 3 and 4, Blanc & Thériez 1998), I predict that where local densities of animals are high, probability of dyadic interactions occurring will increase. Furthermore, as particular vegetation associations may influence the ability of animals to aggregate and gregarity is hypothesized to increase interaction rate, I predict that dyadic interactions are more likely to occur in open vegetation associations, e.g., marshes and grasslands, than in closed vegetation associations, e.g., conifer or mixedwood forests. In addition to explicitly testing for an interactive effect of density and vegetation-openness, I also test intermediate hypotheses looking at habitats that support browse (e.g., deciduous forests), the role of complimentary vegetation associations (e.g., landscape richness), and the affect of anthropogenic trail systems on likelihood of dyadic interaction.

5.3 Methods

5.3.1 Study Site

Riding Mountain National Park (RMNP, Fig. 5.1a) is located in southwestern Manitoba, Canada. RMNP occurs in a transition zone from the Canadian prairies to the northern Boreal Plains ecoregion (Bailey 1968). An elevational gradient exists in RMNP, as eastern portions of the Park rise 475 m from the Manitoba lowlands up the Manitoba escarpment and declines gradually to the western limit of the Park. The change in elevation contributes to vegetative shifts from northern boreal forest with black spruce (*Picea marianna and P. glauca*) and jackpine (*Pinus banksiana*) at higher eastern elevations to a matrix of aspen (*Populus tremuloides*) parkland (Fig. 5.1b) and open vegetation associations (Fig. 5.1c), which are primarily marshes, fens, and fescue (*Festuca* spp.) grasslands (Rowe 1972; Caners & Kenkel 2003). Mixedwood deciduous-coniferous forests occur throughout RMNP (Rowe 1972; Caners & Kenkel 2003), and at low elevations in east RMNP where an east-southeastern aspect occurs, pockets of bur oak (*Quercus macrocarpa*) savannah exist (Rowe 1972; Caners & Kenkel 2003).

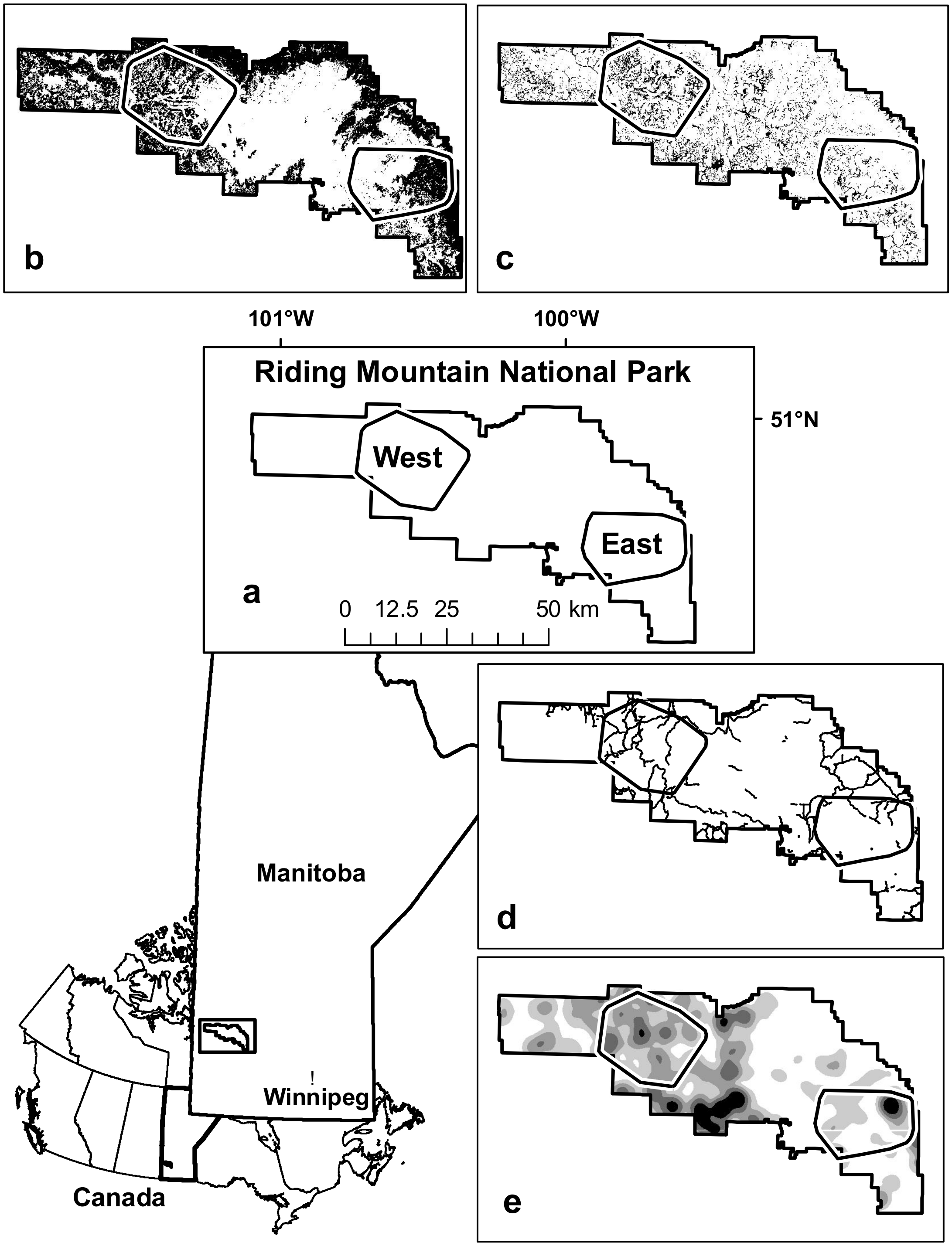

Fig. 5.1. Riding Mountain National Park (3000 km^2; RMNP) is located in southwestern Manitoba, CAN. Elk were sampled in two subpopulations (West and East [a]). RMNP lies in the transition zone of the prairies and northern boreal plain and is dominated by a matrix of predominantly deciduous forest (b, [black]) and open vegetation associations, e.g., marshes, fens, and grasslands (c [black]). RMNP serves the public with trail networks also exist in RMNP (d). Conspecific elk densities also vary between subpopulations (e: 0 [i.e., white]–3 [i.e., black] elk/km^2; 2007 100% census of visible RMNP elk [Parks Canada unpublished data]).

Anthropogenic influences occur within RMNP, e.g., an extensive recreational trail system (Fig. 5.1d), two provincial highways (i.e., 10 and 19), and a townsite (i.e., Wasagaming MB). The majority of human disturbance occurs at the Park boundary. RMNP is surrounded by an agricultural matrix resulting in very low exchange of elk in or out of the region (Brook 2008). Within RMNP there are two subpopulations of elk (Vander Wal unpublished data; Appendix 1) (Fig. 5.1a, East RMNP and West RMNP). Several factors (e.g., habitat, resources) result in each subpopulation having spatially variable conspecific elk densities (Fig. 5.1e). RMNP has a history with TB extending back before the 1950s when cattle grazed within what are now the Park's boundaries (Copeland 2002; Brook 2009). Prior to 1986, when MB was declared TB free, two confirmed cases of TB were detected in RMNP wolves (*Canis lupus*; in 1978). However, from 1991 to 2009 outbreaks involving elk (*n* = 35), white-tailed deer (*n* = 7) and cattle (*Bos taurus*, *n* = 12 herds) occurred (Brook & McLachlan 2009).

5.3.2 Elk Sampling

Between February and March of 2007 and again in 2008 we captured free ranging female elk (*n* = 52) using a net-gun fired from a helicopter (Cattet et al. 2004). Elk were tracked for one year, i.e., in 2008 new individuals were collared and tracked. All elk were equipped with Sirtrack Proximity Logger radio-collars (Sirtrack Ltd., Havelock North, New Zealand), see (Swain & Bishop-Hurley 2007) for an example. Proximity collars have both a traditional VHF (very high frequency) transmitter for relocating animals and an UHF (ultra high frequency) transceiver for logging pairwise interactions (*sensu*

Whitehead & Dufault 1999) among collared elk. See Chapter 2.3.2 for proximity collar programming details and Animal Care Protocol.

I relocated each elk during daylight hours (0800–2100 h) weekly–biweekly by fixed-wing aircraft (Cessna 172) throughout the year. During telemetry flights, I recorded time, date, and position of elk relocations using a Geographic Positioning System (GPS) when animals were either visually observed or when the telemetry receiver operator was confident of being directly overhead based on signal strength using standard methods (White & Garrott 1990). I employed only experienced wildlife telemetry pilots with >10,000 hours of flight time and trained VHF receiver operators. VHF collar relocation error by aerial telemetry was estimated as <250 m (198 m [SE = 17.6, range: 68 m – 381 m], n = 31 known location test collars), which I assessed by locating stationary collars placed on the ground at known points.

5.3.3 Study Design and Global Information Systems

I reconciled spatial relocations of elk with known times of dyadic elk interactions. I assigned UTM coordinates to a dyadic elk interaction if a focal animal interacted with a collared conspecific within ±24 hrs of a telemetry relocation. Of 1954 ($\bar{x}$ = 30 /elk/year; range= 12–39) relocations of elk, 470 ($\bar{x}$ = 9 per elk/year; range = 1–23) were associated with an interaction between collared conspecifics. Using ArcGIS (ESRI, Redlands, California), I created raster layers of average distance to edge, and relative proportion of relevant vegetation derived from the literature (Table 5.1) within a 250 m buffer of each pixel derived from a land cover map with 30 m spatial resolution (LANDSAT–5 satellite imagery collected in 2002 [Manitoba Conservation 2003, unpublished data]). Thus, as the

GIS layers accounted for uncertainty telemetry error, I could assign distance and proportion values directly to relocations.

In addition to physiognomic features, I included a measure of conspecific elk density (Table 5.1). Conspecific elk density was determined from a 100% aerial census of visible elk in RMNP. The census occurred in the winter of 2007 when visibility of elk is greatest (Vander Wal, Brook, & McLoughlin 2011). Linear transects were flown in a fixed wing aircraft (Cessna 172, Wichita, KS) with two trained observers. Each observer was responsible for a 200 m transect directly outside of their window. Transects were flown at an altitude of 120 m and 120 km/hr. Using a GPS, observers recorded the position, as well as number, and age category of all visible elk within the transect. Transects were run to cover 100% of RMNP. Data (Fig 5.1e) are presented as elk density/km^2.

Table 5.1 *A priori* list of limited landscape variables thought to affect annual resource selection and probability of interactions for cervids, particularly female elk in Riding Mountain National Park, Manitoba, Canada, then subsequently derived from a Geographic Information System

Landscape Variable	Description	Rational
Coniferous Forest	Mean distance (m) of all possible relocations from within a 250 m buffer of spatial relocation to nearest predominantly coniferous forest stand	Conifer forest creates thermal cover (Millspaugh et al. 1998; Kunkel & Pletscher 2000; Creel et al. 2005), refuge from predation (Sweeney & Sweeney 1984), or ease of movement (Christianson & Creel 2007). Other oriented behaviours are not conducted simultaneously to vigilance and therefore increase risk of predation. Conversely, dense forests make conspecific detection difficult, therefore resulting in lower probability of dyadic interactions.
Deciduous Forest	Mean distance (m) of all possible relocations from within a 250 m buffer of spatial relocation to nearest predominantly deciduous forest stand	Deciduous forests provide browse for elk (Fortin et al. 2009). However, variable stand density may result in lower detection of conspecifics and thus low probability of dyadic interactions (Cook et al. 1998).
Mixedwood Forest	Mean distance (m) of all possible relocations from within a 250 m buffer of spatial relocation to nearest mixedwood forest stand	Mixedwood forests provide an intermediate strategy to both deciduous and coniferous which may balance forage and cover (Christianson & Creel 2007).
Open Vegetation Associations (e.g., Marsh)	Mean distance (m) of all possible relocations from within a 250 m buffer of spatial relocation to nearest open vegetation association, predominantly marshlands	Open vegetation associations, e.g., grasslands (Boyce et al. 2003; Creel et al. 2005; Hebblewhite, Merrill, & McDonald 2005) and marshlands (Anderson et al. 2005), provide important forage for elk (Hebblewhite et al. 2005; Lung & Childress 2007), however increase risks of predation (Fortin et al. 2009). Moreover, open vegetation associations result in elk group formations as an anti-predator strategy (Hebblewhite et al. 2005; Lung & Childress 2007), therefore an increased probability of dyadic interactions.
Richness	Patch or landscape richness is the total number of different forest patch types (above) that are within a 250 m buffer of spatial relocation	Complex habitats provide complimentary resources for elk to fulfil their life requisites (Fortin & Fortin 2009).
Roads and Trails	Mean distance (m) of all possible relocations from within a 250 m buffer of spatial relocation to nearest road or trail	Wildlife is known to exploit anthropogenic road and trail systems (Kunkel & Pletscher 2000) for their ease of movement (Morris 2003) and reduce predation consequently I predict that such networks will increase the probability of conspecific interactions.
Elk Density	Krigged winter density of visible elk within 250 m from a 100% aerial census conducted in 2008	Density should both affect where animals select to live (Morris 2003) and increased elk density is hypothesized to increase probability of conspecific interactions.

5.3.4 Resource Selection Function (RSF) and Context-Specific RSF Models

All variables, except landscape richness, were standardized to a mean = 1.0. I screened predictor variables for excessive correlations using a Spearman rank correlation matrix for all possible pairs of independent variables (R Development Core Team 2010). If any two variables had an $r_S > 0.7$, I removed the less important variable. I also assessed collinearity using a combination of variance inflation factors (VIF) and variable cluster analysis ([Harrell 2001]; package Design [Harrell 2009]), whereby I eliminated variables with VIF > 10.

