SOCIAL FACTORS DURING FORAGING BOUTS INFLUENCE SEXUAL

SEGREGATION IN ROOSEVELT ELK

by

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ABSTRACT

Spatial patterns of large ungulates occurring at broad scales can often be explained by fine-scale processes that function at the level of an individual animal. To better understand broad-scale sexual segregation, we examined fine-scale processes in a non-migratory population of Roosevelt elk (*Cervus elaphus roosevelti*) in the Redwood National and State Parks, California, USA that exhibited a change in sexual segregation over time. We assessed the potential influence of two fine-scale mechanisms: the availability of forage abundance and social factors during the forage bout. Per capita forage availability was estimated for comparison between two meadow complexes (2005-2016) to determine if selectivity for one meadow complex by males (and thus sexual segregation) could be explained by the constraints of their greater absolute metabolic requirements. To assess the influence of social factors (such as group size, group type, or proximity of conspecifics) during the foraging bouts, focal observations were collected from adult male and female elk from 2009 to 2016. These data were used to conduct AIC model selection analyses to determine the best fit, mixed-effect models for predicting the distance traveled, the variance in turning angles, and the proportion of time the animal spends with its head out of the feeding position during a foraging bout. Interestingly, we found that the availability of forage biomass was likely not the driver for males and females using separate meadow complexes. This study instead found that behavioral differences existing between males and females, as well as between males in single-sex

groups and males in mixed-sex groups may have affected sexual segregation. As group size increased, males in male-only groups tended to move farther and in more direct paths than females in order to avoid other animals. In addition, males in both female and male-only groups were more vigilant than females when foraging in close proximity to conspecifics, yet the time allotted to vigilance increased at a greater rate for males in male-only groups. These asynchronous responses to social factors in male-only versus female groups may explain the exclusive, male-only use of a meadow complex from which females were recently extirpated. We can therefore conclude that sexual segregation, in this population of Roosevelt elk is driven in part by fine-scale foraging behaviors.

I. INTRODUCTION

Understanding characteristics of an ecological system requires recognizing the scale at which patterns function (Levin 1992, Wiens 1989). Fine scale processes explain minute details of an ecological system, whereas broad-scale patterns might require understanding broad scale processes (Wiens 1989). Ecological scales can refer to taxonomic, temporal, or spatial hierarchies in a system and will vary in magnitude depending on the organisms involved (Mayor et al. 2009). Within a region over which ecological phenomena change uniformly, the detailed findings at one scale can be extrapolated to another scale (Wiens 1989). Therefore, ecological patterns understood at fine scales might provide insight to large scale patterns.

Sexual segregation, or the differential use of space between males and females is a prevalent phenomenon among large and sexually dimorphic ungulate species and can occur at multiple spatiotemporal scales (Bowyer 2004, Main et al. 1996). Hence, ungulate spatial and social behaviors provide ideal constructs to examine ecological scaling across a spatial hierarchy, whereby fine-scale patterns often manifest as behavioral differences among individual males and females. These fine-scale patterns might then help explain the broad-scale phenomenon of sexual segregation (Main and Coblentz 1990). For example, variable use of space between male and female giraffes (*Giraffa camelopardalis tippelskirchi*) may be driven by within-habitat differences in use of browse canopy heights rather than across-habitat differences in use of space use (Ginnett and Demment 1999). Male and female mountain sheep (*Ovis canadensis nelsoni*) were found to differ in habitat use across the landscape since females used more rugged terrain likely to protect their young from predators (Bleich et al. 1997). In Alaskan moose (*Alces alces gigas*),

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large males separated from females during winter because they decreased activity levels, reduced travel, and selected open habitats with high forage biomass, all to recover energy reserves lost during the rut (Miquelle et al. 1992). In all these cases, the differential use of space between the sexes can be explained by behaviors of individual males and females, which are necessary for reproductive success.

However, the proximal and ultimate mechanisms through which sexual segregation operate among ungulates have been highly contentious (Bon and Campan 1996, Main and Coblentz 1990, Ruckstuhl and Neuhaus 2002) and many fine-scale behaviors have been posited to provide a mechanism to explain this broad-scale spatial pattern in large ungulates. Proposed hypotheses are usually associated with predator avoidance, body-size dimorphism, social affinities, or activities (Ruckstuhl and Kokko 2002, Bonenfant et al. 2004, Bowyer 2004). Processes of forage selection and intake— which govern the majority of ungulate activities (Senft et al. 1987)—might also be fine-scale characteristics that can be used to explain broad-scale sexual segregation. Notably, these mechanisms can vary with fluctuations in population density and thus have demographic implications (Kie and Bowyer 1999, McCullough 1999).

One potential mechanism for explaining sexual segregation with differences in foraging behavior is the availability of forage biomass. Males possess larger body sizes than females and require greater quantities of forage to meet greater absolute metabolic requirements (Barboza and Bowyer 2000, Mysterud 2000, Ruckstuhl and Neuhaus 2002). Therefore, males should be sensitive to availability of forage and exploit habitats with higher biomass (Main 2008). If a landscape exhibits heterogeneous habitats, then males should be constrained to areas of higher biomass to meet metabolic demands.

A second potential mechanism for explaining sexual segregation with foraging behaviors is the influence of social factors during the foraging bout. The differing life-history strategies in size-dimorphic ungulates lead to intersexual differences in social behavior (Bowyer 2004, McCullough 1999). Males must outcompete other males for reproductive success and, are consequently more aggressive and less gregarious than females (Weckerly 2001, Mysterud et al. 2004). In contrast, female reproductive success relies on the rearing of young which necessitates maintaining body condition and evading predators (Bowyer et al. 1999, Gaillard et al. 2000). Females are therefore less aggressive and more gregarious than males (Weckerly 2001). With higher rates of aggression, males may be more influenced during a foraging bout by other animals in close proximity (Weckerly et al. 2001).

The purpose of this study was to investigate two fine-scale mechanisms linked to foraging behavior and determine if either can be used to explain sexual segregation in large ungulates. To examine these potential fine-scale mechanisms of forage availability or social influences during the foraging bout as they pertain to broad-scale sexual segregation, a population of Roosevelt elk (*Cervus elaphus roosevelti*) was studied in Redwood National and State Parks, California, USA. This population was well-suited for this study because it was non-migratory and it exhibited a change in group sexual segregation throughout long-term observations (recorded each January from 1997 to 2016). In ten years out of the twelve-year period from 1997 to 2009, both males and females were ubiquitous across the landscape, but were segregated by group (exhibiting single-sex groups more than mixed-sex groups). In the last eight years of observation (from 2009 to 2016), males and females were randomly associated with each other across

the landscape (Peterson and Weckerly, *in revision*). The definitive shift in space use at the scale of the group made this population suitable for studying the potential influences on sexual segregation at the broader scale of the entire landscape.

The elk resided in a heterogeneous landscape allowing individuals access to varied forage biomass. The forage biomass was estimated throughout the inhabited meadow complexes to compare the availability across the landscape and assess the use of each meadow by sex. Hypothetically, if availability of forage biomass is the fine-scale mechanism driving sexual segregation, then an area with a greater forage biomass should be used by males more often than an area with less forage biomass.

Moreover, if the fine-scale mechanism driving sexual segregation is related to social factors during the foraging bout, then males and females will exhibit different patterns of forage intake and movement in response to social factors while foraging. The elk in this area are habituated to close-range human presence and were therefore conducive to a behavioral study. Focal observations were conducted on foraging adult males and females to assess the influence of social factors on movement and forage intake patterns. Hypothetically, since males are more vigilant towards conspecifics, they should spend more time with the head out of the feeding position than females (Cameron and du Toit 2005), which will consequently reduce rate of forage intake. And when in close proximity to a conspecific, males should be more likely to move farther distances (Weckerly et al. 2001, Weckerly and Ricca 2014) and in less random and tortuous, or zigzag, paths while foraging (Webb et al. 2009).

The objective here was to determine whether the fine-scale factors of forage availability or social influences during the foraging bout could explain the observed

changes in sexual segregation. Understanding the fine-scale factors that influence the

intersexual differences in space use on a broad-scale provides insight into the distribution

patterns and the consequent management of large ungulate species.

