



Sexual segregation of forage patch use: Support for the social-factors and predation hypotheses



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ABSTRACT

Nearly all species of sexually dimorphic ungulates sexually segregate. Several hypotheses have been proposed to explain this phenomenon, including the social-factors hypothesis (SFH) and the predation hypothesis (PH). Interestingly, previous studies have accepted and rejected each hypothesis within and across species but few studies have simultaneously tested both hypotheses in the same population. In August 2011 and 2012 using 7680 photographs taken with camera traps in standardized forage patches, we tested two predictions of the SFH: 1) foraging efficiency of both sexes would decrease when foraging rate in mixed-sex groups relative to single-sex groups, and 2) activity patterns (i.e., the pattern of temporal use of forage patches on a diel scale) of the sexes would decrease in temporal overlap at the forage patch level (i.e., social segregation) compared to the overall temporal overlap of activity patterns of the population. Also, we tested two predictions of the +PH: 1) the relationship between feeding rates of each sex, and 2) temporal activity overlap would change with changing risk level of forage patches as a result of differing risk perception between sexes. In support of the SFH for temporal segregation, when in mixed-sex groups, mature males and all females decreased feeding rate 30% and 10%, respectively; further, the sexes had similar activity patterns overall (94–95% overlap), though temporal overlap was lower in individual forage patches (68–74% overlap). In multi-male mixed sex groups, at least one male exhibited aggressive posture toward females during all foraging bouts suggesting intersex aggression was the cause of the observed decrease in foraging rates. In support of the PH, the sexes adjusted feeding rate differently in response to changing risk level of a forage patch, encouraging spatial segregation; however, the PH was not supported for temporal segregation because temporal activity pattern overlap did not vary as a function of predation risk. Coupling our results with previous reports indicates that the SFH is supported for only temporal segregation of forage patch use, and the PH may only be supported for spatial segregation in forage patch use. Thus, both social factors and predation risk may interact to encourage sexual segregation.

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1. Introduction

Sexual segregation occurs in most sexually dimorphic ungulates and in cervids in particular (Kie and Bowyer, 1999; Bowyer, 2004; Main et al., 1996). Sexual segregation is a phenomenon where sexes differentially use resources outside of the mating season (Bowyer, 1984; McCullough et al., 1989; Bleich et al., 1997; Kie and Bowyer,

1999; Barboza and Bowyer, 2000) and segregation can occur in space where the sexes use different areas altogether (i.e., spatial segregation) or in time where the sexes use the same space at different times (i.e., temporal segregation or social segregation; Ruckstuhl, 2007). Though mechanisms explaining sexual segregation are unclear, several hypotheses have been proposed. Two commonly supported hypotheses are the social-factors hypothesis and the predation hypothesis, but it is unclear whether either hypothesis necessitates spatial and temporal segregation of forage patch use (Stewart et al., 2011).

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The social-factors hypothesis postulates that social interactions between the sexes can drive sexual segregation. However, the social-factors hypothesis cannot cause consistent spatial segregation (Bowyer, 2004; Stewart et al., 2011). For example, sexual segregation may be the result of aggression between sexes (Weckerly, 2001; Weckerly et al., 2001) but the mechanisms proposed require animals to interact in space so the sexes therefore cannot fully spatially segregate if social factors do indeed drive segregation. This hypothesis could explain temporal segregation in the use of the same space if social interactions encourage the sexes to avoid one another. Aggressive behavior in particular should result in mutual avoidance of the sexes to forage together in a patch. Indeed, fitness consequences could be mutual following aggressive interactions between the sexes if defending a resource and avoiding a defender both detract from other activities such as scanning for predators and foraging. In that case, the associated decreased fitness in both sexes foraging together should be selected against over time yielding temporal or social segregation (Weckerly, 2001; Weckerly et al., 2001). Contrastingly, alternative social factors such as intersexual affinity and social preferences may be the cause of social segregation, but quantifying related factors are often difficult (Michelená et al., 2004; Pérez-Barbería et al., 2005). Few studies have examined whether the sexes foraging together actually causes a fitness consequence. Feeding efficiency may provide a good metric of relative fitness but it is often confounded by forage quality, availability, and handling time (Stewart et al., 2011). Thus, an experiment evaluating the extent to which social-factors can have fitness consequences for both sexes while also accounting for confounding factors such as patch quality is needed.