I modeled probability of (a) resource use via a resource selection function (RSF [see Manly et al. 2002]) and (b) resources use associated with observed dyadic interactions (i.e., context specific resource selection function [CSRSF]) using binary logistic regression. My dependent variable for the RSF was resource used at point of relocation (i.e., 1) or randomly designated available point at the home-range scale (i.e., 95% minimum convex polygon [MCP]) at a ratio of 10 available locations to every known location. The dependent variable for the CSRSF was resources associated with a dyadic interaction (i.e., 1) or available at the home-range scale (i.e., 0). My independent variables (Table 5.1) include forest types (e.g., coniferous, mixedwood, and deciduous), landscape composition (e.g., local [i.e., 250 m radius] richness of forest types), and conspecific density. Density was predicted to modify behaviours of individuals (e.g., resource selection [Morris 2003; McLoughlin et al. 2010]). Furthermore, for gregarious species, such as elk, conspecifics were themselves viewed as a resource (e.g., predator dilution or detection [Lung & Childress 2007]; information gain from social foraging

[Fortin & Fortin 2009]).

I limited my inference to a minimum number of variables of importance derived from the literature (Table 5.1), given this *a priori* process I felt free to create a set of candidate models with all-possible-combinations of independent variables (Whittingham et al. 2005; Whittingham 2006; Anderson 2008; Vander Wal, Brook, & McLoughlin 2011). Additionally, as one of my objectives was to determine changes in individual variable importance, limiting my candidate models would bias my results (Anderson 2008). I determined my most parsimonious model subset from Akaike's Information Criterion difference adjusted for small sample size (ΔAIC_c). I used Akaike weights (w), which weights provide a normalized comparative score for all models and are interpreted as the probability that each model is the best model of the set of proposed models, for multi-model inference ([Burnham 2002]; performed in the R environment for statistical computing [v.2.11 R Development Core Team 2010] with the Multi-Model Inference package [Barton 2010]). Substantial support for a model occurs when $\Delta\text{AIC}_c < 2.0$, thus candidate models with $\Delta\text{AIC}_c < 2.0$ were averaged using the model averaging technique. Model averaging calculates averaged β coefficients and unconditional standard errors for the subset of indistinguishably parsimonious models (Burnham & Anderson 2002). To highlight differences in variable importance between general and context-specific resources I calculated cumulative AIC_c weights (AIC_w) for each independent variable by summing weights of every model containing that variable (Burnham & Anderson 2002). Variables with the highest AIC_w have the greatest influence on resource use. Furthermore, CSRSF represents a subset of location and behaviours modelled in the RSF, thus in addition to AIC_w I compared averaged β coefficients between models to determine which variables contribute disproportionately to the occurrence of pairwise interactions among conspecifics.

5.4 Results

Proportion of edge and proportion of marshes (i.e., open vegetation association) were correlated ($r > 0.7$) and collinear (VIF > 10), as hard edge is a function of the interface between open vegetation associations and closed habitats. As edge did not contribute different information to my model from marshes and one of my main hypotheses was predicated on the influence of open vegetation associations on sociality I chose to exclude edge from my models.

Resource types and local conspecific density where interactions occurred often mirrored selection patterns by elk; however, were the magnitude differed between the CSRSF and RSF. Of the 256 possible models, three CSRSF and four RSF models had $\Delta AIC_c < 2.0$ (Table 5.2). I was able to include all candidate variables in at least one of the model with $\Delta AIC_c < 2.0$ for both the CSRSF and the RSF. Proportion of conifer, mixedwood, and deciduous forest, landscape richness, and the interaction between density and marsh contributed negatively to both models (Table 5.3). However, proportions of conifer and mixedwood were equivocal (i.e., not significantly different from zero) for both models. Conversely, elk density, proportion of marshes, and trails contributed positively to both models. Proportion of marshes was equivocal for both models, as was elk density and proportion of trails for the RSF (Table 5.3).

Table 5.2 Candidate resource and context specific resource (i.e., dyadic interaction) selection models for female elk in Riding Mountain National, Manitoba, Canada 2007 and 2008.

		Model Description[k]	K	AIC_c	ΔAIC_c	ω_i
Resources Selection at Dyadic Interaction	1	CON + DEC + EDEN + RICH + MAR + TRL + EDEN*MAR	8	4181.68	0.00	0.54
	2	DEC + EDEN + RICH + MAR + MIX + TRL + EDEN*MAR	8	4183.28	1.60	0.24
	3	CON + DEC + EDEN + RICH + MAR + MIX + TRL + EDEN*MAR	9	4183.45	1.78	0.22
General Resource Selection	1	DEC + EDEN + RICH + MAR + EDEN*MAR	6	12538.40	0.00	0.45
	2	DEC + EDEN + RICH + MAR + TRL + EDEN*MAR	7	12540.12	1.73	0.19
	3	CON + DEC + EDEN + RICH + MAR + EDEN*MAR	7	12540.13	1.74	0.19
	4	DEC + EDEN + RICH + MAR + MIX + EDEN*MAR	7	12540.28	1.88	0.17

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[k] Abbreviations: Coniferous forest = CON, Deciduous forest = DEC, Elk Density = EDEN, Landscape Richness = RICH, Open vegetation association = MAR, Mixedwood forest = MIX, Roads and Trails = TRL , Interaction between Elk Density and Open vegetation association = EDEN*MAR

Table 5.3 Parameter estimates from model averaged candidate resource and context specific resource (i.e., dyadic interaction) selection models for female elk in Riding Mountain National, Manitoba, Canada 2007 and 2008.

	Parameter[l]	Coefficient Estimate	SE[m]	95% CI	
				Lower	Upper
Resources Selection at Dyadic Interaction[n]	Intercept	-3.33	0.23	-3.79	-2.87
	CON	-0.09	0.08	-0.24	0.06
	DEC	-0.54	0.08	-0.71	-0.38
	EDEN	0.33	0.10	0.13	0.53
	RICH	-0.13	0.05	-0.22	-0.04
	MAR	0.08	0.09	-0.10	0.25
	MIX	-0.02	0.04	-0.11	0.06
	TRL	0.31	0.10	0.12	0.50
	EDEN*MAR	-0.24	0.08	-0.40	-0.09
General Resource Selection[o]	Intercept	-1.76	0.10	-1.95	-1.57
	CON	0.00	0.01	-0.02	0.01
	DEC	-0.07	0.01	-0.10	-0.04
	EDEN	0.05	0.05	-0.05	0.14
	RICH	-0.11	0.02	-0.15	-0.07
	MAR	0.04	0.03	-0.02	0.10
	MIX	0.00	0.00	-0.01	0.01
	TRL	0.00	0.01	-0.02	0.03
	EDEN*MAR	-0.08	0.02	-0.12	-0.03

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[l] Abbreviations: Coniferous forest = CON, Deciduous forest = DEC, Elk Density = EDEN, Landscape Richness = RICH, Open vegetation association = MAR, Mixedwood forest = MIX, Roads and Trails = TRL , Interaction between Elk Density and Open vegetation association = EDEN*MAR

[m] Unconditional SE from Model Average

[n] Hosmer and Lemeshow Goodness-of-Fit test *P* > 0.05

[o] Hosmer and Lemeshow Goodness-of-Fit test *P* > 0.05

For both models, proportion of deciduous and marshes had AIC_w equal to 1 (i.e., were important variables in the model). However, proportion of mixedwood and conifer contributed less to the model, although their contribution to the CSRSF model was greater than that of the RSF: 0.17 and 0.19, respectively, for the RSF; and 0.46 and 0.76, respectively for the CSRSF (Fig. 5.2). Additionally, proportion of trails contributed little to the RSF ($AIC_w = 0.19$) model; however, it contributed greatly to the CSRSF ($AIC_w = 1$; Fig. 5.2).

Although proportion of deciduous forest unequivocally contributed negatively to the RSF model (odds ratio = 0.93 [95% CI 0.90–0.96]), the likelihood of dyadic interactions by proportion of deciduous forest was 62% lower (odds ratio = 0.58 [95% CI 0.49–0.68]; Fig. 5.2.). The probability of selecting habitat based on proportion of trails as a resource is approximately zero (Fig. 5.2). However, the probability of interactions occurring in habitats with high proportions of trails is high (odds ratio = 1.36 [95% CI 1.12–1.64]; Fig. 5.2). Elk density contributed positively, though equivocally, to RSF by elk (odds ratio = 1.05 [95% CI 0.95 – 1.15]; Fig. 5.2). Elk density contributed significantly more to the probability of a dyadic interact (odds ratio = 1.39 [95% CI 1.13 – 1.70]; Fig. 5.2.).

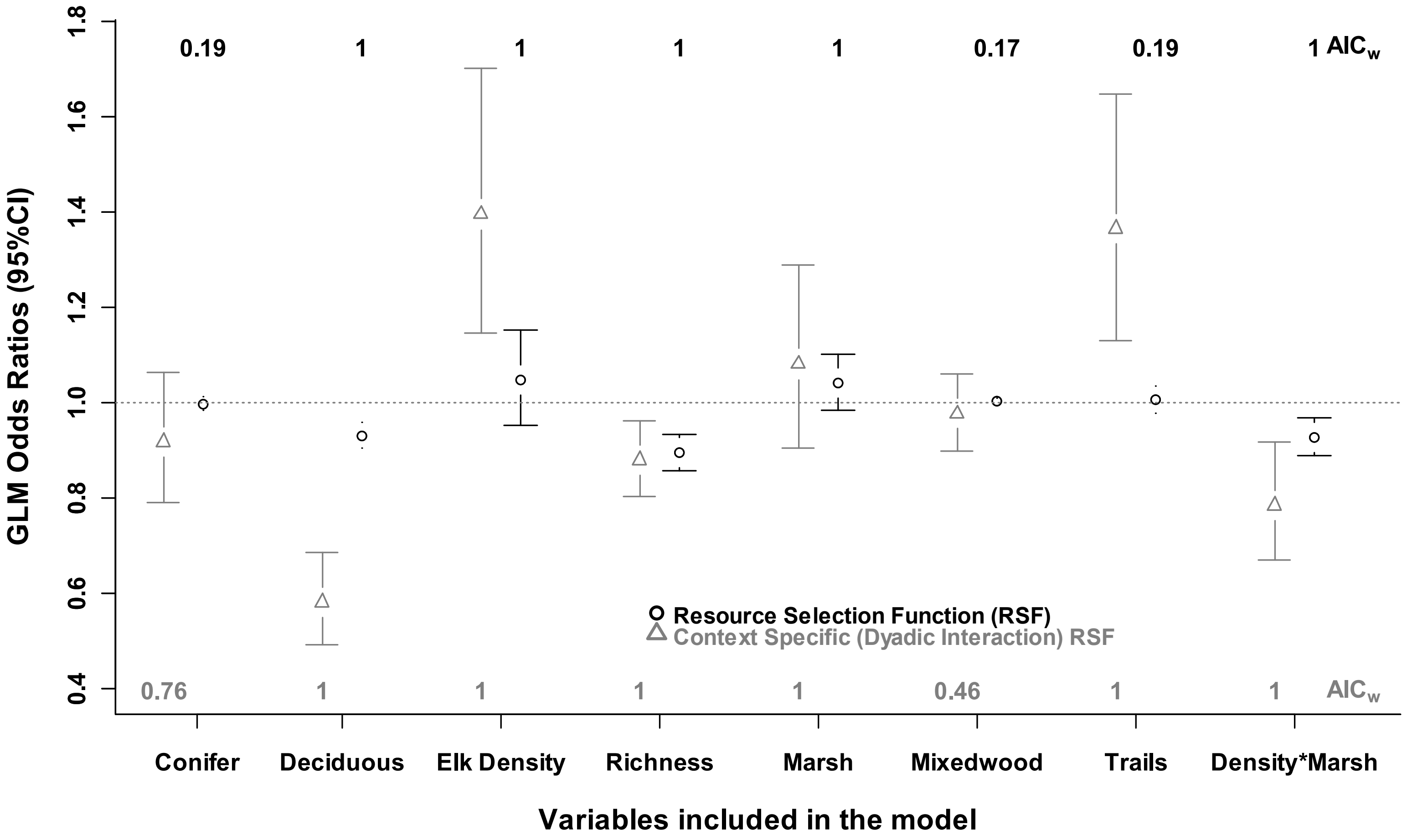

Fig. 5.2. Akaike weights (AIC$_w$), and model averaged odds ratios and 95% CI of the resource selection function (RSF) for elk (in black) and the resources associated with dyadic interaction (i.e., context-specific resource selection function [CSRSF]; in grey). Confidence intervals that do not overlap with 1 contribute either negatively (i.e., < 1) or positively (i.e., > 1) to resource selection or occurrence of dyadic interactions, respectively. Non-overlapping RSF and CSRSF confidence intervals (or marginally overlapping [e.g., elk density], see (Julious 2004) differ significantly between the RSF and CSRSF: deciduous, elk density, and trails.

5.5 Discussion

The interaction between social behaviour and habitat is critical for understanding spatial determinants and the evolution of sociality (Jarman 1974). Further, socially-motivated dyadic interactions are the basic construct for direct horizontal transmission of pathogens (Anderson & May 1979; Begon et al. 2002). Thus, local scale resources are critical to disease transmission (Wright & Gompper 2005; Monello & Gompper 2010). This is evident in my findings, which not only highlight important resources (i.e., components that comprise habitat) for elk, but also identifies which resources affect social behaviours, in particular dyadic interactions. The link between resources and conspecific associations, presuming shared space use correlates with behaviours that may be related to pathogen transmission, has been established (Kjær et al. 2008; Silbernagel et al. 2011). However, records of social interactions occurring in proximity to a given resource are novel.