II. MATERIALS AND METHODS

Study area— This study was conducted in the Prairie Creek drainage in the Redwood National and State Parks, California, USA (41º24' N, 124º02'W) (Fig. 1). The Prairie Creek drainage is made up of two meadow complexes dispersed in a forested landscape which was dominated by coastal redwood (*Sequoia sempervirens*) and included other coniferous species such as Douglas fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), and Western hemlock (*Tsuga heterophylla*). Boyes meadow complex made up a total area of 70 ha and Davison meadow complex (about 2.0 km away) made up 51 ha. This landscape has bracken fern (*Pteridium aquilinum*) and other forbs but was dominated by annual and perennial grass species such as California oatgrass (*Danthonia californica*), redtop (*Agrostis gigantean*), soft chess (*Bromus hordeaceus*), and reed canary grass (*Phalaris arundinacea*) (Harper et al. 1967, Weckerly et al. 2001, Starns et al. 2015). This region of California exhibits a maritime climate with cool summers, rainy winters, and an annual precipitation greater than 150cm with rainfall most prevalent in fall to early spring (Starns et al. 2015). Predators of elk in the parks include black bear (*Ursus americanus*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), and mountain lion (*Felis concolor*) (Bower 1981).

Population dynamics— Population abundance data was collected across 20 years during February in 1997 then each January from 1998 to 2016. Because male and female Roosevelt elk were mostly aggregated during the rut from August to November (Bowyer 1981) and mostly segregated during parturition in April–May (Weckerly 1998), the winter data collection reduced the potential influence that the reproductive seasons might have on sexual segregation. Ten population surveys were conducted each year

(with the exception of 1998–1999 when only five surveys were conducted) by driving on a predetermined route through the study area. All elk observed during the survey were recorded as marked (identified by ear-tags or morphological incongruities) or unmarked (Weckerly 1996). The age class of each elk was identified and groups were categorized as solitary adult males, adult male-only groups, or female groups consisting of adult females, sub-adult (1.5-year-old) males, juveniles (<1.5-year-old) and occasionally a few adult males. Sub-adult females did not exhibit ostensibly distinct morphologies and were included with adult females. Total population abundance was estimated using the highest count among the 10 surveys conducted in a year when sizes of female groups were invariant and all males encountered were marked; otherwise, abundance was estimated using Bowden's mark-resight estimator (Bowden and Kufeld 1995).

To assess the changes in sexual segregation, the SSAS, or sexual segregation and aggregation statistic, (Bonenfant et al. 2007) was calculated for each year of the study to estimate sexual segregation across the two meadow habitats. This was a chi-square statistic that ranged 0–1, comparing the frequencies of observations of males and females in each meadow. The statistic was calculated using the formula:

$$\text{SSAS} = 1 - \frac{N}{XY} \sum_{i=1}^{k} \frac{X_i Y_i}{N_i}$$

where N was the sum of total observed males (X) and total observed female (Y). The data were summed from k groups with a group size of N_i and consisted of X_i males and Y_i females. A randomization procedure was also conducted to project a 95% confidence band from observed data (Bonenfant et al. 2007). A SSAS value above the confidence band suggests sexual segregation between the meadow complexes (males in one meadow

complex, females in the other). A SSAS value below the confidence band suggested that males and females were aggregated in one of the meadow complexes. If the SSAS fell within the confidence band then males and females were regarded as randomly associated among the two meadow habitats.

Biomass estimation— Available forage biomass was estimated during January, from 2005 to 2016, in 570 quarter-meter plots placed along transects dispersed throughout the two meadow complexes in Prairie Creek drainage. Vegetation height was measured to the nearest centimeter at eight equidistant locations within the plot. The cover of palatable grasses, forbs, and shrubs were estimated using Daubenmire coverage classes: 0-5%, 6-25%, 26-50%, 51-75%, 76-95%, and 96-100% coverage (Daubenmire 1968). From 2005 to 2007, clippings down to the ground level of all grasses, forbs, and shrubs in 129 randomly chosen plots were collected, sorted by type (grasses, forbs, or shrubs), dried at 60º C for 48 hours, then weighed to the nearest 0.1 gram. Multiple regressions using the plant heights averaged across the 8 equidistant measurements and coverage classes predicted dried biomass of grasses ($r^2 = 0.84$, $F_{7, 122} = 97.1$, $P < 0.001$) as well as forbs and shrubs ($r^2 = 0.33$, $F_{2, 93} = 24.9$, $P < 0.001$). These regressions were then used to estimate biomass in each of the 570 plots.

From the vegetation transects, forage biomass ($kg \cdot ha^{-1}$) was estimated for each of ten sub-meadow regions in Boyes and Davison meadow complexes. Forage biomass in sub-meadows were summed in each meadow complex to estimate total biomass. Per capita forage availabilities were then estimated as total forage biomass divided by elk abundance estimates in each meadow complex.

Behavioral analyses— Social and forage behaviors of elk were measured through focal observations collected each January from 2009 to 2016. Observations were collected with a digital voice recorder and ranged from four to ten minutes in length. Focal elk were only measured once in each day of sampling. Data collected from focal samples gave insight into forage intake and movement patterns as well as the social factors that may influence the individuals of each sex. Start and end times were annotated when the focal animal lifted its head above its shoulders (i.e., out of the feeding position), and when the focal animal was within one body-length of another, in order to calculate a proportion of time spent in each state (Weckerly et al. 2001). At every one-minute interval, the distance and bearing from the observer were recorded to triangulate the location of the elk, thus enabling the calculation of distance traveled per minute (averaged across the number of minutes of the focal observation) as well as the variance in turning angles during the focal sample. Variance in turning angle was expressed as r (White and Garrott 1990). This metric ranged 0–1, with r values approaching 1.0 indicating more directed movement. Additionally, observations collected in 2015–2016 also included the number of bites taken throughout each observation to calculate a bites·minute^{-1} rate. Supplementary data collected during each focal included the sex of the focal animal, group type, group size, date, time of day, meadow, and sub-meadow where focal animals fed. Group types were female in female group, male in female group, or male in male-only group. Males were distinguished with two group types to assess if their behavior differed when they were associated with females since males were observed joining female groups but not vice versa (Weckerly et al. 2001).

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From the focal observations, 23 mixed-effect regression models were estimated

using the lme4 package (Bates et al. 2014) in program RStudio (RStudio 2014) to predict

the influences on three different factors of a foraging bout: step length (meters of distance

traveled in a min), variance in turning angle (r), and the proportion of time the focal

animal spent with the head up. Linear mixed-effect models were used to predict step

length and variance in turning angle while the models to predict proportion of time with

head up used generalized linear mixed-effects models with a binomial error structure.

Models were estimated using combinations of sex, group type, group size, forage

biomass in sub-meadow, and the proportion of time the focal animal spent within one

body-length of another animal. The minute-length of the focal sample was a confounding

variable and therefore included in each model. The day of each data collection (79 data

collection days in total) was considered the random factor in each model to account for

possible repeated measurements of the same elk across days. The models that best

explained each of the respective response variables were selected using Akaike

Information Criterion (AIC) (Burnham and Anderson 2002). Parameter estimates were

calculated and reported using maximum likelihood estimation, and coefficients of

determination for each mixed-effects model were calculated using the variance explained

by the fixed factors and the random factor (marginal R^2 and conditional R^2, respectively)

(Nakagawa and Schielzeth 2013).

The bite rates from each focal animal in 2015 and 2016 were used to estimate

correlations between bite rate—the most direct measure of forage ingestion measured

(Trudell and White 1981, Ruckstuhl et al. 2003) — and each of the following: variance in

turning angle, step length, proportion of time with head up during the foraging bout, and

estimated biomass in sub-meadow regions where the focal elk was observed. These correlations were estimated to assess the relative strength of associations of the four attributes to bite rate. Determining which social factors the correlate with bite rate will infer the factors measured during all years of focal observations that most influence forage intake rates.

III. RESULTS

Population dynamics— From 1997 to 2016, the total population of Roosevelt elk peaked in 1998 with 133 individuals and declined until it reached the low of 37 elk in 2006. For the last ten years, the range of individuals in the Prairie Creek drainage was 46–80 and averaged 54 individuals per year. The estimated number of males in the population ranged 6–34 while the number of estimated females ranged 18–56 throughout the 20 year study (Fig. 2). These population estimates and the associated sex ratios were used to calculate the sexual segregation and aggregation statistic (SSAS). The SSAS values ranged from 0.032–0.840 and in relation to the 95% confidence band, suggested that males and females were aggregated in the meadow complexes from 1997 to 2011 (Fig. 3). In 2012, males and females were segregated into different meadow complexes. From 2013 to 2016, the SSAS indicated that males and females were randomly associated across both meadow complexes. The proportions of males and females observed in each meadow complex were calculated from sightings across the population surveys conducted in each year (Fig. 4). The number of sightings of elk per year ranged 353–999 (males observed ranged 48–204 and females observed ranged 215–806 per year.) From those sightings, the proportion of males observed in Boyes meadow complex ranged 0.0–0.852 and showed a distinctive increase after 2008, while the proportion of females observed in Boyes ranged 0.0–0.50, but was zero from 2011 through the end of the study in 2016. Conversely the proportion of males observed in Davison meadow complex ranged 0.148–1.0, but markedly declined after 2008. The proportion of females observed in Davison ranged 0.611–1.0, and from 2011 to 2016, females were sighted exclusively in Davison.