The predation hypothesis predicts that predation risk encourages sexual segregation because of differing risk associated with sexual dimorphism (Bleich et al., 1997; Kie and Bowyer, 1999; Bowyer, 2004). Unlike the social-factors hypothesis, the predation hypothesis could cause temporal or spatial segregation because the larger male body size allows them to forage in riskier patches and at riskier times than smaller females (Bowyer, 2004). There have been many studies that support the predation hypothesis as a mechanistic explanation of sexual segregation in white-tailed deer (*Odocoileus virginianus*; hereafter deer); only a few studies demonstrate lack of support, but many of those may have been confounded by interactions between the quality of escape cover and forage patch quality (Bowyer, 2004; Stewart et al., 2011). Thus, an experiment that holds either escape cover or forage patch quality constant is needed.

Explicit tests of multiple hypotheses in the same population may help clarify support for some hypotheses over others (Main et al., 1996). Moreover, an experiment that accounts for confounding variables such as forage patch quality and dimorphism is needed. Also, examination of spatial and temporal segregation simultaneously is rare but necessary to fully understand mechanisms of sexual segregation. We addressed these issues by testing two predictions of the social-factors hypothesis and two predictions of the predation hypothesis using camera trap data of female and yearling and adult male deer collected at standardized forage patches. The first prediction of the social-factors hypothesis (Prediction 1) was that social interactions between males and females would negatively affect feeding rates of both sexes as opposed to single sex groups when interacting in a forage patch. The second prediction of the social-factors hypothesis (Prediction 2) was that male and female activity patterns (i.e., the pattern of temporal use of forage patches on a diel scale) would differ to a greater extent at the forage patch level than the overall activity curves derived from pooled data from all patches. Prediction 1 is an explicit test of the mechanism proposed by the social-factors hypothesis that a decrease in feeding rate by each sex resulting from social interactions would mutually encourage the sexes to temporally segregate the use of forage patches to

maintain feeding efficiency. Prediction 2 is a behavioral test of the social-factors hypothesis to determine if interactions manifest in temporal segregation in use of a forage patch. Female and male activity patterns temporally overlapping less at the forage patch level than across all sites would suggest an avoidance of simultaneous use of the same patch (i.e., temporal segregation). For the predation hypothesis, the two predictions were that the relationship of feeding rates (Prediction 3) and temporal overlap between activity patterns (Prediction 4) should vary as a function of predation risk because of differential vulnerability of the dimorphic sexes to predation. Prediction 3 is a test of the proposed mechanism of the predation hypothesis whereby increased predation risk decreases foraging efficiency of females disproportionately to that of the larger males. Prediction 4 is a test of the behavioral manifestation of the mechanism in that differential predation risk perception between the sexes should yield temporal segregation of a forage patch because larger less-vulnerable males are able to forage at riskier times than females.

2. Methods

2.1. Site description

We conducted our study at Fort Bragg Military Installation (Fort Bragg), located (35°7' N, 79° 9' W) within the Sandhills physiographic region in the lower coastal plain of North Carolina, USA. Longleaf pine (*Pinus palustris*) forests with wiregrass (*Aristida beyrichiana*) understories were the dominant vegetation type (Lashley et al., 2014a). Forests were managed with growing-season prescribed fire on a 3-year fire-return interval (Lashley et al., 2014a). Potential predators of deer included coyotes (*Canis latrans*; Chitwood et al., 2014), bobcats (*Lynx rufus*; Chitwood et al., 2015a), and humans (Chitwood et al., 2015b). During the years of this study, deer were hunted in accordance with North Carolina state hunting regulations from September to January each year except that hunters were restricted to harvest of only males across much of the area.