Open vegetation associations may represent critical resources for elk, which in many circumstances are grazers inasmuch as they are browsers (Banfield 1949; Christianson & Creel 2007). Using open areas to forage results in emergent group properties and encourages fission and fusion events among individuals, groups, and subgroups (Gerard 1995; Fortin et al. 2009). While in open vegetation associations grouping may be response to predation (Hamilton 1971; Hebblewhite et al. 2005). Behaviours such as foraging and vigilance, however, cannot be done simultaneously; hence animals increase group size to decrease individual vigilance and thus increase foraging rates (Jarman 1987; Childress & Lung 2003). Thus in situations with predation pressure, animals may be unlikely to engage in other-oriented behaviours such as close-contact interactions. Similar to me, Weckerly (1999) observed social interactions in open meadows; however, Weckerly's purpose was not to compare their frequency of these interactions to similar behaviours in adjacent forest. In contrast to my results for female elk, Childress & Lung (2003) found that male elk in open vegetation associations were more vigilant toward conspecifics rather than predators, increasing the potential for dyadic interactions. Although my data were insufficient to determine whether this would be the case for male elk in open compared to closed habitats, I did observe interaction rates (i.e., when two focal animals occurred within 1.4 m of each other) that were significantly lower among males compared to females, possibly related to group size (Appendix B) or dominance related visual cues, such as antlers (Chapter 2).

Similarly, local conspecific density (Fig. 5.1e) was important (i.e., $AIC_w = 1.0$) for both resource selection and the likelihood of dyadic interaction. Density increased the likelihood of selection, albeit equivocally. Density unequivocally increased the likelihood of dyadic interactions and did so significantly greater than expected based on selection of conspecifics as a resource. Although, elk may select to be near conspecifics to reduce predation risk (Hebblewhite & Pletcher 2002), exposure to higher conspecific density also increases the likelihood of dyadic interactions, possibly due to an increase in hierarchical behaviours (Weckerly 1999). Increased dyadic interactions may also increase the probability of pathogen transmission (Begon et al. 2002). Furthermore, I predict the distinction between density-dependent selection of resources and density-dependent interactions would become more pronounced as conspecific density increases due to decreased resource selection at high densities (McLoughlin et al. 2006) coupled with increased interaction rates (see Chapters 3 and 4).

I hypothesized that open vegetation association would increase the likelihood of dyadic interactions due to conspecific detection and formation of social groups, which would increase with local conspecific density. However, these two covariates were not correlated in my model. Further, the interaction reduced the likelihood of both resource selection and the occurrence of dyadic interactions (i.e., a negative feedback). Open vegetation associations with increased densities of elk result in avoidance, or decreased probability of selection. Similarly, the interaction between open vegetation association and density decreases the likelihood of dyadic social interaction. Therefore, open vegetation associations with fewer conspecifics were more likely to encourage social interactions among elk. If open vegetation associations have high local conspecific density, I suggest that close-contact dyadic interactions (i.e., within 1.4 m) may be avoided, which suggests that there is a threshold in local density where female elk avoid dyadic interactions. This was shown in Chapter 3 during my density manipulations of captive elk, where moderate local densities (1.05 elk/ha) of elk had higher dyadic interaction rates than high conspecific densities (1.49 elk/ha) where females dyadic interaction rate declined to that similar to low density (0.71 elk/ha).

In addition to natural modifiers of behaviour, such as habitat and density, anthropogenic factors appear to affect likelihood of dyadic interactions (Fig. 5.2). RMNP is a protected area which has maintained trails to facilitate low impact (e.g., foot, bicycle, horse) access to areas within the Park (Fig. 5.1d). At my scale of analysis the existence of recreational trails in RMNP had little effect on resource selection (Fig. 5.2.) and would be considered an unimportant variable (i.e., $AIC_w = 0.19$). However it was important (i.e., $AIC_w = 1.0$) for the social behaviours, increasing the probability of dyadic interaction

(Fig. 5.2). Some ungulates do select roads or trails to ease travel (e.g., bison, *Bison bison* [Fortin & Fortin 2009]), which may occur during winter to reduce bioengergetic costs (e.g., elk and mule deer [Parker, Robbins, & Hanley 1984]; moose, *Alces alces* [Leblond, Dussault, & Ouellet 2010]). Had this occurred with RMNP elk I would have expected to see the use of roads and trails to differ from what is available on the landscape. Clearly, elk do use the trail systems, otherwise dyadic interaction would not occur on them. Animals using established trails will result in close-contact interactions.

The RMNP elk population is an ideal system for understanding the impact of social behaviours on disease, as they are infected with TB, which is a pathogen of human-social and economic concern (Nishi et al. 2006; Brook & McLachlan 2006). Options for managing disease in protected areas are limited, as typically eradicating a species which itself is showing no population-level effects from the disease, such as elk in RMNP (Parks Canada unpublished data), would be anathema and run counter to organizational mandates, which include “protecting wildlife” and “ensuring ecological integrity”. However, the extreme level of concern from farmers around RMNP about risks to their cattle herds can create political pressure which requires that ‘no action’ is not an acceptable response. Part of a best practices approach to controlling pathogens in wildlife populations is to understand first the mechanisms which permit transmission (Tompkins et al. 2011). This includes understanding how habitats which constitute locations for environmental contamination of transmission (Duffield & Young 1985; Williams et al. 2002) affect social interactions among a suspected reservoir host, i.e., opportunities for direct horizontal transmission (Menzies & Neill 2000; Williams 2005). With empirical data, agencies responsible for managing wildlife populations can proceed to change environmental conditions that will alter the behaviours of elk, i.e., a “bottom-up” approach, rather than “top-down” or cull-based approach. For example, agencies can manage for habitats that discourage large groupings of animals (i.e., decreased local densities) such as dense forests. My results suggest that the interaction between density and open vegetation association is not intuitive; hence managing for less open vegetation association may be more sustainable than population reductions. At the very least habitat manipulation needs to be done in conjunction with population reductions to observe lasting effects. An additional option may be decreasing the dyadic interaction rates and possible opportunities for pathogen transmission via limiting the number of trails which animals may exploit.

I highlight that social behaviours are affected by habitat. I focus on two categories of results. One that identifies resources that positively affect social behaviours and one that identifies where resources associated with behaviours differ from those generally selected. In some instances, the relationship between the behaviours and resources did not differ from what I would expect based on resource selection (RSF), e.g., use of open vegetation association and occurrence of dyadic interactions in open vegetation association. However, contrary examples existed where resources, such as proportion of deciduous forests, proportion of trails, or conspecific density, were more likely to affect the odds of an interaction occurring than would be expected based on the RSF alone. Although there are clear implications and options for managing social behaviours that relate to pathogen transmission, I also illustrate that trade-offs among complex habitat types have likely influenced other-oriented behaviours in social cervids.

5.6 Literature Cited

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Chapter 6: General Discussion

Review

My objectives were (1) to explore factors that affect sociality in gregarious cervids and (2) to do so in a manner meaningful to understanding pathogen transmission in elk, especially in RMNP. My thesis had three major themes, sociality, conspecific density, and information transfer—which is analogous to pathogen transmission. Specifically, I explored the effects that season (Chapter 2), sex (Chapter 2 and 3, Appendix A and B), conspecific density (Chapter 3–5, Appendix B), habitat (Chapter 5 and Appendix B), relatedness (Appendix A), and group size (Appendix B) had dyadic interaction rates and durations (Fig. 1.1).

6.1 Theory

Understanding the ecology and evolution of social behaviour may be among the great pursuits in biology (May 2006; Sherratt & Wilkinson 2009). Research in this arena has predominantly focused on benefits to social behaviour rather than costs (Krause & Ruxton 2002). Although there must be a net benefit outweighing costs for sociality to accord a fitness advantage (Silk 2007), appreciating these costs, and the dynamics of the cost-benefit balance, is critical for understanding relationships among social animals. Here I have explored intrinsic (e.g., sex and relatedness) and extrinsic (seasonality, conspecific density, and habitat) factors which may affect the costs of being social (e.g., contracting transmissible disease). I have shown that seasonality (Chapter 2), sex (Chapter 2 and 3), density (Chapters 3, 4, and 5), and habitat (Chapter 5) do affect social behaviour.

I found that interaction rates and durations (i.e., when two focal elk were within 1.4 m of one another) varied between sexes and among seasons (Chapter 2). Seasonal interaction rates ebb in summer, when elk also have low exposure to group size (Appendix B [Fig. B.4]). My results indicate that two seasons exist for social interactions. Summer, when feeding for females is constrained by caring for calves and males employ a forage maximizing strategy. The second season is autumn-winter, which includes mating behaviours for both sexes and when females are gestating and predation risk on males is highest due to post-rut recovery. An extension of the habitat-dependent sociality hypothesis (Chapter 5) would suggest that foliage in summer may also reduce the ability for conspecifics to detect one another and consequently interact.

Inter-sex interactions were infrequent, and in a polygamous mating system those that do occur result in few males mating with many females (Vos, Brokx, & Geist 1967). Additionally, female-female dyads interacted more frequently than male-male dyads—a trend I also observed during my experimental manipulations of conspecific density (Chapter 3). Inter-sex differences in interaction rate may be due to female elk forming groups of mixing matrilineal subgroups (Geist 1982); however, my pairwise relatedness data did not corroborate this idea (Appendix A). In addition to interacting more frequently, female groups were larger than those of males, though this too exhibited phenology (Appendix B [Fig. B.4]). Further exposure to group size was modified by habitat and conspecific density (Appendix B [Figs. B.1 and B.3]).

Season and sex-specific interaction rates and durations, however, revealed to me more than the existence of inter-treatment differences (see Chapter 2). Rather, sex-specific routes of information transfer (or pathogen transmission) seem to result from sexual and spatial segregation. If routes of transmission (Fellous & Koella 2009) and susceptibility to disease (Lindsey & Altizer 2009) can be sex-specific then a pathogen that affects reproduction or survival (i.e., individual fitness) will have sex-specific consequences on behaviour. Ultimately, host behaviours that minimize transmission should be selected for. Sexual segregation may evolve to maintain specific strategies of pathogen transmission if the mechanics of transmission differ between the sexes (i.e., transmission in females is based on repeated exposure, whereas in males transmission relies on prolonged exposure). Conversely, sexual segregation may be the prerequisite for different strategies that minimize pathogen transmission.

Sex-specific interaction rate and duration were also modified by conspecific density (Chapter 3; also see group size Appendix B). In a review, Bowyer (2004) highlights the necessity of evaluating effects of sex in segregated cervids, which may result in sex-specific ecological niches (Mysterud 2000). In addition to differences in resource selection (Weckerly 1993; Bleich, Bowyer, & Wehausen 1997), segregation has resulted in sociality having a sex-specific response to changing conspecific density (Chapter 3). Whereas male-male interactions increased predictably with increased conspecific density, female-female interactions increased from low to medium density and then decreased at high density.

My field design was dichotomous; I was therefore unable to replicate completely the results from the experiment in RMNP. Interaction rates at conspecific densities in the field were significantly different: animals in western RMNP had higher interaction rates than the lower-density eastern subpopulation (Chapter 4). These results provide further evidence that sociality is density-dependent. However, the relationships that animals form are predicated on repeated encounters. I found that interaction heterogeneity (i.e., the number of individuals with whom a given focal individual interacts) was density-dependent among socially familiar individuals (i.e., elk that interacted ≥ 3 times); however, for unfamiliar individuals social familiarity did not vary with conspecific density (i.e., frequency-dependent). Social familiarity is not predicated on genetic relatedness as interaction rates did not covary with genetic relatedness (Appendix A).

The influence of density may affect dominance hierarchies. Females existing in dominance hierarchies are less likely to be aggressive to each other when individuals are known or related to each other (e.g., primates [Perry et al. 2008], red deer [Thouless and Guinness 1986], sheep [Guilhem et al. 2000]); however, my field data suggest that social interactions did not reflect pairwise relatedness (Appendix A). Wild female elk are also thought to form philopatric groupings. However, philopatry may result in increased intraspecific competition, which confounds kin-based fitness benefits that sociality may confer (West, Pen, & Griffin 2002). Some costs of competition include decreased access to resources, and increased levels of stress and competition because of this lack of resources (Lung & Childress 2007). Competition typically leads to lower body weight and reduced performance (e.g., Mysterud et al. 2001, Stewart et al. 2005); however, females likely place less a cost on high group size than males (Appendix B). Changing density may also affect sexual selection. Average male mating success is expected to decrease as density increases (Gaskin, Futerman, & Chapman 2002; Zhang & Zhang 2003; Härdling & Kaitala 2005; Kokko & Rankin 2006). One possible mechanism may be when male–male interference and competition increase (Zhang & Zhang 2003; Kokko & Rankin 2006; Wang et al. 2009) females become choosier (Shelly & Bailey 1992; Kokko & Rankin 2006; Wang et al. 2009), or some males become more likely to be engaged in courtships to other males (Gaskin et al. 2002).

Conspecific density, however, is also related to habitat (Morris 2003) and the resources which comprise habitat (McLoughlin et al. 2006; McLoughlin et al. 2010). The interaction between social behaviours and habitat is critical for understanding spatial determinants and the evolution of sociality (Jarman 1974). Open vegetation associations may represent critical resources for elk, which in many circumstances are grazers inasmuch as they are browsers (Banfield 1949; Christianson & Creel 2007). While in open vegetation associations grouping may be response to predation (Hamilton 1971; Hebblewhite, Merrill, & McDonald 2005). Using open areas to forage influences an individual's ability to detect conspecifics and results in emergent group properties which encourage fission and fusion events among individuals, groups, and subgroups, (Gerard & Loisel 1995; Fortin et al. 2009), and increase the likelihood of interacting (Chapter 5). Although I found that open vegetation associations did have a positive effect on the likelihood of dyadic interactions, counter-intuitively the interaction between open vegetation associations and conspecific density decreased the likelihood of close-contact interactions (Chapter 5).