Available forage biomass—Biomass estimates calculated for both meadow complexes from 2005 to 2016 indicated that biomass in Davison ranged from 8,257 (± 2.94 SE) to 19,432 (± 4.97 SE) kg and averaged 14,325 (± 3.92 SE) kg. Forage biomass in Boyes meadow ranged from 10,058 (± 3.25 SE) to 19,307 (± 3.64 SE) kg and averaged 14,178 (±3.41 SE) kg. The forage biomass estimates at the meadow complex scale were divided by the respective population estimate for each meadow complex to report a per capita forage availability (Fig. 5). The total population estimated for Davison meadow from 2005 to 2016 ranged from 32 (± 1) to 51 (± 0) individuals while the population estimates in Boyes meadow ranged from 3 (± 0) to 10 (± 0). Boyes meadow had significantly more per capita forage biomass in every year between 2005 and 2016 with the exception of 2012.

Behaviors during foraging bouts— From 2009 to 2016, 547 focal observations were collected from adult females ($n = 329$), adult males in female groups ($n = 67$) and adult males in male-only groups ($n = 151$). From 117 focal observations collected in 2015 and 82 collected in 2016, Pearson's correlation coefficients were estimated between bite rates and the following: step length, turning angle variance, proportion of time with head up and estimated biomass in the sub-meadow where the focal elk was observed (Fig. 6). The correlation estimates indicated that proportion of time with the head up had the strongest association with bite rate relative to the other three behaviors.

One model was selected from each of the three different AIC analyses of the three response variables (Table 1). Although the model selection analyses indicated seven models for step length and three models for variance in turning angle had ΔAIC < 2.0, the models chosen for each had the smallest AIC value, the fewest number of parameters,

and most predictors in the model were statistically significant (Table 2). The additional predictors in all remaining models with ΔAIC < 2.0 had predictors that were statistically insignificant. Furthermore, competing models did not exhibit substantially greater Log-likelihood values than the selected models and were therefore not considered to be better fit models. The model selected for the response variable proportion of time with the head up had the smallest AIC that was clearly much smaller than any other model.

Step length was influenced by length of the focal observation and group size (Table 2). As group size increased, so did step length. The fixed factors accounted for 8.1 percent of the variation in the response variable (marginal r^2) and the fixed factors and random factor accounted for 9.6 percent of the variation in step length (conditional r^2).

The variance in turning angle depended on length of the focal observation and the interaction between group types and group size. This interaction indicated that the effect of larger group size on the variance in turning angle was more dramatic for males in male-only groups than for males or females in female groups (Fig. 7). As group size increased, males in male-only groups traveled in more direct paths more so than both males and females in female groups. It should also be noted that the range of group sizes of male-only groups were much narrower than males or females in female groups. The marginal and conditional r^2 values for this model were 4.1 and 4.8 percent, respectively.

The model selected to explain the proportion of time an elk had its head up suggested that length of the focal observation, forage biomass in the sub-meadow, group type and proportion of time spent within one body-length of a conspecific animal were influential (Table 2). Forage biomass was inversely related to time the head was up. There also was an interaction between group type and proportion of time spent within one

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body-length of a conspecific animal. The nature of the interaction was such that an increasing proportion of time spent within one body-length of a conspecific did not have as much of a positive effect on the proportion of time spent with the head up for females as it did for males in female groups and especially for males in male-only groups (Fig. 8). The variance in the response variable explained by the fixed factors (marginal r^2) and random factor (conditional r^2) for this model were 2.9 percent and 8.0 percent respectively.

IV. DISCUSSION

A novel finding in this study was that a fine-scale foraging process was coupled to sexual segregation. The process was that behavior during a foraging bout was affected by social factors, which drove differential space use between sexes. Little evidence was found to support the influence of forage biomass availability within the meadow complexes on the spatial distribution of females and males. Previous studies have shown that males will be confined to places with greater forage biomass to meet absolute metabolic requirements (Clutton-Brock et al. 1987, du Toit 2005, Shannon et al. 2006). In this study, Boyes meadows consistently exhibited greater per capita forage biomass than Davison meadows from 2005 to 2016 (Fig. 5). If forage availability had driven meadow use by males, then males should have been observed in high proportions in Boyes meadow earlier in the study since they would have been constrained to the area with higher forage biomass. Though direct measurements of forage intake were not collected, the greater per capita availability of forage in Boyes is likely not the cause for the shift in sexual segregation patterns throughout the study.

The shift in use of the two meadow complexes by male and female Roosevelt elk was observed over twenty years of observation within the Prairie Creek drainage. Early on in the study, when the population was high in abundance, males and females within meadow complexes tended to be segregated by group (Weckerly et al. 2004, Peterson and Weckerly 2016, *in revision*) although individuals were considered sexually aggregated in meadow complexes (Fig. 3). Later in the study when population abundance was lower and females no longer occupied Boyes meadow complex, male and female elk were randomly associated both within groups and across meadow complexes. Though the

sexes were randomly associated, males frequented Boyes meadow complex more often after females became scarce and then disappeared from the area. Since the availability of forage biomass was not influential in this shift in space use, this study instead suggests that different foraging behaviors between males and females were likely driving the distributional change by males.

Intersexual differences in foraging behavior are related to either forage search, handling, and movement patterns or bite rate, ingestion, and the time allotted to feeding (Underwood 1983). Models selected for step length and variance of turning angle associated the movement patterns of an animal to size of the elk group. As group size increases, animals will travel in more direct paths and move farther distances (Table 2). When there are more elk in a group, each animal travels farther to seek out forage (Mårell et al. 2002, Shrader et al. 2007). Males in male-only groups are especially influenced by increasing group sizes and direct movement in straighter paths much more-so than females or males in female groups. At small group sizes, males might travel in more tortuous paths to increase forage efficiency in order to meet the greater absolute metabolic demands than females (de Knegt et al. 2007). When group size increases, so too does the potential for rival males to be in close proximity and engage in aggressive bouts, thereby decreasing forage ingestion. Therefore in large, male-only groups (5–10 individuals in this study), males display more directed movement to mitigate interactions with potential rivals so that more time can be devoted to foraging (Weckerly et al. 2001, Vander Wal et al. 2012).

The bite rate correlation analyses suggested that the proportion of time spent with the head up has the greatest impact on the number of bites elk take. Specifically, the

greater proportion of time spent with the head up, the less time will be allotted to feeding

and consequently, fewer bites will be taken during the bout. The model selected for

predicting the proportion of time an animal with the head up indicates that vigilance in

males will increase with the time spent within one body-length of another animal (Fig. 8).

Furthermore, proximity of conspecifics influenced males in male-only groups more than

males in female groups, suggesting that in winter, males are the more vigilant sex and are

probably more vigilant towards other males. The lack of association between proximity

and vigilance for females is likely because vigilance in females is directed outward

towards detecting predators (Lung and Childress 2006, Li and Jiang 2008, Li et al. 2012).

Therefore, males in male-only groups will be the most influenced by conspecific

proximity since all conspecifics might be potential competitors.

Sexual segregation observed in this population of elk was affected by the

disparate influences from social factors between males and females. Through the early

years of the study, abundance was high so there was a higher abundance of adult males in

the population and subsequently, male-only group sizes were larger in size. These larger

male-only groups likely drove sexual segregation by group (Peterson and Weckerly 2015,

in revision) even though the sexes were aggregated in the two meadow complexes. Rates

of male-male aggression increase concomitantly with male-only group sizes (Weckerly

2001, Weckerly et al. 2001) and when large groups of males enter female groups, females

might avoid interactions with males, which forces them closer together and might

increase female-female aggression between females of different social rank (Weckerly et

al. 2004). Females are likely to avoid large male groups, so at high abundance—which

has been shown to be correlated with larger male group sizes—sexual segregation by

group is likely to occur (Peterson and Weckerly 2016, *in revision*). At low abundance, when more per capita space is available for use, males can expand their spatial patterns to utilize separate spaces from females (McCullough 1999). Greater separation between females and males might also reduce rates of aggression for both sexes (Weckerly 1999, Weckerly et al. 2001, Weckerly et al. 2004) and influences on forage ingestion from large group sizes and close proximity of animals could thus be mitigated (Weckerly et al. 2001, Ruckstuhl et al. 2003, Fortin et al. 2004).