2.2. Data collection

In August of 2011 and 2012, we established 100 standardized forage patches with ~20 kg of corn (*Zea mays*) and monitored each with a single camera trap (i.e., 50 sites established August 1 and 50 sites established August 8) and cameras were able to detect researchers consistently out to a maximum distance of 21 m with the maximum width of 8 m (see Lashley et al., 2014b for study design details). Each forage patch was established for 14 days to allow deer to adopt the new forage patch into their daily foraging activity and then we refreshed the corn and activated cameras to take pictures for 14 days and as frequently as every 3 min (Jacobson et al., 1997). After the 14 days of camera trapping, we collected all pictures and tallied the group size, sex, age of the oldest male, group type (mixed- or single-sex), group feeding rate by sex, time and date of the picture, and distance of the forage patch to escape cover. Distance to escape cover is known to affect the perception of risk (Crowell et al., 2016) and should change in relative importance to animals with differing vulnerability to predators (Camp et al., 2012). We considered a deer to be in a feeding posture if its head was below its stomach line and appeared to be actually feeding or approaching the food source (i.e., feeding; Lashley et al., 2014b). We determined sex based on the presence or absence of antlers; if the head was not visible the picture was discarded. Also, we discarded pictures containing a spotted fawn and other taxa to reduce their influence on individual deer feeding rates (Lashley et al., 2014b). We discarded pictures of single deer to analyze the effects of forag-

ing in mixed- versus single-sex groups on individual feeding rates of males and females because we were interested in conspecific interactions. However, photographs of single deer were used to generate activity curves to avoid biases associated with excluding solitary individuals (Monteith et al., 2007). We classified males into one of two age classes, yearling (<2yr) and adult (\geq 2yr), based on the number of antler points. We derived this classification from 10 years of hunter harvest data at Fort Bragg, whereby \sim 90% of yearling males had \leq 4 antler points (3.18 ± 0.05 antler points [mean;SE], $n = 1014$) and 90% of mature males had \geq 5 antler points (7.07 ± 0.04 antler points [mean;SE], $n = 1266$). Based on hunter harvest data, the majority of inaccuracy in this method at Fort Bragg was associated with broken antlers. Therefore, we discarded any pictures where antler points could not be tallied or antlers were broken.

2.3. Data analysis

To test Prediction 1 (that feeding rate would be lower when sexes foraged together), we used linear mixed models in program R (R Development Core Team, 2011) to examine the effects of group type on feeding rate of each sex. Feeding rate was the response variable and group type was the explanatory variable. Based on our criteria, four group types were possible: 1) Single-sex female, 2) Single-sex male, 3) Mixed-sex with adult male, and 4) Mixed-sex with yearling male. We compared feeding rates of females when feeding with a mature male and when feeding with a yearling male to female feeding rates when feeding in single sex groups. Also, we compared feeding rates of mature males foraging in mixed-sex groups to males foraging in single-sex groups. Group size was reported previously as the most important variable affecting white-tailed deer feeding rate (Lashley et al., 2014b), so we controlled for group size in the model by including group size as a random effect. We assumed that forage patches were independent because uniquely marked males and females were never observed in multiple forage patches.

To test prediction 2 (that male and female activity patterns would differ to a greater extent at the forage patch level than the overall activity curves derived from pooled data from all patches), we used a temporal overlap analysis in the Overlap Package within program R. Specifically, we fit kernel density functions to camera trap pictures of male and female deer (Ridout and Linkie, 2009). First, to avoid biases associated with small sample sizes, we selected only camera trap locations that contained \geq 100 detections of males and \geq 100 detections of females during 2011 which was determined to produce robust activity curves (Lashley unpublished data) and repeated the selection of sites for 2012. This yielded fourteen camera trap locations in 2011 and 17 locations in 2012 (5 camera trap locations common to both years) for which we estimated the coefficient of overlap, a quantitative measure of temporal overlap ranging from 0 to 1, with 1 representing identical activity pattern curves of males and females. The forage patch was the experimental unit for this analysis producing one unique coefficient of overlap value per forage patch per year. Further, we calculated the overall coefficient of overlap based on the pooled activity pattern for males and females producing one unique coefficient of overlap value in 2011 and one in 2012 from all one hundred forage patches. This allowed us to compare the average coefficient of overlap at the forage patch level to the overall coefficient of overlap from all camera locations. A lower coefficient of overlap at the forage patch level compared to the coefficient of overlap from all camera locations would indicate temporal segregation of forage patch use to a greater degree than expected by the population-level temporal segregation.