The final theme of my thesis was information transfer, which is analogous to direct horizontal pathogen transmission (Wilson 1975). Pathogen transmission is predicated on contacts among individuals (Anderson & May 1979; May & Anderson 1979), which is further decomposed into probability that contacts are between infectious and susceptible individuals and whether the contact successfully transmits the infectious agent between hosts (Begon et al. 2002). Traditionally transmission is assumed to be frequency- or density-dependent (Lloyd-Smith et al. 2005). One critical difference between the two models is that thresholds for pathogen establishment or fade-out (i.e., critical community size [Bartlett 1957]) exist for density-dependent models, however are absent in frequency-dependent systems. Some models have suggested an intermediate strategy may exist (Schauber & Woolf 2003; Smith et al. 2009; Cross et al. 2010). The mechanisms of frequency- or density- dependent transmission are predicated on social behaviour upon which pathogens capitalize on to infect new hosts. Mechanisms of transmission are not typically studied for logistical reasons (see Tompkins et al. 2011).

I have studied the mechanisms of transmission in different conspecific density treatments. Experimental (Chapter 3) and field (Chapters 4) results clearly show that interaction rate is density-dependent. However, pathogen transmission is also contingent on interaction quality (i.e., duration, Chapter 2, 3, 4, and Appendix A) and the number of socially familiar individuals with whom a focal animal interacts (i.e., heterogeneity of interactions) (Chapter 4, Appendix B). Interaction quality did not vary between the two field conspecific density treatments (Chapter 4); however, within-herd interaction durations did vary with the conspecific densities used in the experimental manipulation (Chapter 3). Moreover, heterogeneity of interactions varies between frequency and density dependence contingent on the level of familiarity between individuals (e.g., withn vs. between group transmission). This suggests that some relationships, i.e., potential transmission events, may be density-dependent, whereas others may be frequency-dependent, revealing mechanisms for an intermediate strategy of pathogen transmission.

6.2 Application

In this thesis, I address a management issue where a paucity of local ecological information has resulted in a void within which some management decisions have been based on expert-opinion rather than evidence from within the elk-TB system in RMNP. Due in part to previous research (see Brook [2008]), I was able to approach the host-pathogen relationship between elk and TB in RMNP from a sociobiological perspective. Thus, I have focused on how evolved social behaviours upon which pathogen transmission is predicated are affected by intrinsic and extrinsic factors. This work contributes to a growing body of scientific results unravelling the complexities or of TB in RMNP.

Three thesis chapters (3, 4, and 5) and two appendices (A and B) present some evidence that the social behaviours upon which pathogen transmission is predicated may exhibit some form of density dependence. Chapter 3 demonstrates clear within-herd density effects on social behaviours. Chapter 4 illustrates that interaction rates differ between subpopulations, and—among more familiar individuals—heterogeneity of interactions also differed between west and east RMNP. Local conspecific density had an effect on occurrence of interactions (Chapter 5). That interaction rate and duration did not covary with relatedness was also evidence for density-dependent pathogen transmission (Appendix A). Further, there was evidence that density and habitat are affecting group size between subpopulations (Appendix B). Ecological complexity, however, exists in most instances. For example, where male interaction rates clearly increased with density, female rates peaked at an intermediate density and then declined at high density during our experiment (Chapter 3). Similarly, though interaction rates were clearly density-dependent in the field, heterogeneity of interactions were frequency-dependent for weak relationships (i.e., few interactions), which may highlight difference in within vs. between group transmission of pathogens (Chapter 4). Though local conspecific density increased the likelihood of interaction, so too did a suite of resource covariates, and the statistical interaction between open-habitat and conspecific density was further confounding (Chapter 5).

Communicating uncertainty in science is a formidable task. Yet, it is imperative to consider such uncertainty in future management decisions regarding TB and ungulates in RMNP. There exists a great deal of evidence to suggest that pathogen transmission within elk in RMNP is density-dependent. Therefore one may assume that maintaining an elk population in west RMNP at a similar conspecific density to the eastern subpopulation may, over a given time scale, result in disease fade-out.

A top-down approach to reducing the subpopulation is to cull elk. Culling social animals, however, may change interaction rates, durations, or heterogeneity, risking increased incidence of disease (see Woodroffe et al. 2009). Further, the logistics of maintaining smaller population size needs to be considered. Conversely, a bottom-up approach may achieve a similar end. It is also clear that habitat modifies behaviours of elk within RMNP, thus relief from population suppression will result in elk population numbers increasing and again becoming a viable environment for TB host-pathogen coexistence. Conversely, modifying habitats such that they are less suitable to elk and discourage dyadic interactions may sustainably reduce conspecific interactions. This may be as simple as limiting current habitat modifications (e.g., prescribed burns) or minimizing trail systems which are not frequented by Park visitors.

Two pertinent caveats to these conclusions exist. Here I focus exclusively on social behaviours and cannot comment on what role environmental contamination (i.e., fomites) may have on transmission of TB. A common criticism of an autecological approach is that though this thesis spans the scale of DNA to population, it does not comment on community interactions. Thus, little is known about the role of inter-specific transmission of TB from white-tailed deer to elk.

6.3 Concluding Remarks

Here I present a sociobiological approach to understanding the mechanisms of pathogen transmission. I submit that within this document there is much that has been learned about important social behaviours and much knowledge that can and is transferred into evidence-based management. Many questions, however, remain unanswered, both locally for host-pathogen interaction in RMNP and more generally about the eco-evolutionary dynamics of social behaviours.

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Appendix A: Social interactions, relatedness, and population structure in a gregarious cervid: implications for pathogen transmission

Author contributions: EVW, José Andrés, and Paul C. Paquet designed research; EVW and JA performed research; EVW and JA analyzed data; and EVW, JA, and PCP wrote the manuscript.

A.1 Abstract

Pathogen transmission is an inherently multi-spatial process. At the local scale, social behaviors, such as close-contact interactions, are a critical mechanism for direct transmission of pathogens among hosts. Host populations, however, exist in patchy often isolated environments, which may create a continuum of genetic and social familiarity. Such variability can have an important effect on pathogen spread locally and at the landscape-scale. Elk dispersal was assessed through spatially explicit genetic analyses. At a regional scale, the elk population is composed of at least three distinct clusters associated with two protected areas: Duck Mountain Provincial Park and Forest, east, and west Riding Mountain National Park. These genetic data are consistent with apparent prevalence of tuberculosis. To understand better the dynamics and distribution of the disease we used a combination of close-contact logging biotelemetry and genetic data to identify the mechanisms of pathogen transmission. Our results indicate that elk have complex social structures and that contact within family groups was not a significant mechanism of disease transmission. Here we show that the combination of landscape-scale genetics, relatedness, and local-scale social behaviors is a promising approach, to not only understand and predict landscape-level pathogen transmission within our system, but within all social ungulate systems affected by transmissible diseases.

A.2 Introduction

Social behaviors of individual hosts are critical in disease ecology (Altizer et al. 2003; Tompkins et al. 2011); particularly pair-wise interactions, which influence the horizontal transmission of infectious pathogens (Joly et al. 2006; Blanchong et al. 2007, 2008). Behaviors that influence close-contact interaction rates within social groups are known to be important factors explaining the local spread of a wide range of infectious diseases in natural populations (e.g. Ramsey 2007; Woodroffe et al. 2009; Wendland et al. 2010). However, the process of transmission occurs over multiple spatial scales (Cross et al. 2005) and social interactions are not the only factor explaining the transmission of pathogens. In many wildlife species different social groups exist as assemblages of spatially delimited populations inhabiting a landscape of patchily distributed habitats (e.g., red deer, *Cervus elaphus* [Coulson et al. 1997], wild boar, *Sus scrofa* [Gabor et al. 1999], blackbuck antelope, *Antilope cervicapra* [Isvaran 2007]), and the spread of infectious diseases also depends on host dispersal and movements between demes (e.g. Blanchong et al. 2007; Pope et al. 2007; Blanchong et al. 2008; Cullingham et al. 2009; Grear et al. 2010).

Different population scale approaches, including landscape genetics, have been applied to understand disease transmission in natural populations (see Archie, Luikart, & Ezenwa 2009; Beik & Real 2010 for reveiws). In the cases where the parasite is closely associated with a particular species, population genetic analyses of the host are a valid tactic to study infectious dynamics (Beik & Real 2010). One major advantage of this method is that it can reveal and predict disease transmission pathways by assessing the landscape permeability from the host point of view (e.g. chronic wasting disease [Blanchong et al. 2008; Cullingham et al. 2009], and racoon rabies [Cullingham et al. 2009]). However, this type of approach overlooks crucial mechanistic factors (e.g. probability that individuals make potentially transmissible contacts) known to affect infection dynamics (see Matthews 2009; Tompkins et al. 2011).

Despite the crucial importance that integrating social interactions with population substructure has in the study and management of infectious diseases, so far, very few studies have simultaneously considered at these two factors. Here I integrate individual (i.e. mechanistic) and population-level approaches (see Fenton et al. 2002) to better understand the spread potential of bovine tuberculosis (TB) among ungulates in a fragmented prairie-parkland ecosystem.

Bovine tuberculosis exists within a host–parasite continuum affecting a wide range of species worldwide (Daszak, Cunningham, & Hyatt 2000). However, in North America (north of 32° latitude) tuberculosis is primarily associated with three geographically separated populations of wild, social ungulates. In the northern boreal plains (Alberta-Northwest Territory, CAN) bison (*Bison bison*) is the only confirmed reservoir for tuberculosis in the wild (Wobeser 2009). Conversely, elk is suspected to be the primary wild reservoir in the prairie-parkland of Manitoba, CAN. (Lees 2004; Nishi, Shury, & Elkin 2006), whereas in the temperate forest biome of Michigan, USA, tuberculosis is mostly found in white-tailed deer (Schmitt et al. 1997). Of the wild cervids with tuberculosis, elk has the most complex social structure (Vos, Brokx, & Geist 1967; Geist 1974).

The elk population of The Riding Mountain Region (RMR, Manitoba), therefore represents a unique opportunity for studying pathogen transmission from local social scales of behavior to large-scale landscape phenomena. After the elk demographic collapse associated with post-European colonization (O'Gara & Dundas 2002), the RMR population has remain relatively isolated. Currently inhabits a fragmented landscape of protected areas (Riding Mountain National

Park [RMNP], and Duck Mountains Provincial Park and Forest [DMPP&F]) surrounded by agricultural land. From 1991 to 2009, clusters of tuberculosis have been detected in the population (Nishi et al. 2006; Brook & McLachlan 2009), The observed variance in apparent prevalence across the region (most of the infected individuals are found in western RMNP [Parks Canada unpublished data]) implies the existence of biotic and/or abiotic factors affecting disease spread. Here I hypothesized that dispersal dynamics and social interactions are the two main factors explaining the observed pattern of tuberculosis apparent prevalence. I use 30 microsatellite loci to examine elk dispersal dynamics using spatial Bayesian clustering and spatial principal component analyses. My *a priori* prediction is that limited dispersal would result in discrete clusters that reflect the spatial distribution of tuberculosis in the region. Moreover, I used a combination of close-contact logging biotelemetry and genetic data to test whether the frequency and duration of social interactions that could potentially result in the transmission of tuberculosis is affected by the degree of genetic relatedness. Specifically, I tested if interactions have a sociobiological basis (i.e., animals who interact are more closely related) or are they a function of population structure (i.e., animals interactions are a function of their spatial distribution, not their genetic relatedness).

A.3 Methods

A.3.1 Study area

The Riding Mountain Region includes Riding Mountain National Park (RMNP; 3000 km^2) and the Duck Mountain Provincial Park and Forest (DMPP&F; 3,800 km^2) are in southwestern Manitoba, Canada (Fig. A.1). The region lies in the transition from the prairies and the more northern Boreal Plains ecoregion (Bailey 1968). An elevation gradient exists in RMNP: the eastern portions of the Park rise 475 m from the Manitoba lowlands up the Manitoba escarpment and decline gradually to the western limit of the Park, resulting in variation in vegetation (Caners & Kenkel 2003) and in local climate. Both reserves are surrounded by agricultural matrix resulting in little known exchange of individuals in and out of the region. Riding Mountain National Park and DMPP&F are connected by the remnants of a once extensive corridor, fragmented over the last five decades by agricultural expansion (Walker 2001). Riding Mountain National Park is also bisected by a provincial highway and electrical transmission lines across the top of the escarpment.

A.3.2 Elk sampling

We captured free ranging elk (*n* = 312) from 2005–2008 using a net-gun fired from a helicopter (Cattet et al. 2004). Location of capture was recorded and available for most individuals (*n* = 172). Tissue and hair samples were obtained from the ear and frozen until processed for genotype analysis. In 2007 and 2008 I captured and fit 49 (23 females and 26 males) and 55 (35 females and 20 males) elk, respectively, with Sirtrack Proximity Logger radio-collars (Sirtrack Ltd., Havelock North, New Zealand). See Chapter 2.3.2 for proximity collar programming details and Animal Care Protocol.

