

Sex-based differences in density-dependent sociality: an experiment with a gregarious ungulate

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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 with respect to true conspecific density and not group size. However, insight into this line of research may be far-reaching—from understanding density dependence in sexual selection to improving models of disease transmission. Using elk (*Cervus elaphus* Linnaeus) held in enclosures, we 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 we 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. We highlight a sexually dichotomous, density-dependent response in sociality that has yet to be reported. In addition to furthering our understanding of sociobiology (e.g., implications of time constraints presented by density on dyadic interactions), our results have implications for managing communicable disease in gregarious species of livestock and wildlife.

Key words: behavior; *Cervus elaphus*; density dependence; disease transmission; elk; interaction rate; proximity-logging radio collars; sexual selection; sociality.

INTRODUCTION

Understanding the 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 the 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 the 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. Most of our 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). Estimating density as a predictor of sociality is made difficult by confounding effects by arbitrary delineations of a group's range boundary, the role of patchy resources, the effect of fission and fusion within and between groups, and immigration and emigration across study boundaries. For animals living in natural or seminatural settings, research remains limited, especially concerning social responses to true conspecific density and not only to group size. The applications of knowledge obtained by conspecific density, however, may be far-reaching, from understanding density dependence in sexual selection (Kokko and Rankin 2006) to improving models of pathogen transmission and management (Ferrari et al. 2004, Dobson 2005,

Manuscript received 6 January 2011; revised 13 June 2011; accepted 16 June 2011. Corresponding Editor: B. P. Kotler.

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Lloyd-Smith et al. 2005, Matthews 2009, Kirkpatrick and Altizer 2010, Tompkins et al. 2011).

Though poorly studied, it makes sense that effects of conspecific density on sociality may depend on sex, particularly where social behaviors have evolved in the context of sexual segregation. Sexual segregation occurs in most vertebrate classes (Ruckstuhl and Neuhaus 2005), and many mammals, especially cervids, remain in sex-specific groupings outside the breeding season (Main et al. 1996). Several hypotheses have been presented for the evolution of sexual segregation, including ideas founded on sex-based differences in predation risk, foraging and body size, reproductive strategy, and social preference (Bon and Campan 1996, Main et al. 1996, Ruckstuhl and Neuhaus 2000, Pérez-Barbería et al. 2005). Here we focus on the “social preference” hypothesis, which predicts that males and females will aggregate by sex due to social affinity. Proximally, segregation is thought to reduce sexual harassment of females by males (Bon and Campan 1996, Cransac et al. 1998, Darden and Croft 2008) and aid in the development of sex-specific behaviors, e.g., fighting (Clutton-Brock et al. 1982, Weckerly 2001) or rearing young (Clutton-Brock et al. 1982). Ultimately, segregation may reduce intraspecific competition (Geist and Petocz 1977) and instances of sexual harassment, leading to increases in individual performance (Chapman et al. 2003). Given that the impetus for social intercourse may differ between the sexes, interactions may have sex-specific costs and benefits and be differentially affected by changing conspecific density.

Using a gregarious, large herbivore as a model (captive elk [*Cervus elaphus* Linnaeus] feeding on naturally available forage in 7–20 ha enclosures), we conducted a series of sex-stratified experiments to test how the frequency of dyadic pairings (interaction rate) and their quality (duration of individual pairwise interactions and summed total duration of interactions per dyad) responded to manipulations in population density. The latter relationship has received very little attention before in a wild ungulate; however, measuring duration of interactions may be as important as quantifying the number of interactions over time when we consider, e.g., implications of density-dependent sociality to the spread of disease.