To test Prediction 3 (that the relationship in feeding rates between the sexes changes as a function of predation risk), we

modeled the difference in male and female feeding rate (i.e., male feeding rate – female feeding rate) at a forage patch as a function of distance to escape cover, which served as a proxy for predation risk. The forage patch served as the experimental unit, the difference in feeding rate was the response variable, and the distance of the patch to escape cover was the explanatory variable. In this study area, because of the unique land management practices, the majority of high quality cover is relegated to drainages where moisture prevents fire from consuming understory plants, and deer heavily select those areas for escape cover (Lashley et al., 2014a, 2015a,b). If the relationship between feeding rates is altered by distance to escape cover, that would indicate the sexes are perceiving predation risk differently.

To test Prediction 4 (that temporal overlap between activity patterns change as a function of predation risk), we modeled the coefficient of overlap of each forage patch to determine if temporal segregation varies as a function of distance to escape cover. The forage patch served as the experimental unit, the generated coefficient of overlap was the response variable, and the distance of the patch to escape cover was the explanatory variable.

3. Results

We collected 40,540 photos of deer that were used to generate activity curves and analyzed 7680 photos meeting our criteria to determine the effect of foraging in single versus mixed-sex groups on individual foraging rates of males and females. We recorded 4390 pictures of females, 2338 of mature males, and 952 of yearling males. Mixed-sex and single-sex groups comprised 1715 and 5965 photos, respectively. Thus, single sex groups were almost 3.5 times more likely to be encountered than mixed-sex groups. Single-sex female groups had a mean group size of 2.2 (SD=0.51), single-sex male groups had a mean group size of 2.2 (SD=0.41), mixed-sex mature male groups had a mean group size of 2.1 (SD=0.29), and mixed-sex yearling male groups had a mean group size of 2.7 (SD=1.1). The percentage of detections of males in forage patches ranged from a minimum of 11% to a maximum of 77%, with a median of 48% and a mean of 45%. Thus, on average, the sex ratio across cameras was slightly skewed towards females. Also, males appeared to have high intersex aggression as aggressive posture was observed in all foraging bouts when multiple males were in the group (Fig. S1).

3.1. Social factor hypothesis

3.1.1. Prediction 1

Mature males spent 30.2% less time feeding ($T = 4.6$, $P < 0.001$) when females were present than when foraging in single-sex groups (Fig. 1). Females spent 9.6% less time feeding ($T = 2.1$, $P = 0.03$) when mature males were present than when either yearling males or no males were present (Fig. 1). Yearling males spent 12% more time ($T = 4.9$, $P < 0.001$) feeding when females were present than in single-sex groups (Fig. 1). Also, males and females both had lower feeding rates in mixed-sex groups than single-sex groups at a given group size. However, males were still able to increase feeding efficiency with increasing group size when feeding in mixed-sex groups and females were not able to do so (Fig. S2).

3.1.2. Prediction 2

The coefficient of overlap between male and female activity patterns at the forage patch level ranged from 0.38 to 0.91 with a median of 0.71. Female and male overall activity patterns had a high coefficient of overlap in both years (2011=0.95 and 2012=0.94;