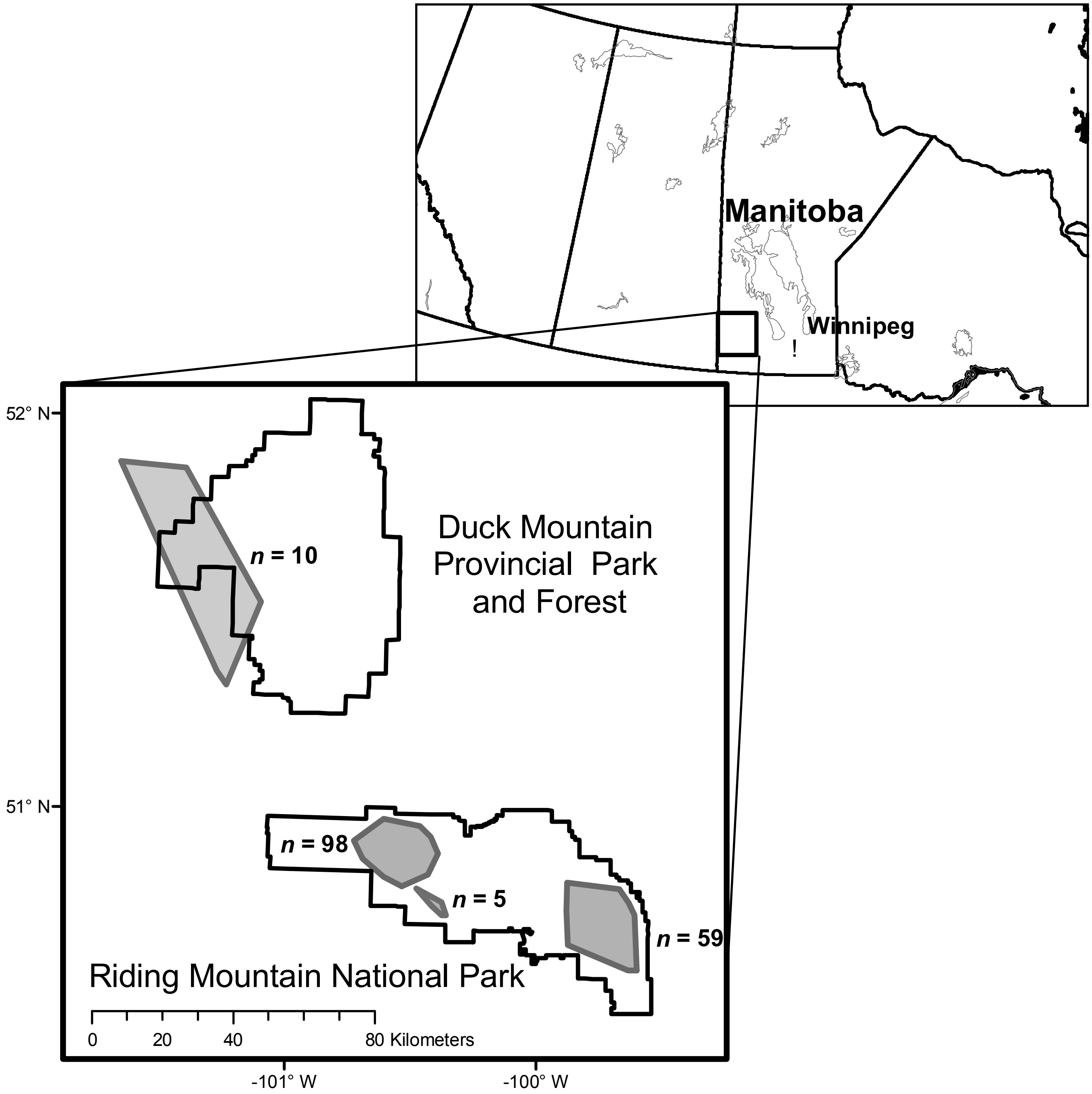

Fig. A.1 Riding Mountain National Park and Duck Mountain Provincial Park and Forest, Manitoba, CAN. Areas in gray are minimum convex polygons delineating the outer boundaries of samples from unique population clusters designated by GENELAND analysis.

A.3.3 Genotyping, population structure, and landscape analyses

Genomic DNA was isolated from 315 ear plug samples using DNAdvance^{TM} (Agencourt ®) following the manufacturer's instructions. I checked for genotyping errors using MICROSATELLITE TOOLKIT version 3.1 (Park 2001), and estimated null alleles and large allele dropout in MICRO-CHECKER version 2.2.3 (Van Oosterhout et al. 2004).

The population genetic structure was examined using the Bayesian clustering method implemented in GENELAND version 3.2.1 (Guillot, Mortimer, & Estoup 2005). This method uses geo-referenced individual multilocus genotypes for the inference of the number (K) and spatial distribution of clusters (subpopulations) in Hardy-Weinberg and Linkage Equilibrium. Given the recent history of the sampled population(s) I expected low genetic differentiation, if any, among clusters. Therefore, it was assumed that a Dirichlet (*i.e.* correlated frequency) model and proceeded as follows to determine the number and composition of genetically differentiated subpopulations. A potential problem with this approach is that the sampling schemes and deviations from random mating not related to barriers to gene flow can have a strong influence on the detection and interpretation of genetic structure. More specifically, spatial Bayesian clustering can result in the overestimation of genetic structure for data sets characterized by continuously distributed individuals and spatially autocorrelated allele frequencies (Schwartz & McKelvey 2009; Frantz et al. 2010). To avoid these potential problems and to corroborate the results of the Bayesian approach a multivariate analysis was also used. Spatial Principal Component Analysis (sPCA, Jombart 2008) makes no assumptions regarding Hardy–Weinberg equilibrium or linkage equilibrium and incorporates Moran's I (Moran 1948, 1950) to detect spatial structure in the data. I performed all calculations in R 2.11.1 (R Development Core Team 2010) using the

ADEGENET (Jombart 2008) and ADE4 (Dray & Dufour 2007) packages. Finally, I carried out conventional FST and AMOVA analyses in the inferred clusters using ARLEQUIN 3.11 (Excoffier, Laval, & Schneider 2005) and GENEPOP 4.0 (Rousset 2008).

A.3.4 Social interactions and relatedness

Here I was interested in social behaviors of epidemiological relevance. The change in infectious individuals over time can be modeled as:

$$\frac{dI}{dt} = Scpv \text{ (Begon et al. 2002)}$$

where, S, is the number of susceptible individuals, c is the contact rate, p is the probability that a contact is with an infectious host, and v is the probability of successful transmission, a parameter that it is likely to be related with contact duration. Therefore, I focused on the quantity (i.e., rate) and quality (i.e., duration) of contacts between individuals. As a proxy measure for p I estimated the conspecific interaction rate (*sensu* Whitehead & Dufault 1999). Similarly, as a proxy for v I measured interaction duration. That is, I assumed that longer interactions increase the likelihood of successful pathogen transmission. I did not, however, know incidence of pathogen transmission in RMR.

Interactions are predicated on social behaviors among individuals. Thus I aimed to quantify the rate of these dyadic interactions. Interaction frequency was partitioned into four categories: 0; ≥ 1; ≥ 10; and ≥ 100 dyadic interactions. I categorized interactions to represent differing degrees of social familiarity. Animals that did not interact within 1.4 m of one another were not considered socially familiar. As the threshold of interactions increased from 1– 100 I assumed that animals were a) increasingly socially familiar, and b) more closely associated. Similar to many social cervids, elk segregate sexually outside of the breeding season (see Main & Coblentz 1990; Ruckstuhl & Neuhaus 2002; Bowyer 2004 for reviews). Thus, I divided dyadic interaction rates and duration by sex-specific dyad: female-female, male-male, and female-male.

I estimated pedigree relationships between male-male, male-female and female-female dyads using Lynch and Ritland (R_{LR}) (Lynch & Ritland 1999) as implemented in IDENTIX (Belkhir, Castric, & Bonhomme 2002). I chose this index because it shows the best performance in natural populations of outbred vertebrates (Csillery et al. 2006), and because it performs well in substructured populations (Casteele, Galbusera, & Matthysen 2001; Oliehoek et al. 2006; Csillery et al. 2006). The distribution of R_{LR} values among all individuals for which I had genetic data (n = 312) was evaluated, without respect to interaction rates to determine the overall degree of pair-wise relatedness of elk in the studied area as well as within the distinct genetic clusters for which I had interaction data (n = 104). I bootstrapped (n = 1000 iterations) relatedness of a) the population, b) animals that did not interact within a cluster, c) animals that interacted $\geq$ 1, $\geq$ 10, $\geq$ 100 times, samples permitting. Furthermore, randomized general linear models (Manly 1998) were used to test the relationship between pair-wise relatedness and median duration of dyadic interactions. Median interaction duration per dyad was transformed ($\log_{10}$) to improve normality. All analyses were implemented in R 2.11.1 (R Development Core Team 2010).

A.4 Results

A.4.1 Population Structure

The full dataset consisted of 30 microsatellite loci scored for 312 individuals drawn from Riding Mountain National Park and the Duck Mountain Provincial Park and Forest. No significant pairwise linkage disequilibrium was detected. Potential null alleles were detected in only 1 locus due to homozygote excess for most of the allele size. Over the entire dataset the number of alleles per locus ranged from only two (Locus C127) to 14 (Locus T156), with a mode of 5. Observed heterozygosity averaged over all loci was 0.620, ranging from 0.844 (locus T193) to 0.210 (Locus BL25). Overall, loci conformed to HW proportions for each locus and only four loci (T26, T126, RBP3 and BM848) show significant deviations. GENELAND analyses consistently identified 4 population clusters (K; Fig. A.1). Individual animals had a probability of 0.8–0.9 of belonging to the assigned cluster (Fig. A.2), providing strong support for the clustering result. The clusters defined by the posterior probabilities were named as follows: (a) the DMPP&F individuals; (b) west RMNP individuals; (c) east RMNP individuals, and (d) small group of individuals south-central RMNP. Mean F_{ST} calculated by GENELAND range between 0.0845–0.0423. Similarly, the mean θ_{ST} (GENEPOP) between the inferred clusters range from 0.116 to 0.0074. R_{ST} analyses yield very similar genetic differentiation values. AMOVA analysis revealed that almost all genetic variation resides within clusters, and that only a small (3%) but significant (P <0.0001) of the genetic variation is related to differences among the inferred clusters.

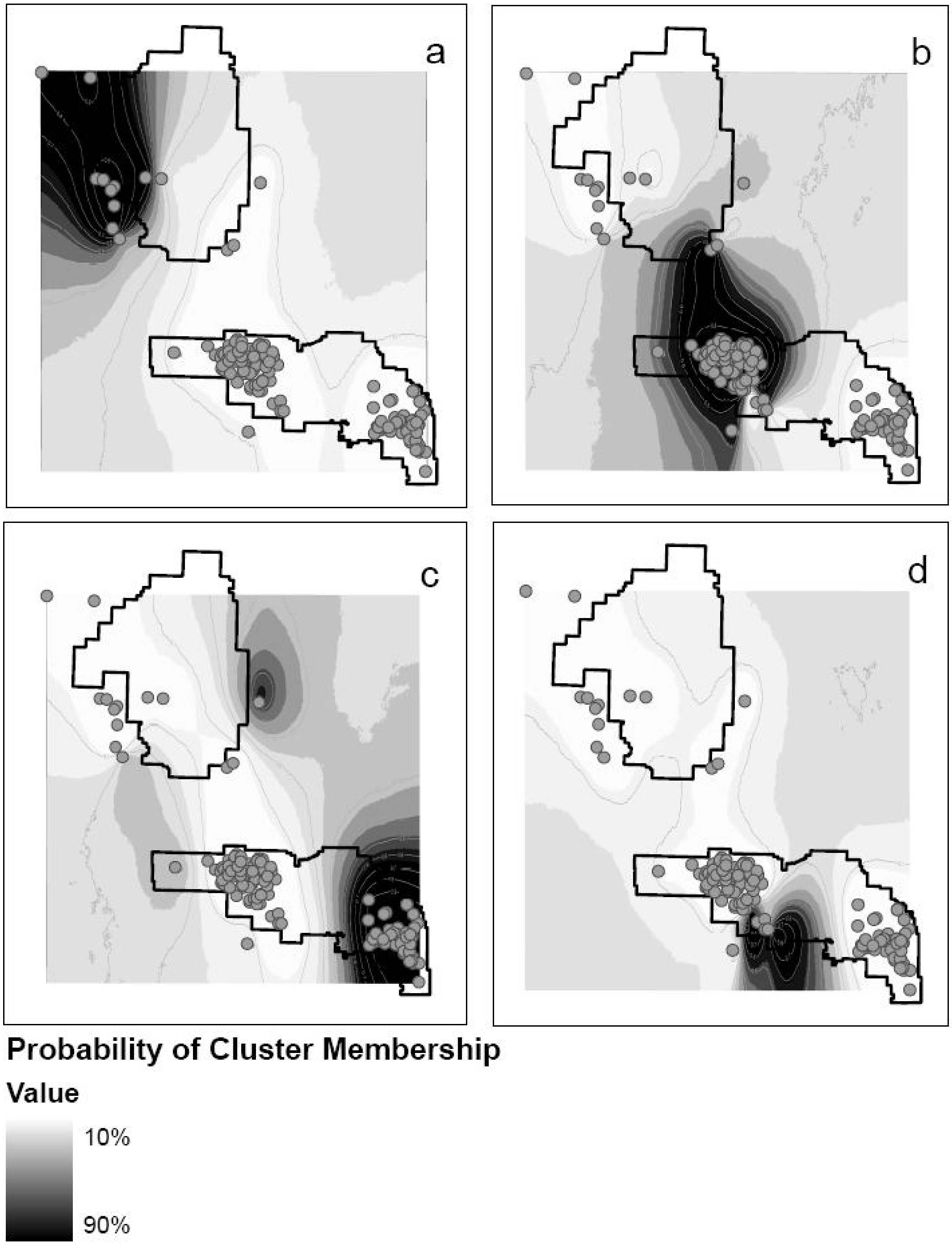

Fig. A.2 Spatial Bayesian clustering of posterior probabilities of population membership and genetic discontinuities from the spatial model in GENELAND for the sampled elk. Contour lines indicate the predicted spatial position of genetic discontinuities. Black areas indicate a high probability of group membership (≥ 90%). Four genetic clusters were identified, each depicted in one of the maps: (a) subpopulation in Duck Mountain Provincial Park and Forest, (b) subpopulation in west Riding Mountain National Park, (c) subpopulation in east Riding Mountain National Park, and (d) small subpopulation in south-central Riding Mountain National Park.