We quantified interaction rates and their duration for elk using novel proximity-logging radio-collars (see Swain and 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, we defined interactions *sensu* Whitehead and Dufault (1999). Based on predictions drawn from previous laboratory studies (e.g., Blanc and Thériez 1998, Gaskin et al. 2002) and field studies (e.g., Weckerly 1999, 2001, Weckerly et al. 2001), we hypothesized that interaction frequency would

increase with density due to increased opportunities for aggressive competitive interactions. We also reasoned that interaction duration would decrease as density increased due to interference resulting in less time a given dyadic pairing could interact uninterrupted; or that if agonistic interactions were involved, which are often short occurrences for social ungulates (e.g., Weckerly 1999), we would observe reduced lengths of interactions than at lower density (although many short agonistic interactions may still result in increased total duration of time interacting). We believed that responses in interaction frequency and duration would vary between the sexes, assuming selective pressures for gregariousness differs by sex. For example, if smaller females naturally aggregate in response to safety in numbers more than male elk, which are primarily vigilant for monitoring conspecifics and not predators (Childress and Lung 2003), we might expect longer and more frequent durations of interactions compared to males on the whole and in the face of increasing density. Our results support this idea, and we highlight a sexually dichotomous, density-dependent response in sociality that has yet to be reported.

METHODS

Data collection

We based our analysis on data collected outside the breeding season in summer 2007 for two captive herds of adult elk (14 females, age 7.6 ± 3.3 yr [mean \pm SD], minimum age 6 yr; and 10 males, all aged 6 yr) located at the Specialized Research Centre field plots of the Western College of Veterinary Medicine in southeast Saskatchewan, Canada. Our research followed Animal Care Protocol number 20060067 of the University of Saskatchewan, following guidelines of the Canadian Council on Animal Care. All animals used in our experiments were adults. Males were polled (i.e., had their antlers removed) 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 our experiment was located in rural Saskatchewan, the merits of avoiding habituation remain. To avoid potential complications, we handled animals only twice throughout the entire experiment: to apply and remove Sirtrack Proximity Logger radio-collars (Sirtrack, Havelock North, New Zealand). All elk were handled for collar fitting by corralling and immobilization in a livestock processing chute and squeeze facility.

We programmed each Sirtrack proximity collar (Goodman 2007) to activate and collect data whenever one collar came within 1.4 m of another collar ($1.42 \pm$

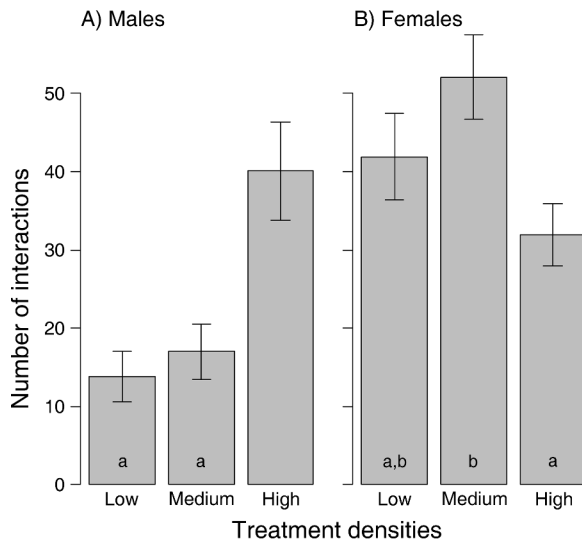


FIG. 1. Frequency of interactions for proximity-collared captive (A) male ($n = 10$) and (B) female ($n = 14$) elk at low, medium, and high experimental densities in Saskatchewan, Canada, 2007. Data are means with 95% confidence intervals. Means of histogram bars sharing a lowercase letter do not differ significantly (i.e., $P > 0.05$). For males, low, medium, and high density equaled 0.75, 1.02, and 1.49 elk/ha, respectively; for females the respective densities were 0.71, 1.05, and 1.43 elk/ha. Proximity was logged when two elk were within 1.4 m or less. Each density treatment lasted for seven days.

1.00 m [mean \pm SD]; 1.42 \pm 0.20 m [mean \pm SE). Collars deactivated recording an encounter each time a pair separated for >30 s and a distance of 1.98 \pm 1.60 m (mean \pm SD), 1.98 \pm 0.32 m (mean \pm SE). These collars allowed for both a count of the number of interactions between animals wearing collars, and also recorded interaction length in seconds.

Elk tend to spend most of their time in single-sex groups (Altmann 1952, Clutton-Brock et al. 1982); hence, we created two separate experiments (one for each sex), each with three possible density treatments (low, medium, and high), which we 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, 1.02 elk/ha, and 1.49 elk/ha, respectively). Our high density constructs were not unrealistic for elk under natural conditions (e.g., 2.15 elk/ha in Beneke Creek Wildlife Management Area, Oregon, USA [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). Our experiment mimicked these natural condi-

tions where forage is not limiting by allowing elk to feed only on naturally abundant available forage without supplementation.