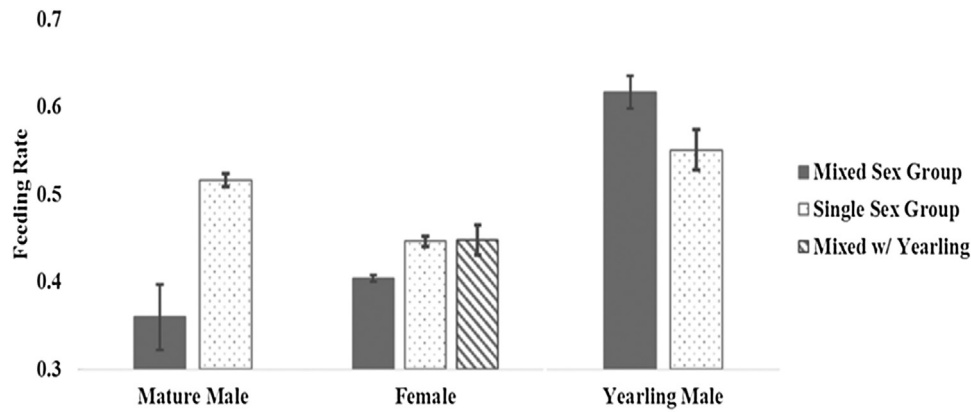


Fig. 1. Feeding rates (mean and SE) of mature male, female, and yearling male white-tailed deer in mixed- and single-sex groups based on camera trap detections at Fort Bragg Military Installation, North Carolina, USA, August 2011 and 2012. Mature male feeding rate was lower when foraging in mixed-sex groups ($T=4.6$, $P<0.001$), female feeding rates were lower when feeding in mixed-sex groups with mature males ($T=2.1$, $P=0.03$), and yearling male feeding rates were greater when feeding with females than with other males ($T=4.9$, $P<0.001$).

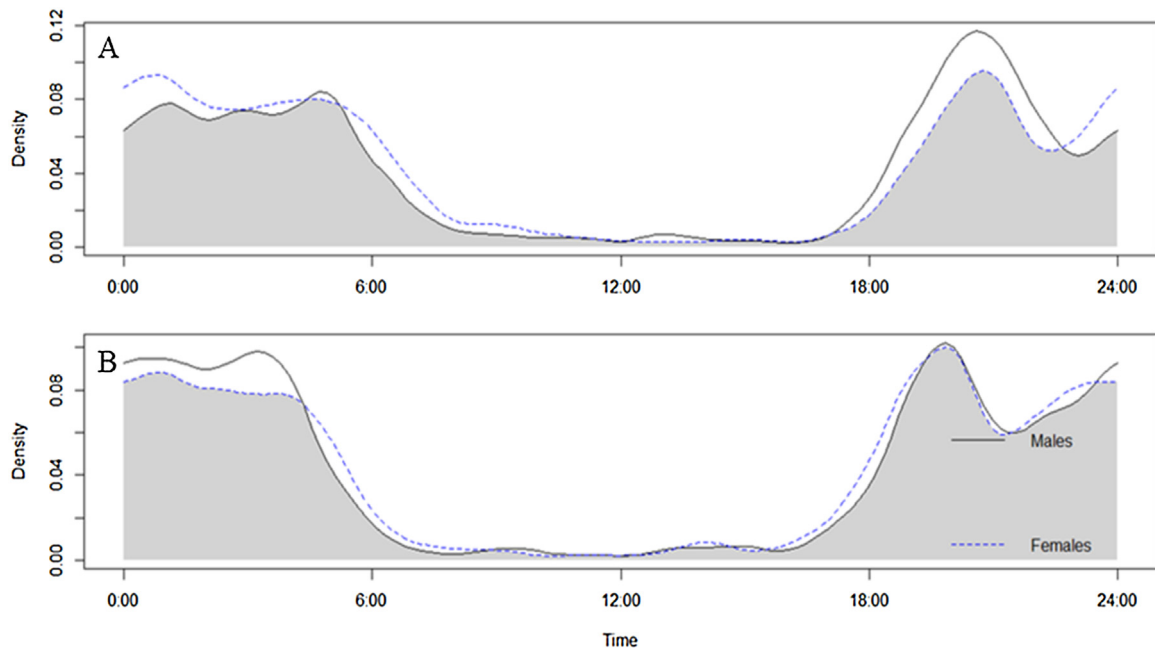


Fig. 2. Overall temporal overlap of male and female deer activity patterns in August 2011 (Overlap = 0.95; A) and 2012 (Overlap = 0.94; B) at Fort Bragg Military Installation, North Carolina, USA. Males and females have similar activity patterns when considering activity from all forage patches.