Since not all males and females could be uniquely identified, the influence of social hierarchies on foraging behaviors could not be assessed (Weckerly 1999, 2001). It is possible that subordinate animals might be influenced to move farther or be more vigilant to dominant animals while foraging, however, forage intake is not always greater for dominant animals since they must devote time and energy to maintain their high social status (Barroso et al. 2000, Jørgensen et al. 2007). Furthermore, disturbances from anthropogenic activities (i.e., domestic dog barking, unusual noises) that may have stimulated vigilance and movement were not evaluated. However, in areas of high human presence, rates of vigilance have been shown to remain constant regardless of group size, suggesting that populations habituated to human presence do not perceive humans as predator threats (Manor and Saltz 2003).

Previous studies have shown that different responses between the sexes to non-human predator threats might be a fine-scale mechanism for influencing sexual segregation (Bleich et al. 1997, Bleich 1999). It was assumed that such factors were likely not influential in this area since vulnerability to predators is probably lower in meadows with flat terrain than in the surrounding forests. In densely vegetated forests

with broken terrain mountain lions are more likely to ambush, subdue, and kill a much larger prey such as elk (Atwood et al. 2009, Underwood 1982). The inclusion of social rank, types of vigilance or areas of increased risk from predators in the mixed-effect regression models probably would have strengthened the marginal r^2 values for each of the three response variables, though it is not likely that these variables would have altered findings. The foraging patterns of female and male elk in my study were similar to patterns described in other populations of size-dimorphic ungulates (Ruckstuhl 1998, Yearsley and Barbería 2005, Shannon et al. 2006).

Many behavioral studies have exploring differences between the sexes have failed to measure changes in behavior of one sex dependent on the group type (Pérez-Barbería et al. 2005, Ruckstuhl 1998, Ruckstuhl and Kokko 2002). This study presented the opportunity to compare behaviors when a male is in a male-only group to when a male is in a female group. When in a female group, movement patterns of males were similar to females, increasing in distance and turning angle variance with group size, though the males in female groups were more vigilant than females. Males in male-only groups were more influenced by increasing group size and increasing proximity of conspecifics than males in female groups. We can therefore conclude, that differences exist not only between males and females, but between males in female groups and males in male-only groups as well. Individual males may alternate between male-only groups or female groups (to increase intra-sexual competition or increase breeding opportunities, respectively) to benefit reproductive success (Isvaran 2005, Pelletier et al. 2006).The alternation between group types for males might therefore explain why variation exists in male behaviors conditional to the group type.

This study revealed a fine-scaled mechanism that could be coupled to large scale sexual segregation and provides a more accurate understanding of the social factors that actuate differences in foraging behavior between the sexes as well as between female and male-only groups. The dissonant foraging behaviors could then also explain sexual segregation at the level of the group early in the study since population abundance then was high and there was little available space to use, compelling males and females to aggregate in the same meadows but use different parts of the same meadows (Weckerly et al. 2004). Though intersexual differences in behavioral processes may not exclusively explain sexual segregation (Bowyer and Kie 2004, Michelena et al. 2008, Yearsley and Barbería 2005), we have presented a fine-scale mechanism for explaining the shift in the broad-scale spatial patterns of a large ungulate population. Understanding the processes functioning at each scale of a phenomenon has become increasingly vital to knowing what mechanisms drive ungulate population dynamics and spatial distribution within an ecosystem (Levin 1992, Bowyer and Kie 2006).

Table 1. Summary of model selection analyses of 23 mixed-effect regression models to predict the influence of three response variables collected within foraging bouts of Roosevelt elk (*Cervus elaphus roosevelti*): step length, variance in turning angle, and proportion of time the focal elk spent with the head up (out of the feeding position). These models were estimated using combinations of the observed variables: sex, group type (Type) [female in female group, male in female group, or male in male-only group], group size (Size), available forage biomass (kg) estimated in sub-meadows focal animals were observed (Biomass), and the proportion of time the focal animal spent within one body-length of another animal (Proximity). The length of the focal sample in minutes (Length) was a confounding variable included in each model and each day of data collection was considered as the random factor for each model. Interactions in the models are denoted with an asterisk (*). Delta (Δ) denotes the difference in AIC between a model and the model with the smallest AIC, LL was the log-likelihood, nPar was the number of parameters estimated in each model with nPar - 1 for the binomial regression.

Fixed predictors	nPar	Step length		Var. turning angle		Prop. time head up	
		Δ	LL	Δ	LL	Δ	LL
Intercept	3	38.95	-1601.3	9.69	49.26	2887	-24065
Length	4	1.72	-1581.7	6.06	52.07	1883	-23212
Size + Length	5	0.80	-1580.2	7.95	52.13	1170	-23204
Sex + Length	5	3.68	-1581.7	7.98	52.11	933	-23086
Type + Length	6	2.39	-1580.0	5.50	54.35	727	-22982
Proximity + Length	5	0.67	-1580.2	7.61	52.30	909	-23074
Biomass + Length	5	3.64	-1581.7	7.06	52.57	1084	-23161
Sex + Size + Length	6	**0.00**	**-1578.8**	9.53	52.34	857	-23047
Sex * Size + Length	7	2.00	-1578.8	7.35	54.43	565	-22900
Type + Size + Length	7	1.77	-1578.7	1.94	57.13	727	-22981
Type * Size + Length	9	4.84	-1578.3	**0.00**	**60.10**	466	-22848
Sex + Proximity + Length	6	2.32	-1580.0	9.59	52.31	536	-22886
Sex * Proximity + Length	7	4.32	-1580.0	11.5	52.33	222	-22728
Type + Proximity + Length	7	1.50	-1578.6	7.27	54.47	361	-22798
Type * Proximity + Length	9	3.87	-1577.8	10.91	54.65	57	-22644
Sex + Size + Biomass + Length	7	1.16	-1578.4	10.68	52.76	766	-23000
Sex * Size + Biomass + Length	8	3.16	-1578.4	8.57	54.82	494	-22863

Table 1, Continued: Summary of model selection analyses

Type + Size + Biomass + Length	8	2.95	-1578.3	3.23	57.49	647	-22940
Type * Size + Biomass + Length	10	5.99	-1577.8	0.94	60.63	405	-22817
Sex + Proximity + Biomass + Length	7	4.19	-1580.0	10.33	52.93	490	-22862
Sex * Proximity + Biomass + Length	8	6.17	-1579.9	12.32	52.94	196	-22714
Type + Proximity + Biomass + Length	8	3.13	-1578.4	7.31	55.45	280	-22756
Type * Proximity + Biomass + Length	10	5.49	-1577.8	10.88	55.66	**0.00**	**-22614**

Table 2. Parameter estimates ($\underline{B_i}$) and standard errors (*SE*) from selected models in AIC analyses (each with $N = 547$) for predicting step length, variance in turning angle, and proportion of time the focal elk (*Cervus elaphus roosevelti*) spent with the head up (out of the feeding position). The length of the focal sample (Length) was a confounding variable in every model. Size refers to the size of the group the focal elk was in, sex indicates male or female, and type refers to the group type and consists of three categories: female in female group, male in female group, or male in male-only group. Proximity refers to the proportion of time the focal elk spent within one body-length of another animal. Biomass was the estimated biomass of available forage for the sub-meadow where the focal elk was observed. Interaction parameters are indicated with an asterisk (*). Reference categories were female for sex and female in female groups for type.