We herded elk between treatments without direct handling. Each treatment ran for seven days. We 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 data set to ensure that any confounding data from the herding event was not included.

Statistical analyses

We analyzed our data in the R environment for statistical programming (R Development Core Team 2010). Replicates were pooled and we tested for differences in treatments using mixed-effects generalized linear models (GLMM). We added random intercepts to the GLMM for individual (to control for unknown behavioral 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. We were able to normalize interaction duration and its sum, however, with a natural-logarithm transformation. We based our models on these distributions, respectively.

RESULTS

The frequencies at which male interactions occurred between low- and medium-density treatments were not significantly different (Fig. 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 $P < 0.001$). Individual interaction duration per male dyad was longest at low density (Fig. 2A). All treatments were significantly different with respect to interaction duration (Fig. 2A; P -adjusted multiple comparison z score of a generalized linear model: low-medium $P < 0.001$; low-high $P < 0.001$; medium-high $P = 0.027$). However, decrease in duration did not change the overall trend toward increased interaction as the sum of time a dyad spent interacting was significantly greater at high density (Fig. 3A; P -adjusted multiple comparison z score of a generalized linear model: low-medium $P < 0.138$; low-high $P < 0.001$; medium-high $P < 0.001$).

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. 1B; P -adjusted multiple comparison z score of a generalized linear model: low-medium $P = 0.333$; low-high $P = 0.264$;

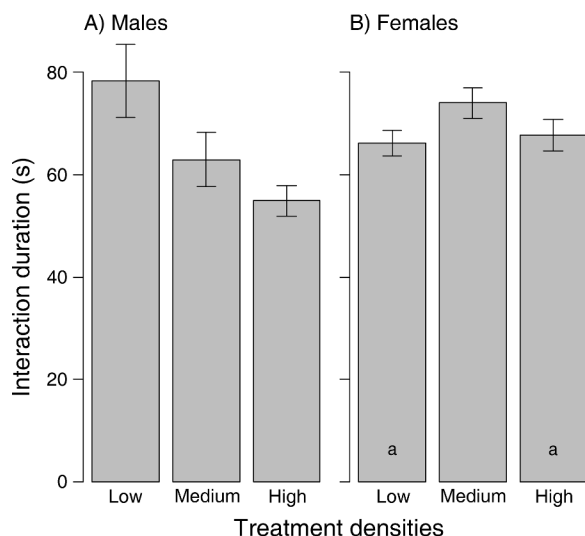


FIG. 2. Interaction duration for proximity-collared captive (A) male ($n = 10$) and (B) female ($n = 14$) elk at low, medium, and high experimental densities in Saskatchewan, Canada, 2007. Data are means with 95% CI. For further details, see Fig. 1 legend.

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 $P < 0.001$). A similar trend (i.e., an increase at medium density) occurred for total duration of interaction (Fig. 3B; P -adjusted multiple comparison z score of a generalized linear model: low–medium $P < 0.001$; low–high $P = 0.008$; medium–high $P < 0.001$).

DISCUSSION

Our 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 we had predicted, but for females we noted the greatest number of interactions occurring at an intermediate density. These trends were clearly evident in our replicated study, and we suggest they are biologically meaningful.

We 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 et al. 2007). Benefits include reduced predation risk and associated reductions in vigilance, allowing for more time feeding or resting (Lima 1987, Roberts 1996). Some costs include de-

creased access to resources, and increased levels of stress and competition because of this lack of resources (Lung and Childress 2007). In natural situations, if the costs exceed the benefits an animal may leave the group (Weckerly et al. 2001, Krause and Ruxton 2002); however, in our 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 defenses against predation. Childress and 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 behavior is mainly antipredator. 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 behaviors than females. Females are undoubtedly affected in a similar fashion to male elk in that increased density and competition typically leads to lower body mass and reduced performance (e.g., Mysterud et al. 2001, Stewart et al. 2005); however, females likely place less of a cost on high group size than males. 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 (*Odocoileus virginianus* [Zimmerman]) male groups were spaced farther apart and were more aggressive to each other than were female groups. Weckerly et al. (2001) also found that total time spent within ≤ 1 body length was