Fig. 2). However, the coefficient of overlap at the patch level averaged 0.74 (± 0.03 ; SE) in 2011 and 0.68 (± 0.04 ; SE) in 2012 (Figs. 3, S3).

3.2. Predation hypothesis

3.2.1. Prediction 3

Adult male feeding rates decreased relative to female feeding rates as distance to escape cover increased, indicating that fear perception was different between males and females when holding patch forage quality constant (Fig. 4).

3.2.2. Prediction 4

The coefficient of overlap did not change as a function of distance to cover, indicating that differences in fear perception of the sexes did not cause temporal segregation of forage patch use (Fig. 5).

4. Discussion

Our results support the social-factors hypothesis, demonstrating that mechanisms related to social interactions may result in reduced feeding efficiency of both sexes and encourage mutually-driven temporal sexual segregation in deer. Further, the substantial decrease in activity pattern overlap between males and females at the forage patch level may indicate that social interactions could encourage temporal sexual segregation. Other studies have reported similar coefficients of overlap in species commonly considered to have differing modes of activity (Farris et al., 2015). Because male and female interactions decreased the feeding rate of both mature males and females in our study, social interactions between the sexes may outweigh the increased feeding efficiency of larger groups and explain some the decrease in activity pattern temporal overlap of the sexes at the forage patch level. Interestingly, although males and females had greater feeding rates in

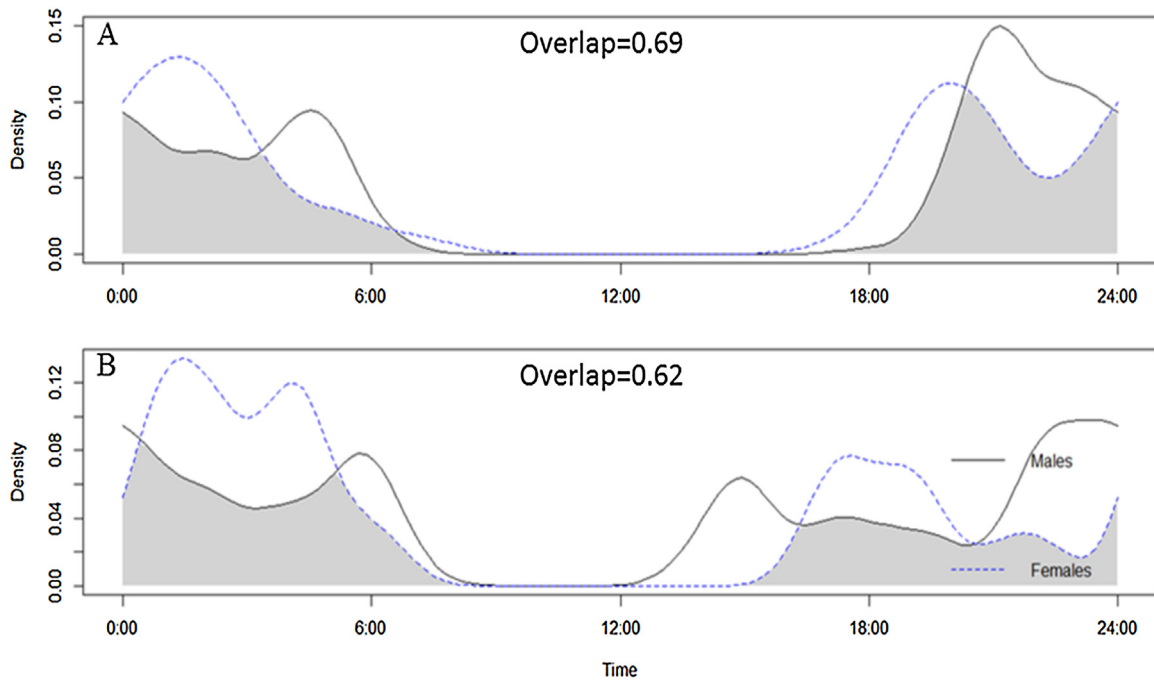


Fig. 3. Forage patch level temporal overlap of male and female deer activity patterns in August 2011 (A) and 2012 (B) at Fort Bragg Military Installation, North Carolina, USA. Males and females temporally segregate the use of single forage patches indicating that interactions between the sexes encourage mutual avoidance of foraging together in support of the social-factors hypothesis.