A global permutation test on the eigenvalues derived from a sPCA with a minimum neighbor connection network revealed global structure ($P = 0.0013$) but no significant local structure ($P = 0.273$). Analyses of the scree - and bar plots of the eigenvectors (see Jombart et al. 2008) suggest that the first 2 global axes were more extreme values than the other axes and were retained (Fig. A.3). The individual scores on theses two principal axes are plotted onto the sampled area (Fig. A.3b). The first scores show strong spatial structure ($I = 0.616$) clearly differentiate the West RMNP individuals from the rest (Fig. A.3c). The second scores also show strong spatial structure ($I = 0.542$). DMPP&F individuals have high negative scores on the second axis whereas RMNP individuals, especially those in the East, tend to have positive scores. These second scores do not show sharp boundaries between patches but a progressive change from the NW to the SE, suggesting that this global structure may be a cline (Fig. A.3d). Combining both axes, I retrieved a genetic structure similar to the one predicted by GENELAND, confirming the spatial patterning in the genetic differentiation.

A.4.2 Relatedness and Social Interactions

Largely, population-scale mean pair-wise relatedness did not differ significantly from animals that of animals who interacted ≥ 1 or ≥ 10 (Fig. A.4) or ≥ 100 times within the east or west RMNP clusters. In four cases (Fig. A.4d, f, k, and i), however, elk that were sampled and did not interact were more closely related than the population mean. These groups were not more related than animals that did interact within the same cluster (suggesting samples sizes were too small to discriminate). This result became clearer when I compared sampled individuals against population cluster, rather than the total population (Fig. A.4).

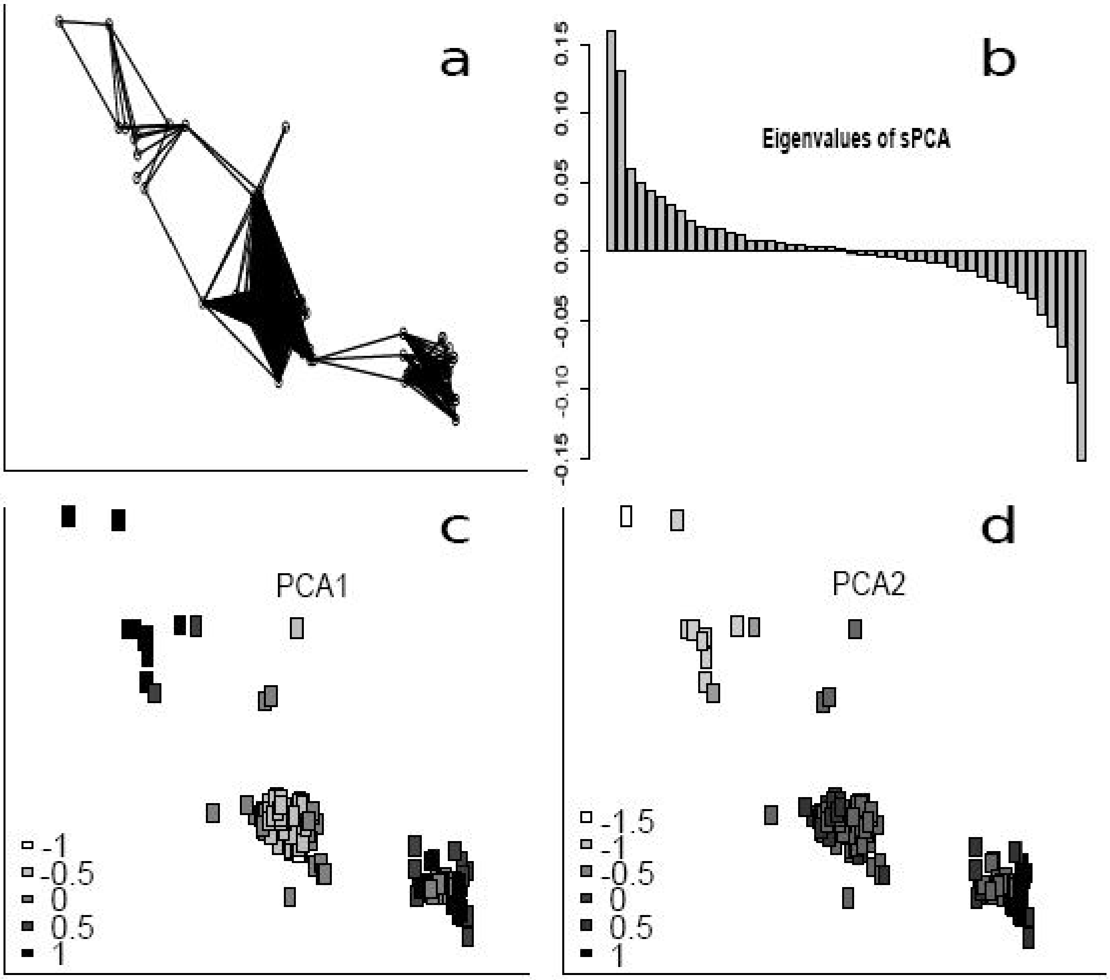

Fig. A.3 Analysis of global eigenvalue scores for the spatial principal component analyses (sPCA) performed on the genotyped elk (at 30 microsatellites) from Riding Mountain National Park (2005-2008). All plots are positioned according to their spatial coordinates. (a) Connection network (produced by minimum neighbour distance) used in the analysis. (b) Global and local eigenvalues of the analysis. (c) First axis PCA scores. (d) Second axis PCA scores. Large black squares correspond to high positive autocorrelation scores, whereas large white squares correspond to high negative scores. Gradual variation in autocorrelation scores represents clinal, isolation-by-distance genetic variation (d).

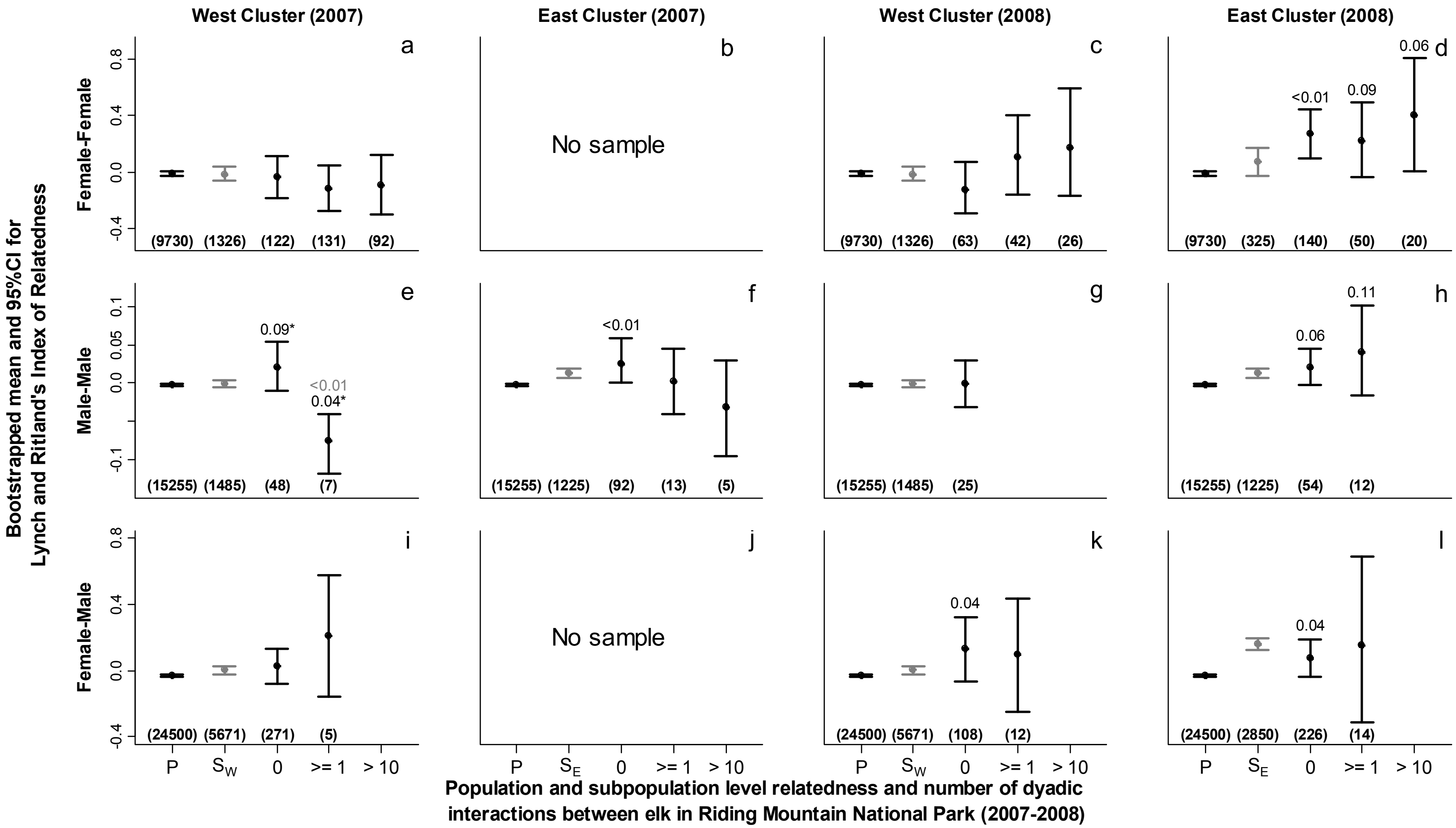

Fig. A.4 Bootstrapped sex-specific pair-wise relatedness by dyadic interaction frequency (i.e., degree of social association) dissected by subpopulation cluster in (east and west Riding Mountain National Park [RMNP, MB, CAN]) and sample year (2007 and 2008) for 104 elk in RMNP. All test statistics with $P < 0.15$ comparing non-interacting (0) and interacting ($\geq$ 1 and $\geq$ 10) dyads with the pair-wise population relatedness (P) appear in black, and with pair-wise subpopulation relatedness (east [S_E] and west [S_W]) appear in gray. *P*-values in west cluster male-male (e) compare between non-interacting dyads to interacting dyads within the subpopulation (indicated with *).

In all cases, both animals that did not interact and animals that did interact were not more related to one another than they were to the mean relatedness of the population cluster (Fig. A.4, $P > 0.05$). For males from the west cluster sampled in 2007 (Fig. A.4e), individuals that did interact were less related than the population mean, the cluster mean, and less related than males whom did not interact. This result was not replicated in 2008 due to low sample size (Fig. A.4g), nor was it apparent in males from the eastern cluster (Fig. A.4f and h). Similarly, no linear relationship is apparent between pair-wise relatedness and interaction duration female-female dyads (Fig. A.5a): $P = 0.95$ ($t = 0.07$, randomized t distribution 95%CI 1.98 —1.89; $n = 222$); male-male dyads (Fig. A.5b) $P = 0.15$ ($t = 0.81$, randomized t distribution 95%CI 2.11– -2.00; $n = 34$); and female-male dyads (Fig. A.5c) $P = 0.23$ ($t = -1.47$, randomized t distribution 95%CI 1.99 —1.98; $n = 30$).

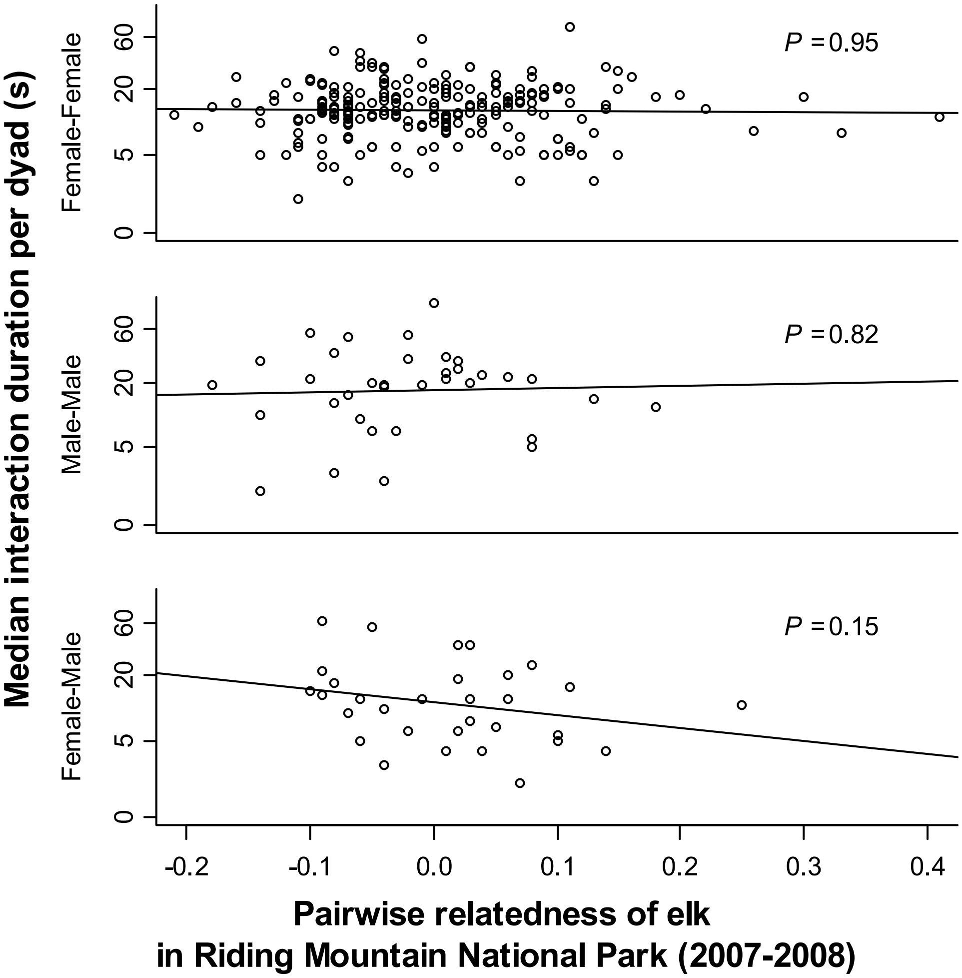

Fig. A.5 Relationships between interaction duration and pair-wise relatedness - Lynch and Ritland (R_{LR}) - in Riding Mountain National Park (2007–2008).