|	Step length		Var. turning angle		Prop. Time head up	
Fixed predictors	$\underline{B_i}$	*SE*	$\underline{B_i}$	*SE*	$\underline{B_i}$	*SE*
Intercept	**4.72**	**0.299**	**0.433**	**0.015**	**-2.03**	**0.09**
Length	**-1.18**	**0.189**	**-0.023**	**0.009**	**-0.270**	**0.006**
Size	**0.584**	**0.244**	0.029	0.016	-----	-----
Sex (male)	0.833	0.497	-----	-----	-----	-----
Biomass	-----	-----	-----	-----	**-0.055**	**0.007**
Proximity	-----	-----	-----	-----	**0.044**	**0.007**
Type (male in female group)	-----	-----	-0.051	0.034	**0.394**	**0.018**
Type (male in male-only group)	-----	-----	**0.714**	**0.276**	**0.144**	**0.015**
Type (male in female group) * Size	-----	-----	0.046	0.052	-----	-----
Type (male in male-only group) * Size	-----	-----	**0.505**	**0.219**	-----	-----
Type (male in female group) * Proximity	-----	-----	-----	-----	**0.097**	**0.020**
Type (male in male-only group) * Proximity	-----	-----	-----	-----	**0.228**	**0.013**
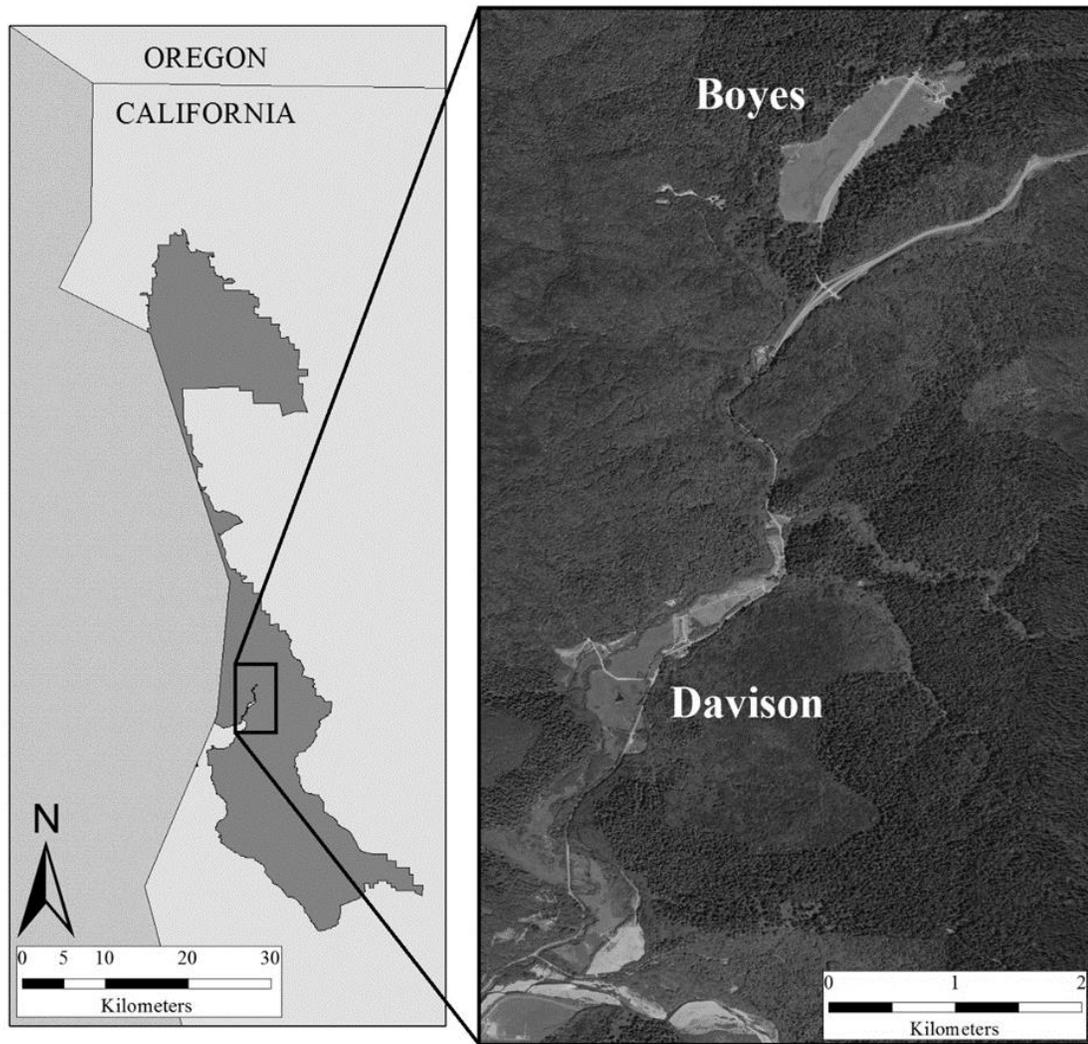
Figure 1. Map of study area
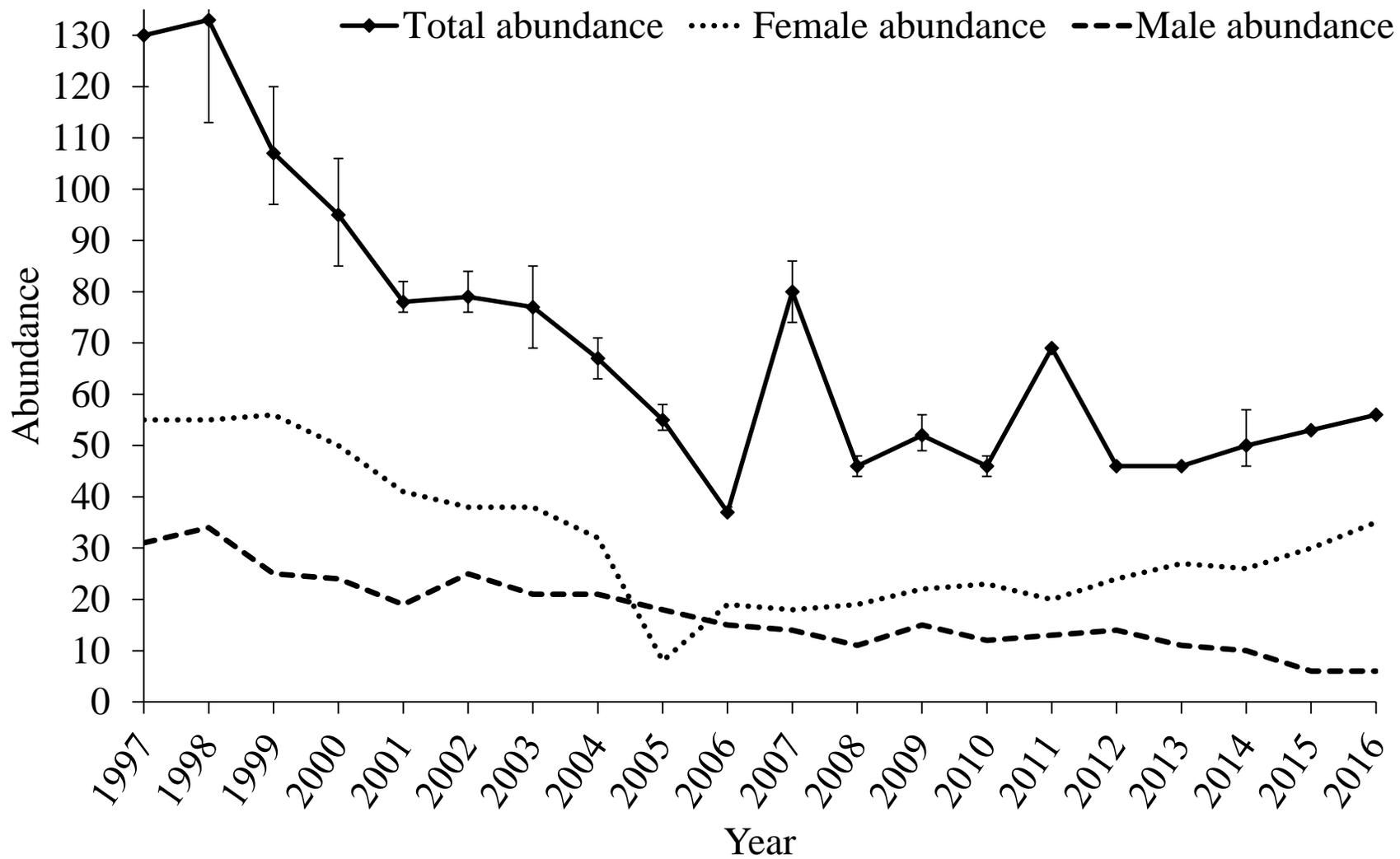
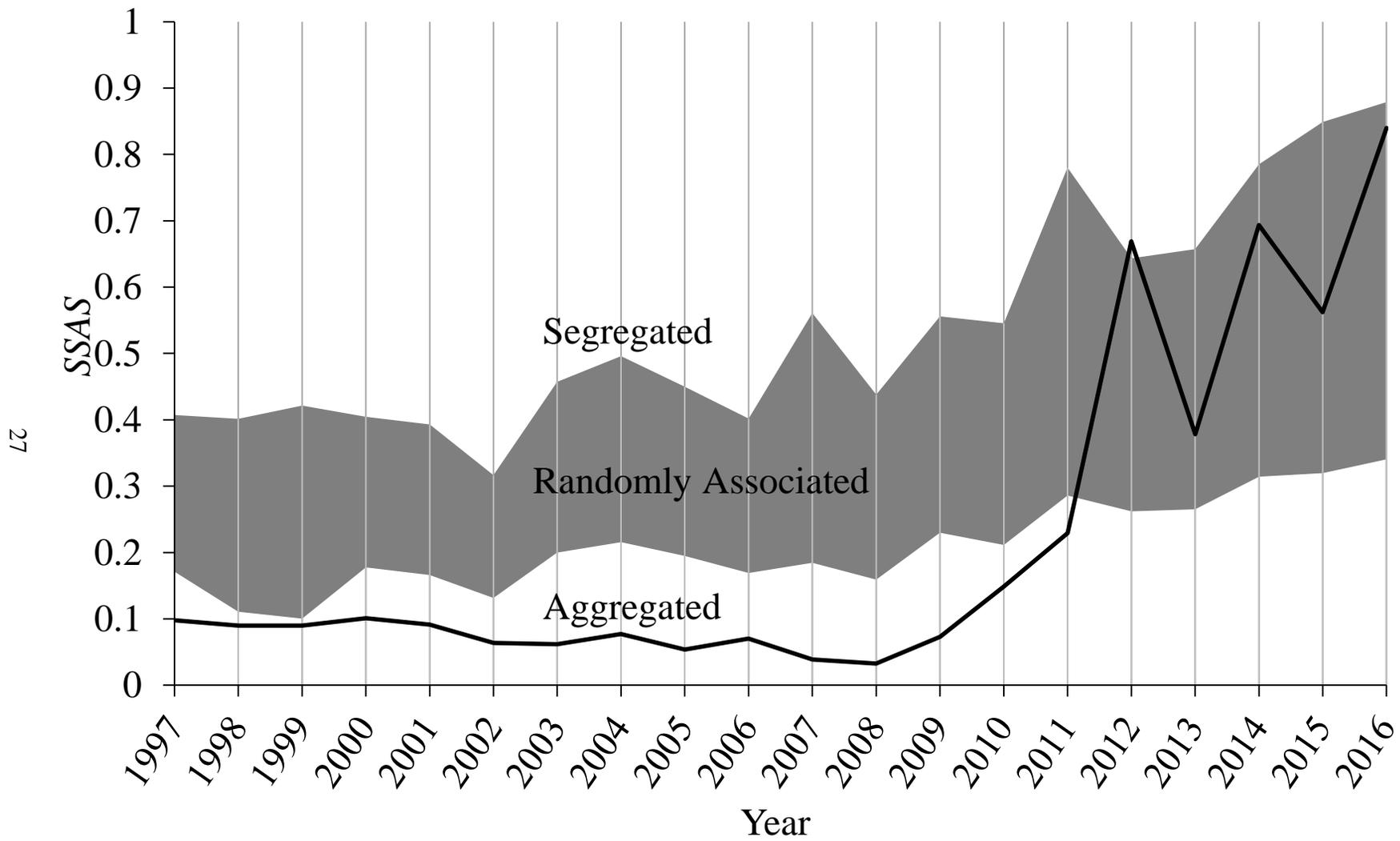**Figure 2.** Population abundance across twenty years