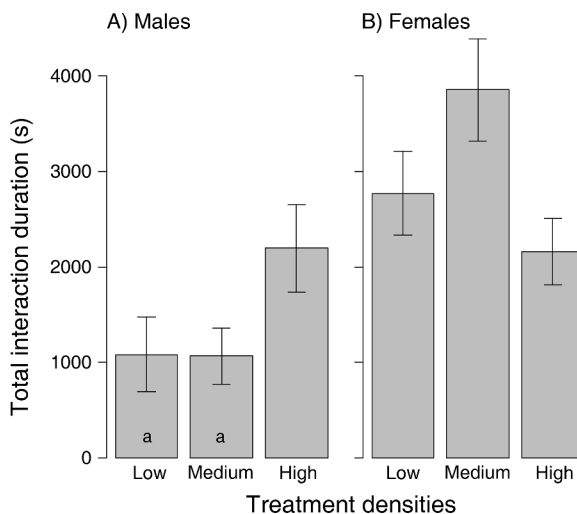


FIG. 3. Summation of interaction duration per dyad for proximity-collared captive elk at low, medium, and high experimental densities in Saskatchewan, Canada, 2007. Format is as in Fig. 2.

higher for female than male elk; however, aggressive behavior at that spatial scale was more common among males. This mirrors the trend we observed at a smaller scale. In addition, using group and body size of male elk, Weckerly (2001) found that large males occur in smaller groups and often avoid interacting aggressively with similar-sized males. Weckerly (2001) suggested this likely related to the costs of aggression (e.g., risk of injury) as large males did not exhibit similar avoidance with smaller males. Our results corroborate this finding, as males when unable to disperse at high density had higher interaction rates.

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 our experiment, it is likely that the females we 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. Our techniques for measuring interaction duration differed, making direct comparison difficult. Notwithstanding this caveat, and predicated on Weckerly's (1999) observations, we observed much longer interactions for females than expected for conflict (Fig. 2B), suggesting the possibility that we 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.

Despite total duration of dyadic interactions having increased with density, the duration of individual interaction for males declined significantly as density increased and the number of interactions increased in the male herd. This suggests the opposite compared to females: that aggressive interactions increased for males with population density. Our 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 for density-dependent theory on sexual selection (Kokko and Rankin 2006) may be important. With increasing density, average male mating success is expected to decrease (Gaskin et al. 2002, Zhang and Zhang 2003, Hårdling and Kaitala 2005, Kokko and Rankin 2006) possibly because when local population density increases, male–male interference and competition increase (Zhang and Zhang 2003, Kokko and Rankin 2006, Wang et al. 2009), females become choosier (Shelly and Bailey 1992, Kokko and Rankin 2006, Wang et al.

2009), or some males become more likely to be engaged in courtships to other males (Gaskin et al. 2002). Our data suggest that elk under high-density situations continue to invest more time in interacting; however, due likely to interference and to time constraints, social behaviors 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.

Our 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 (*Morbillivirus* spp.), and tuberculosis (*Mycobacterium* spp.); and transmission is generally assumed to be directly density- (McCallum et al. 2001) or in some cases ratio- (Begon et al. 1999) dependent. 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 our understanding of disease transmission. Furthermore, classic disease models predominantly assume increased transmission with increased contact between animals (see Hethcote 1976, 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 behaviors 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.

Our observations differed from our 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 and Altizer 2010, Tompkins et al. 2011). 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. 2A). These results have some practical management implications. For example, we 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. Our 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, our 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.

ACKNOWLEDGMENTS

We thank Parks Canada Agency, Riding Mountain National Park, the Natural Science and Engineering Research Council (Canada), the University of Saskatchewan Western College of Veterinary Medicine Specialized Livestock Research Centre, and PrioNet Canada for in-kind and financial support. We also thank F. Messier, P. Paquet, T. Shury, M. Woodbury, and R. McCormack for making this study possible. Further, we thank M. Boyce and one anonymous referee for their thoughtful reviews.

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