A.5 Discussion

The spread of infectious diseases in natural populations is innately a spatial process. Here I have combined close-contact biotelemetry and genetic data to shed light into bovine tuberculosis prevalence and dynamics in one of the three main reservoirs of the disease in North America, the prairie-parkland population of elk (Manitoba, CAN). Spatially explicit genetic analyses of the host indicate reduced gene flow at the regional level. At this scale, the elk population is composed of at least three distinct clusters associated with two protected areas: Duck Mountain Provincial Park and Forest (DMPP&F), east, and west Riding Mountain National Park (RMNP). Although narrow habitat corridors are still present in the agricultural matrix surrounding both parks that appear to connect RMNP and DMPP&F, these corridors have been fragmented over the last five decades (Walker 2001) and are bisected by several roads. As a result, although individual elks are highly mobile (Kie, Ager, & Bowyer 2005) my results suggest that in natural circumstances, movements are generally more restricted and/or dispersers between the two parks rarely interbreed. Telemetry data support this interpretation. Between 2004–2009 only 3 of 415 elk (all juvenile males) actively tracked with biotelemetry in and around RMNP moved across the 30 km separating the north-west part of RMNP and the southern border of the Duck Mountain Provincial park (Brook 2008; Parks Canada unpublished data). Hence, the contemporary agricultural expansion seems to represent an anthropogenic barrier that impedes movement between northern and southern demes.

The analyses also reveal the existence of a north-south cline that it is likely to represent a transitional zone between historically divergent subpopulations (Turner 1906; Green 1933;

Banfield 1949). Thus, the interplay between historical and contemporary factors (Brook 2009), with the superimposition of an anthropogenic barrier upon a zone that was already transitional might explain the sharp genetic discontinuity observed between DMPP&F and RMNP. The discontinuity between the east and the west areas of RMNP may also be related with anthropogenic habitat fragmentation, due in part to a provincial Highway 10 and a 50-m access strip for a high-tension power line. Abundant observational and telemetry evidence show that the power line corridor is certainly permeable to the movements of elk. However, the influence of Highway 10 on elk movements is less clear. Main roads have been identified as dispersal barriers in other large highly mobile herbivores, including red deer (Epps et al. 2005; Pérez-Espona et al. 2008). However, in red deer the effect of roads on gene flow needed to be explained in conjunction with the effect of other landscape features (Pérez-Espona et al. 2008). In fact at a fine-grained spatial scale elk have been shown to avoid disturbance, such as roads and highways (Lyons 1983; Anderson et al. 2005; Dodd et al. 2007). Furthermore, local habitat studies indicate that the environment parallel to Highway 10 has a low probability of use by elk (Parks Canada unpublished data), suggesting that in this case the combination of a semi-permeable barrier with highway infrastructure indeed act as barrier to dispersal. In fact, no elk that has been actively tracked with radio telemetry ($n > 400$) has been recorded moving from the east cluster to the west cluster in RMNP or vice versa (Brook 2008; Parks Canada unpublished data).

Understanding permeability and the selectiveness of host dispersal barriers can be used to infer disease dynamics and understand heterogeneity in the spatial distribution of infectious diseases (e.g. Blanchong et al. 2008). Here I hypothesized that dispersal dynamics and social interactions are the two main factors explaining the observed pattern of tuberculosis prevalence. During the last decade, clusters of tuberculosis have been detected in the studied population

(Nishi et al. 2006; Brook & McLachlan 2009). While the apparent prevalence has remained higher in the west side of the RMNP (9%; i.e., 41/460), the number of diseased animals in the east side of the Park (< 1%; i.e., 1/154) and in DMPP&F (<1%; i.e., 1/116) has remained low (Fig. A.6; Parks Canada unpublished data, but see Rousseau & Bergeson 2005 for partial description disease testing protocol, and Rohonczy et al. 1996; Surujballi et al. 2009 for TB assay descriptions used therein). This suggests low connectivity between infected and uninfected demes. My results clearly show that genetic structure is in fact related to landscape features that are likely to influence elk dispersal, and that this structure reflects the spatial variation in tuberculosis prevalence.

Contacts, or close-contact interactions, are a critical parameter affecting pathogen transmission and ultimately disease prevalence. Thus, social behaviors that influence the process of disease transmission are key factors explaining the distribution and spread of diseases (Altizer et al. 2003). Previous studies of white-tail deer suggest that, in social cervids, contacts within family groups are a key factor explaining the transmission of infectious diseases (Farnsworth et al. 2006; Joly et al. 2006; Blanchong et al. 2007; Grear et al. 2010).

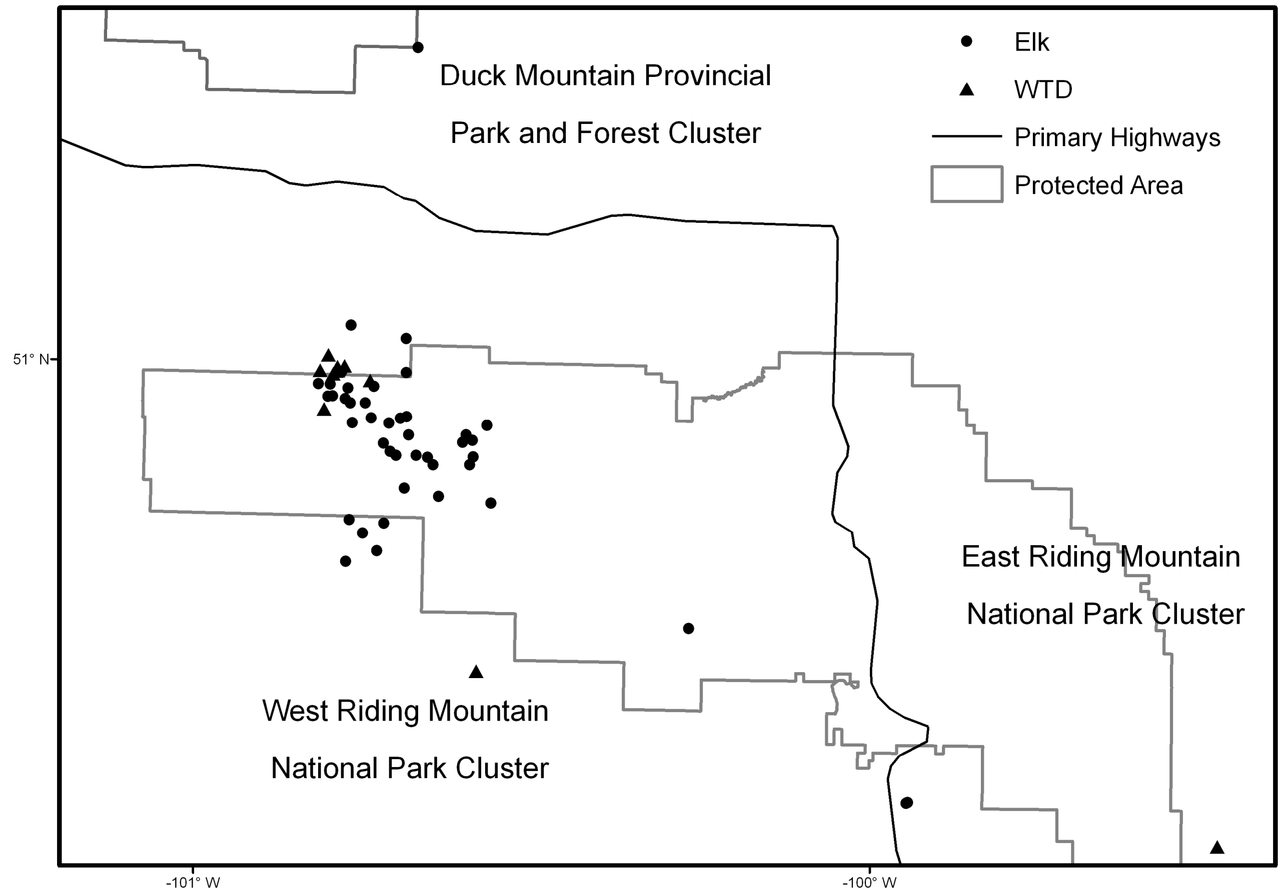

Fig. A.6 Spatial locations of bovine tuberculosis positive elk (n = 42) and white-tailed deer (WTD; n = 11) from 1991–2010 illustrating the grouped distribution of disease occurrence in the Riding Mountain Region. Only three of 54 cases of tuberculosis in wildlife have occurred outside of the western Riding Mountain National Park (RMNP): one elk which was assigned to the Duck Mountain Provincial Park and Forest subpopulation, one elk on the margin of the east and west RMNP cluster, and one WTD in the east end of RMNP. *).

In white-tailed deer systems individuals form small stable matrilineal groups (Mathews & Porter 1993; Miller et al. 2011). Accordingly, at small spatial scales (3–4 km), disease transmission is likely to be socially constrained and driven by interactions among relatives. In contrast, my data clearly show that social interactions in elk are not necessarily based on the genealogical relationship between individuals and two important epidemiological parameters, the close-contact interaction rate (p) and the probability of successful pathogen transmission (v), do not covary with genetic relatedness. Elk form relatively large groups with mixing matrilineal subgroups (Geist 1982), and at small scales these groups seem to mixed freely (Millspaugh et al. 2004). This results in a very different type of social unit that has important implications.

In matrilineal systems, such as the white-tail deer, transmission is most likely to occur within a social group. This may affect the heterogeneity of contacts (i.e., the number of unique individuals that are contacted), which could also have implications for transmission (Cross et al. 2004; Cross et al. 2005). Furthermore, in matrilineal systems pathogen transmission is thought to be frequency-dependent (Miller et al. 2000; Gross & Miller 2001; Wasserberg et al. 2009). In this type of model highly virulent pathogens (*i.e.,* those causing high mortality rates) may lead to local population extinctions. Though this is not universally assumed to be true (see Schauber & Woolf 2003; Smith et al. 2009; Cross et al. 2010), it still remains a chosen model for transmission (e.g., white-tailed deer, Grear et al. 2010). That I failed to detect similar structuring among elk social units, provides some evidence that highly virulent pathogens in elk may display density-dependent transmission, and thus have critical community sizes (Bartlett 1957) and thresholds for pathogen establishment or fade-out (Lloyd-Smith et al. 2005). Further evidence for thresholds may exist given the distribution of tuberculosis in the Riding Mountain Region (RMR; Fig. A.6) which also mirrors different conspecific densities of elk (i.e., west RMNP has higher elk densities than DMPP&F and East RMNP), and appear to affect interaction rates (Chapter 4). However, habitat-density relationships (see Morris 2003) and behaviors upon which transmission is based result from complex social interactions, which may influence transmission (Chapter 5 and Appendix B).

Pathogen spread is a multi-spatial process (Cross et al. 2005; Cross et al. 2009; Heisey et al. 2010). These results provide small-scale mechanistic (i.e., interaction rates and durations) and landscape-scale evidence (i.e., presence of population structure) which reinforce the importance of a multi-spatial approach to avoid erroneous conclusions regarding relatedness and social behaviors upon which pathogen transmission is predicated and the likelihood of inter-deme transmission within a regional population. Moreover, tuberculosis is oftentimes a community-level pathogen among ungulates (Aranaz et al. 2004; Wobeser 2009). In the RMR, further investigation into the population-scale genetic structure and local-scale social behaviors of white-tailed deer is warranted due to the contrast between low-likelihood of exchange of elk among RMR subpopulations and the distribution of tuberculosis in the region (Fig. A.6). White-tailed deer may prove to be a more effective vector for landscape-scale tuberculosis transmission. The combination of landscape-scale genetics, pair-wise relatedness, and local-scale social behaviors is a promising approach, to not only understand and predict landscape-level pathogen transmission within my system, but within all social ungulate systems affected by transmissible diseases.

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Appendix B: Group size

B.1 Methods

B.1.1 Relocations and group size estimates

Free ranging elk in Riding Mountain National Park (RMNP) were captured (*n* = 313; 178 F [144 west and 44 east], 135 M [80 west and 55 east]) from 2002–2009 using a net-gun fired from a helicopter (Cattet et al. 2004). We equipped each animal with a Very High Frequency (VHF)-radio collar (Telonics, Mesa, AZ, and SirTrack, Havelock North, New Zealand). Elk were located during daylight hours (usually 0800–1900 hr) 1–16 times every 2 weeks by fixed-wing aircraft (Cessna 172 [Wichita, KS, USA]). During telemetry flights the location of the animal was collected with a Global Positioning System at the point where the animal was visually observed. Subsequently the observers would count number of conspecifics neighbouring the focal individual.

B.1.2 Statistical analysis

Group size was designated as exposure to conspecifics, i.e., group size equalled the number of elk in the vicinity. Group size observations may be affected by visibility biases (see Vander Wal, Brook, & McLoughlin 2011 for details). Thus I binned the observations into groups following Hebblewhite & Pletcher (2002) to visualize trends in group size between subpopulations and sexes. Alternately repeated observations of group size for a focal individuals were averaged to calculate a measure of mean unadjusted (i.e., not binned) group size for each focal individual.