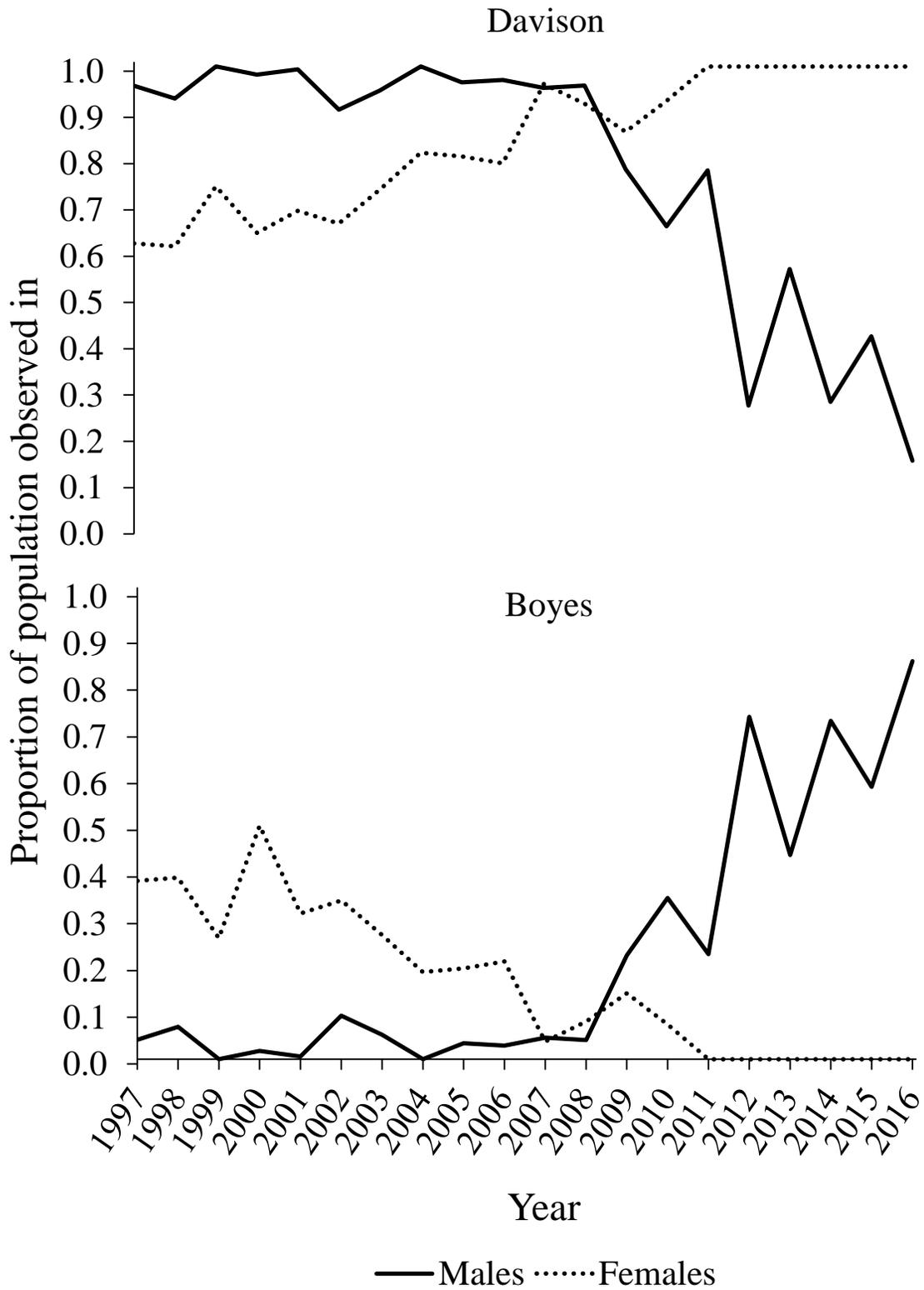**Figure 3.** Sexual Segregation and aggregation statistic

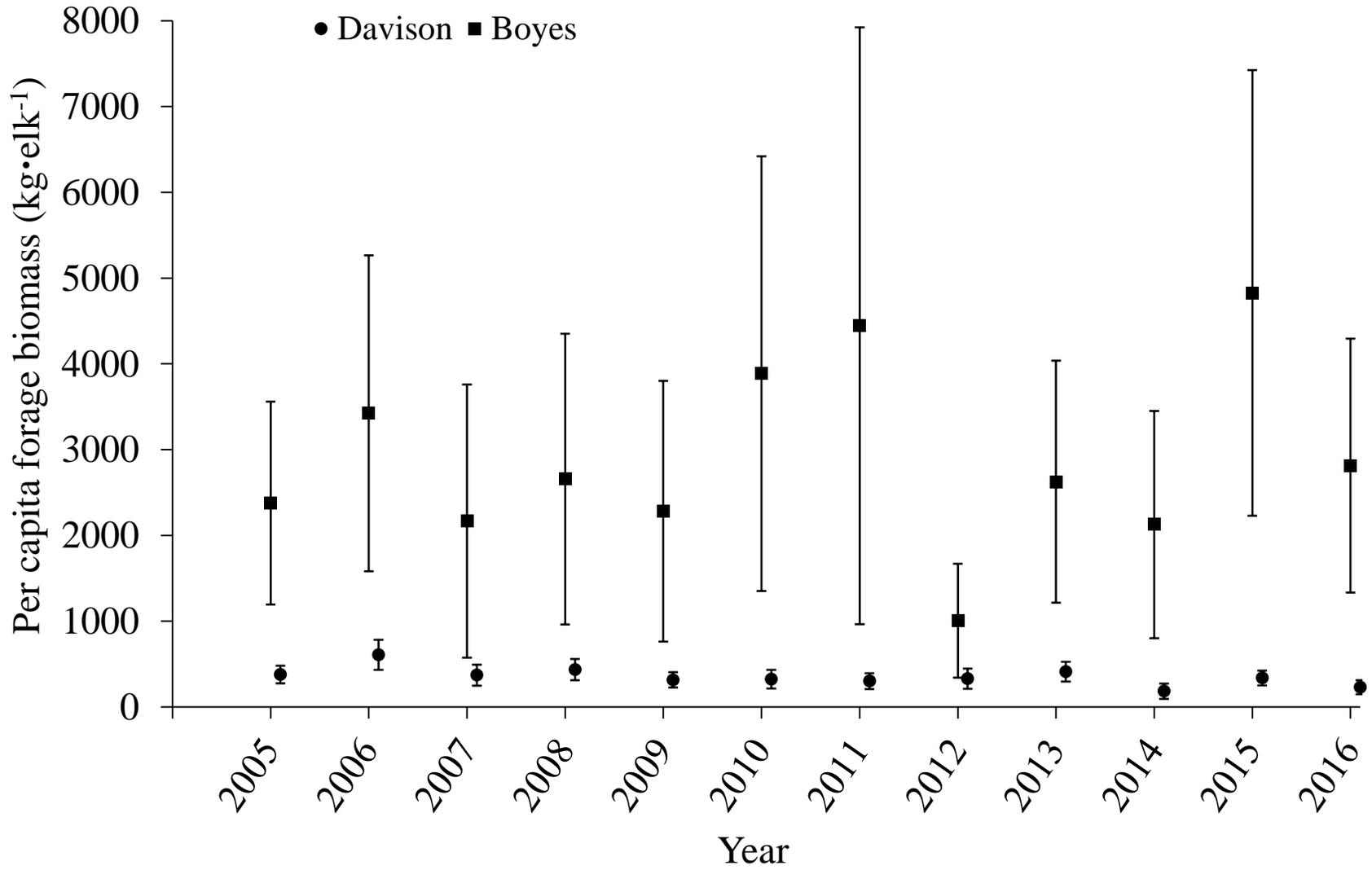**Figure 4.** Proportion of males and females sighted in each meadow
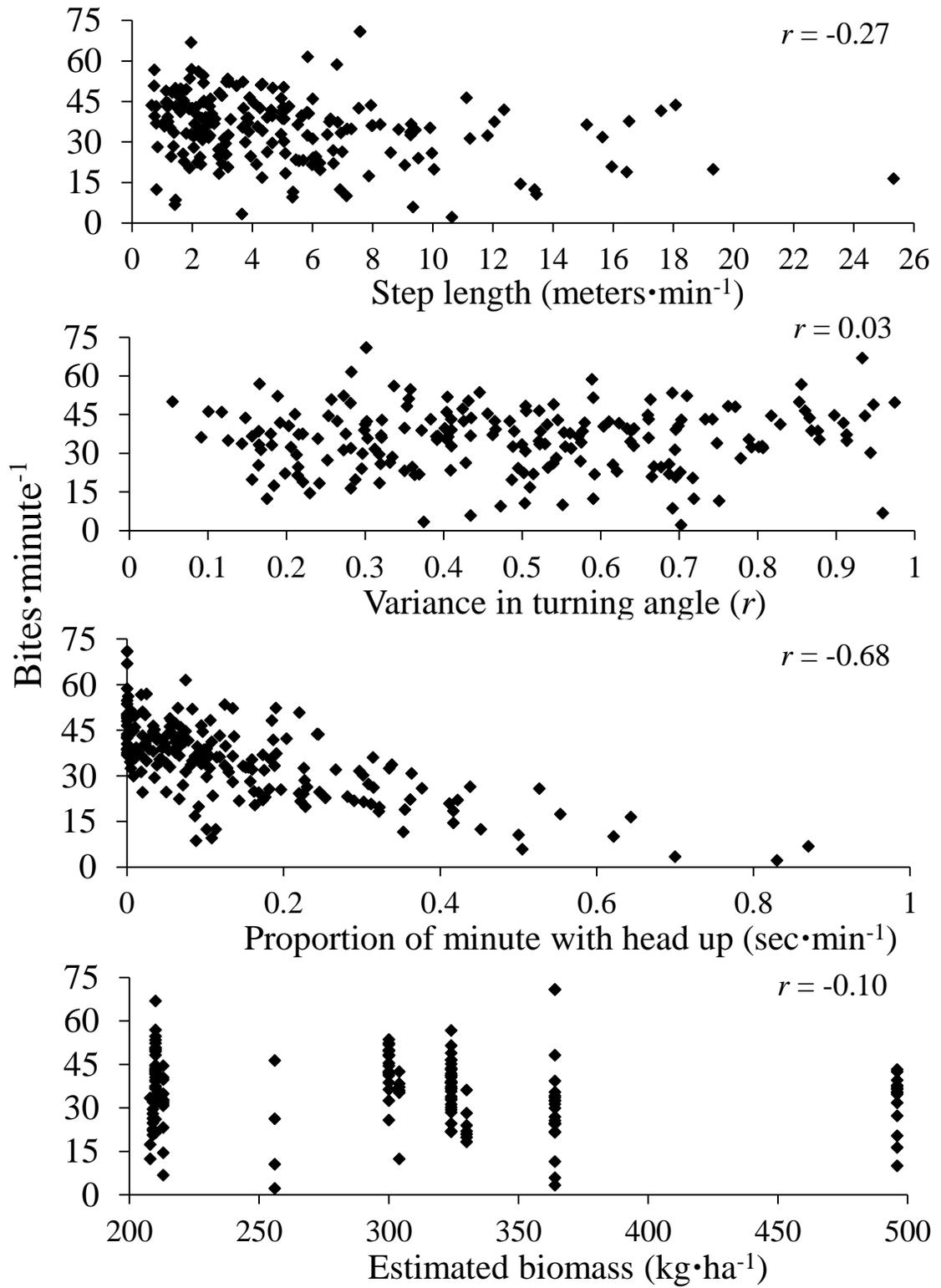
Figure 5. Per capita forage biomass for each meadow
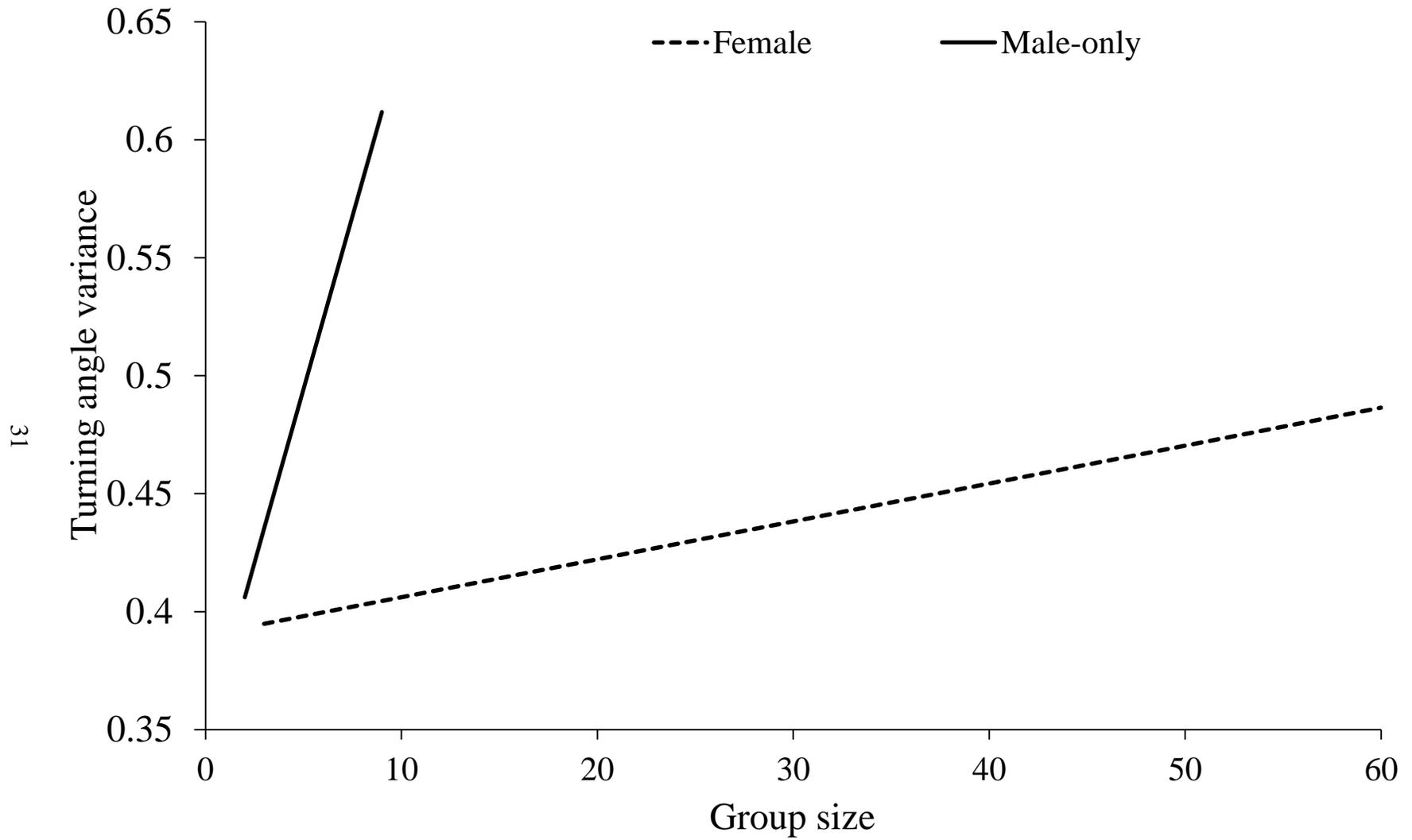
Figure 6. Bite rate correlations