Data were divided by sex, as elk segregate sexually (Main & Coblentz 1990). Riding Mountain National Park has two distinct subpopulations (Appendix A) which differ in density of elk (Chapter 4) and also vary in habitat composition. As habitat and density both affect sociality (Chapter 5), here I tested differences between subpopulations as a proxy for the habitat-density interaction. Specifically, I tested whether mean unadjusted group size differed by sex (i.e., male and female) and habitat-density. Group size data were skewed right. Given that the data were overdispersed I used a generalized linear model with a poisson distribution. Generalized linear models were run in R (R Development Core Team 2010), and I used the multcomp package (Hothorn, Bretz, & Westfall 2008) for post-hoc multiple comparisons tests.

B.2 Results

Group size was affected by habitat-density, though the results were sex-specific (Fig. B.1). Female group size differed between subpopulations: west RMNP females had a higher group size than eastern females ($z = 4.66$, $P < 0.001$); however male groups did not differ between subpopulations ($z = 2.31$, $P = 0.09$). In fact contrary to expectation, habitat-density resulted in group sizes of western males not differing in group size from females in eastern RMNP ($z = -0.62$, $P = 0.92$); although western males did have smaller groups than western females ($z = -6.60$, $P < 0.001$), and eastern males had smaller groups than western females ($z = -7.26$, $P < 0.001$). Similarly, females in the east did have larger groups than males in the east ($z = -2.63$, $P < 0.04$), although the difference is minimal. These trends, however, were not universal across bins (Figs. B.2 for sex and B.3 for subpopulation). Similarly, exposure to group size may also vary seasonally (Fig. B.4).

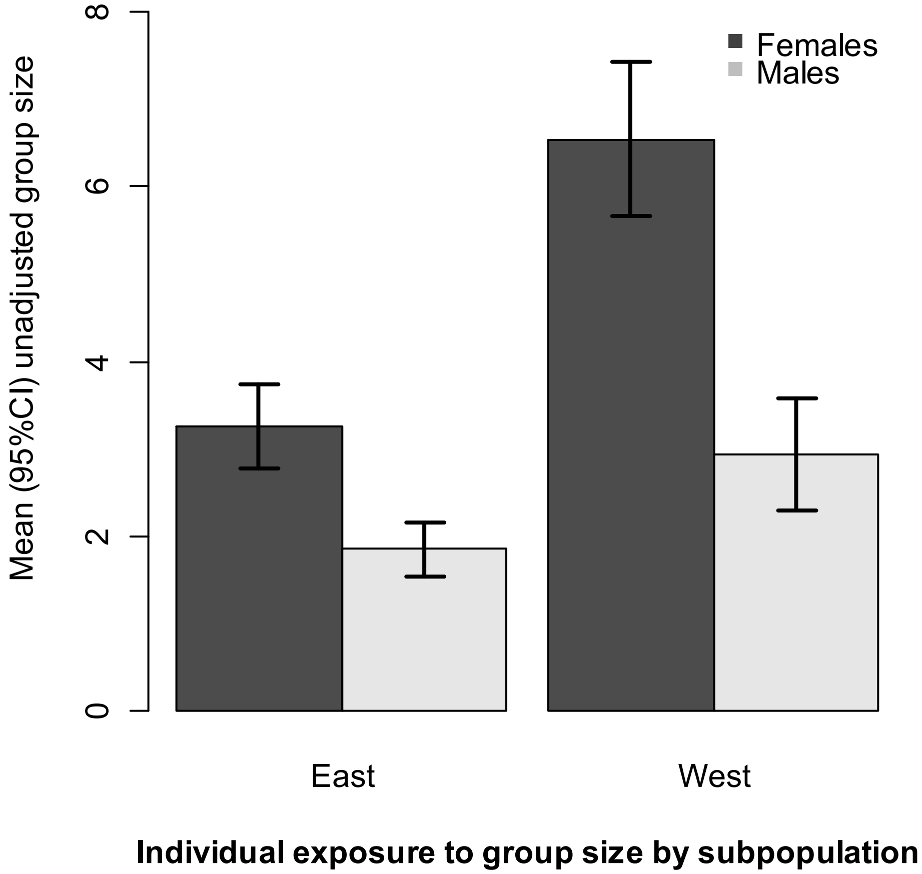

Fig. B.1 Mean unadjusted group sizes for individual elk (*n* = 313) by sex and subpopulation in Riding Mountain National Park from 2002–2009.

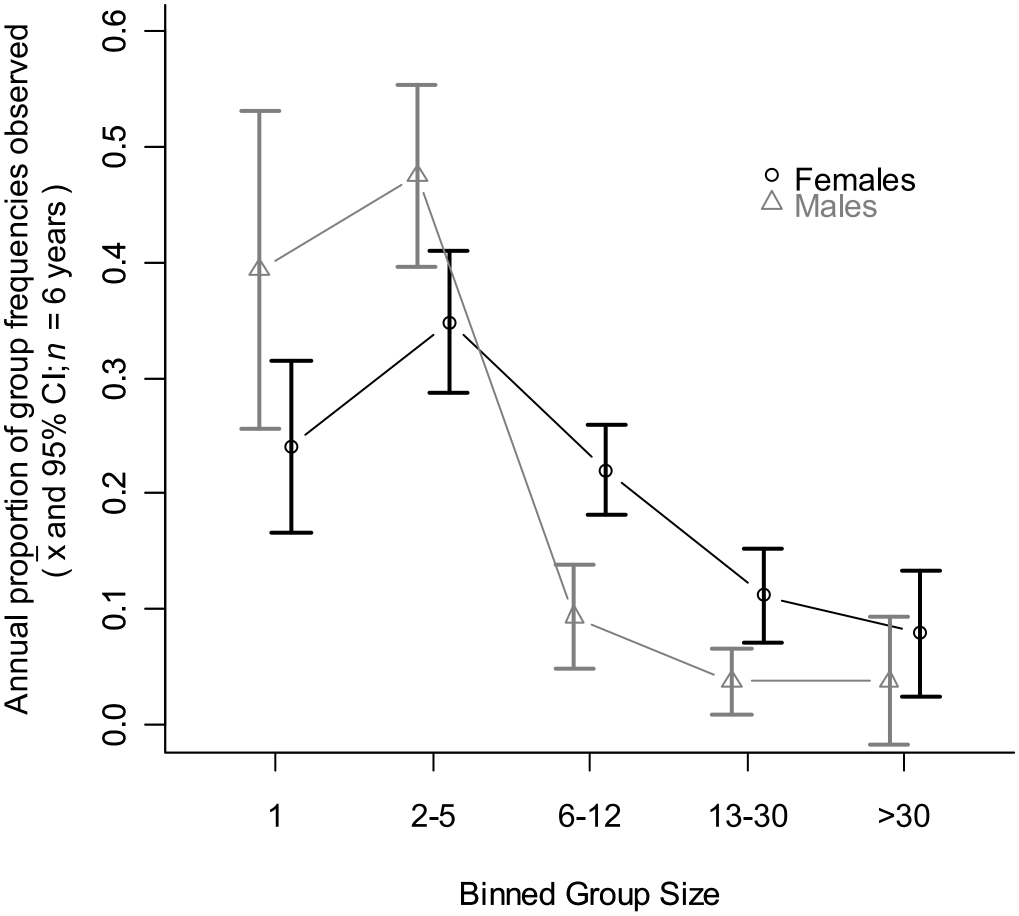

Fig. B.2 Binned proportion of observed frequencies of group size for individual elk (*n* = 313) by sex in Riding Mountain National Park from 2002–2009..

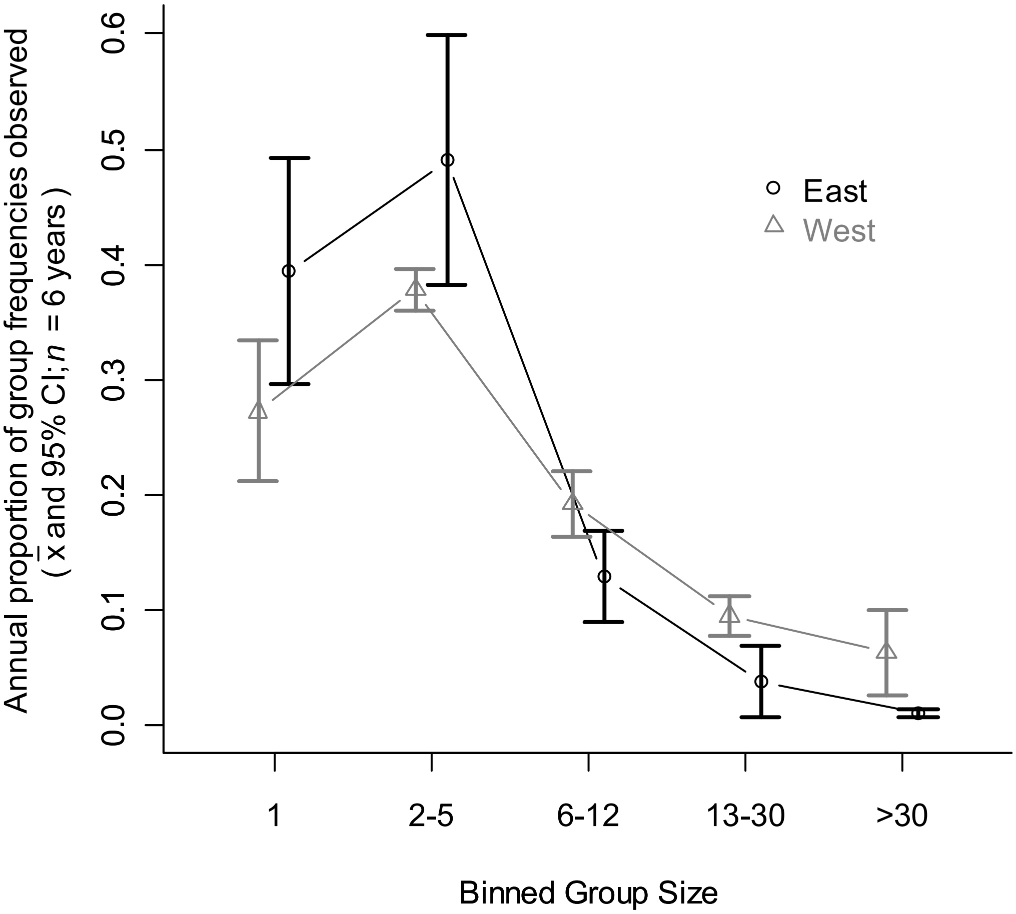

Fig. B.3 Binned proportion of observed frequencies of group size for individual elk (*n* = 313) by subpopulation in Riding Mountain National Park from 2002–2009.

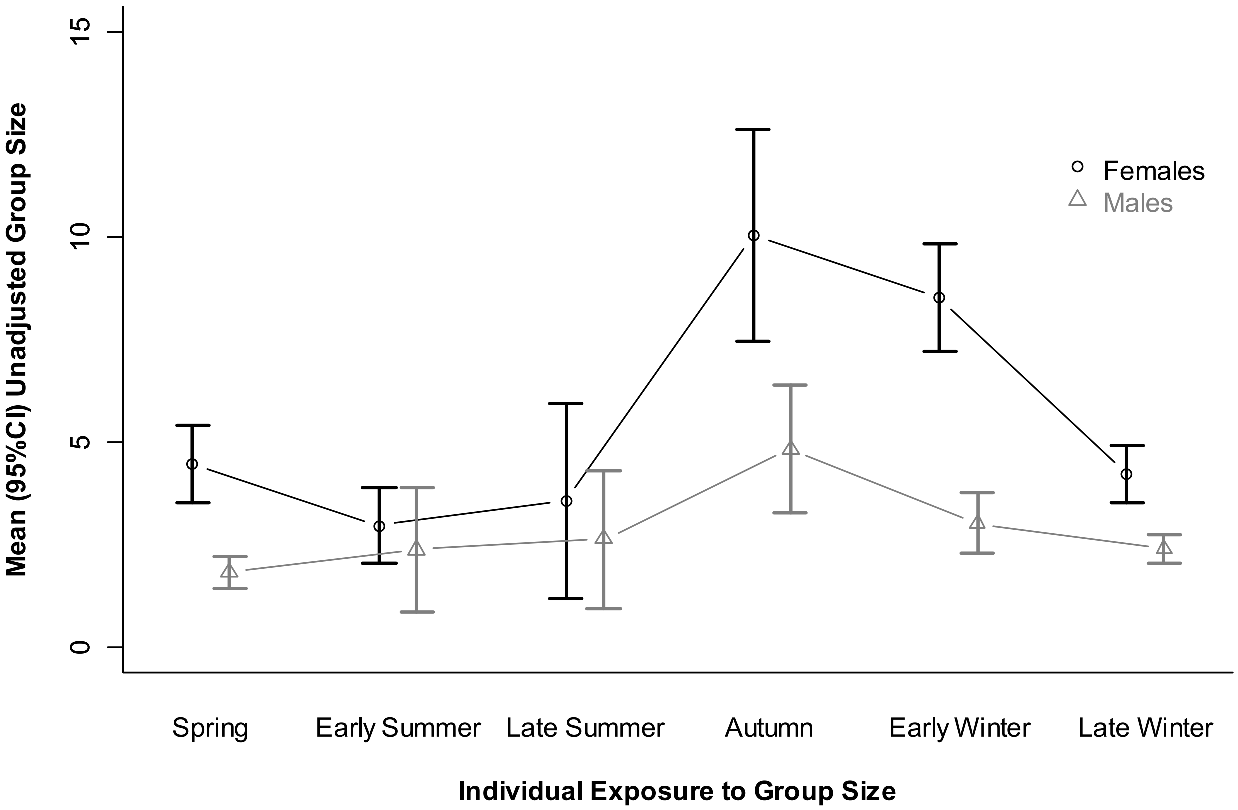

Fig. B.4 Mean unadjusted group sizes for individual elk (*n* = 313) by sex and season in Riding Mountain National Park from 2002–2009.

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