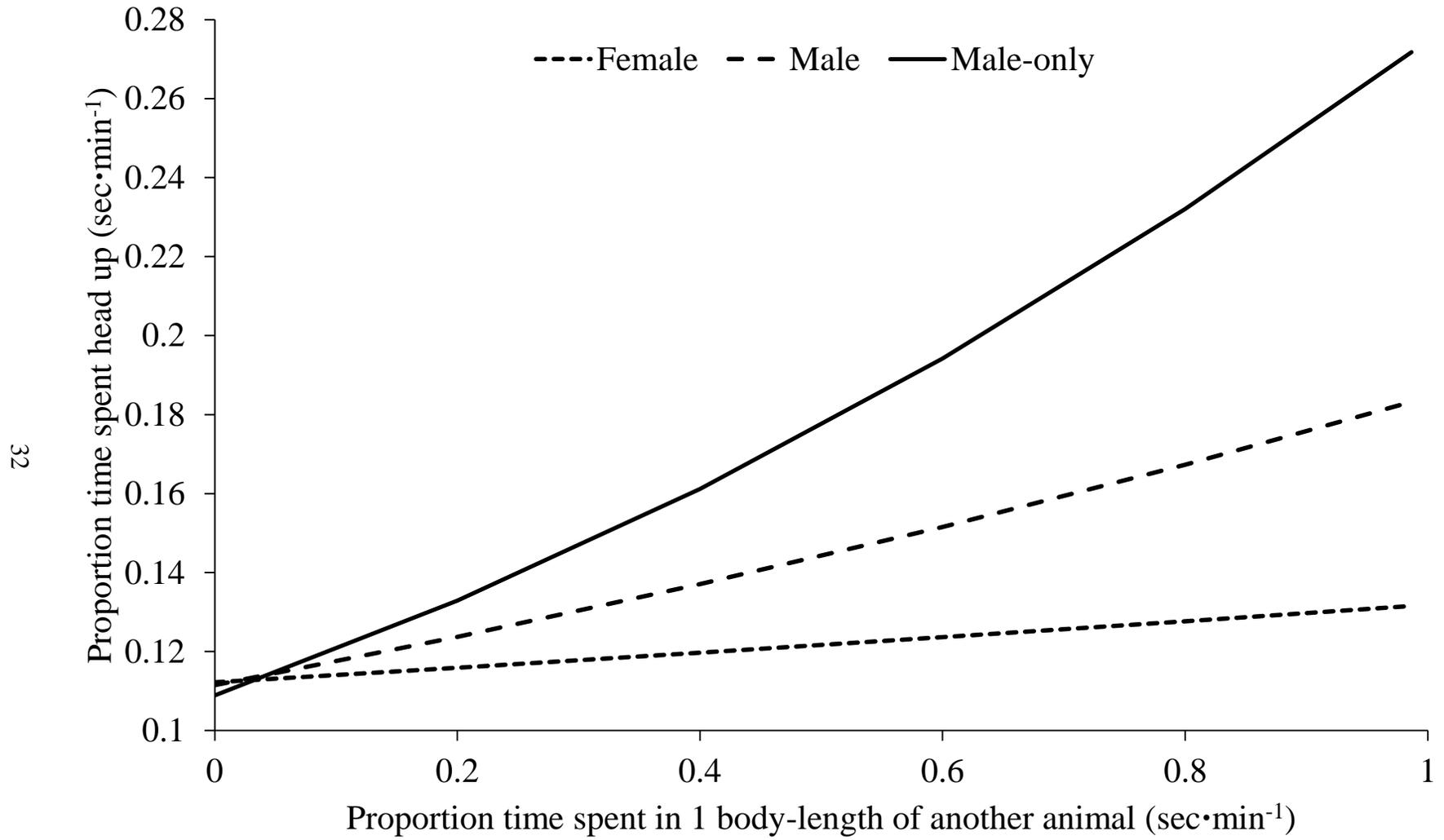**Figure 7.** Predicted turning angle variance with selected model

Figure 8. Predicted proportion of time head up with selected model

APPENDIX SECTION

Figure 1. The study area in the Prairie Creek drainage of Redwood National and State Parks, on the ocean coast in Humboldt County, California, USA (park boundary shown on the left). The image on the right is an aerial photograph showing the two meadow complexes—Boyes (70 ha) to the north and Davison (51 ha) to the south—interspersed in old and second-growth redwood-conifer forests.

Figure 2. The population abundance of Roosevelt elk from 1997 to 2016 in the Prairie Creek drainage of Redwood National and State Parks. The total population (adult males and females, sub-adults, and juveniles) abundance estimate is represented by the solid line. Abundance was estimated from population surveys using Bowden's estimator unless female group sizes were invariant across observations and all encountered males were marked, in which case, the highest count was used for abundance. The abundance of adult females observed in the population across the 20 years is represented by the dotted line and adult male abundance observed is represented by the dashed line.

Figure 3. The sexual segregation and aggregation statistic or SSAS (black line) from 1997 to 2016 of male and female Roosevelt elk in Prairie Creek drainage of Redwood National and State Parks, California, USA. The gray 95% confidence band represents SSAS values that would indicate that males and females were randomly associated between the two meadows. A SSAS above the gray band indicates males and females were observed in separate meadows, and SSAS values below the gray band indicates that males and females were spatially aggregated.

Figure 4. Line chart showing the proportion of male and female (also included juveniles and sub-adult male) elk sighted in Boyes and Davison meadow complex during surveys of Roosevelt elk (*Cervus elaphus roosevelti*) in the Prairie Creek drainage of Redwood National and State Parks, California, USA, 1997–2016.

Figure 5. Plot showing the estimated total biomass available per individual elk each year from 2005 to 2016 in two different meadow complexes (Davison and Boyes) in the Prairie Creek drainage of the Redwood National and State Parks, CA, USA. The error bars represent 95% confidence intervals for each estimate of per capita forage biomass.

Figure 6. Scatterplots showing associations between four variables and bite rates of Roosevelt elk (*Cervus elaphus roosevelti*) in the Prairie Creek drainage of the Redwood National and State Parks, California, USA, 2015–2016. Variables were step length (distance traveled per minute), variance in turning angle during a foraging bout, proportion of time spent with the head up (out of the feeding position), and the amount of available forage biomass estimated for each sub-meadow regions the elk were observed in.

Figure 7. Plot showing the predicted turning angle variance for the selected model in relation to group size. Group types displayed are male-only and female. Males in female groups were not statistically different from females in female groups and were therefore omitted from the graph. This relationship was predicted with the length of the focal sample held constant at the mean focal sample length. Displayed are the range of group sizes across all focal samples ($N = 547$). Female group size ranged 3–60 individuals and male-only groups ranged 2–9 individuals.

Figure 8. Plot showing the predicted proportion of time spend with the head up for the selected model in relation to group type and proportion of time spent in 1 body-length of another elk. . Predicted values are back transformed from the logit scale. This relationship is predicted using values back transformed from the logit scale and both the average length of the focal samples and estimated biomass were held constant. The data represents the range of proportions the focal animals spent within one body-length of another elk observed across all focal samples ($N = 547$).

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