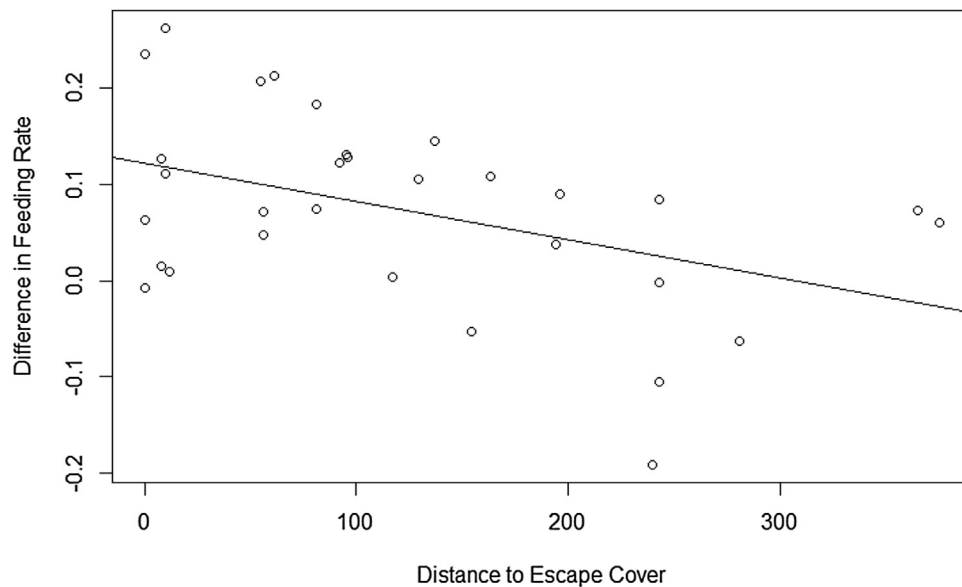


Fig. 4. The difference in feeding rates of male and female deer as a function of distance of the forage patch to escape cover. The change in values from positive to negative indicates that the feeding rate of males is decreasing relative to the feeding rate of females as distance to escape cover increases ($R^2 = 0.19$, $F_{29} = 6.67$, $P = 0.02$).

single-sex groups of a given group size, only males increased feeding efficiency when foraging in mixed-sex groups. Thus, the cost of foraging in mixed-sex groups may be much greater for females than males.

We should expect males and females to be temporally sympatric in patch use because their overall activity across all camera locations was similar. However, deer clearly temporally segregated their use of forage patches. Notably, [Bowyer et al. \(1996\)](#) warned that the degree of sexual segregation measured depended on the scale of measurements and that improper scale of measurements may result in improper conclusions. The scale-dependent differentiation in the degree of sexual segregation may, at least in part, be a

result of one potential mechanism causing temporal sexual segregation (i.e., mutually antagonistic social interactions). Therefore, this scale dependency provides evidence that other hypotheses (e.g., predation or gastrocentric hypotheses; [Barboza and Bowyer, 2000](#); [Jenks et al., 1994](#)) that do not require male and female interaction may not fully explain the observed temporal segregation of patch use. Moreover, different scales may be required to address different hypotheses with the same data. For example, although possible, we did not attempt to test predictions of the activity-budget hypothesis proposed by [Conrath \(1998\)](#) and [Ruckstuhl \(1998\)](#) primarily because many studies have rejected this hypothesis as a mechanistic explanation of spatial segrega-

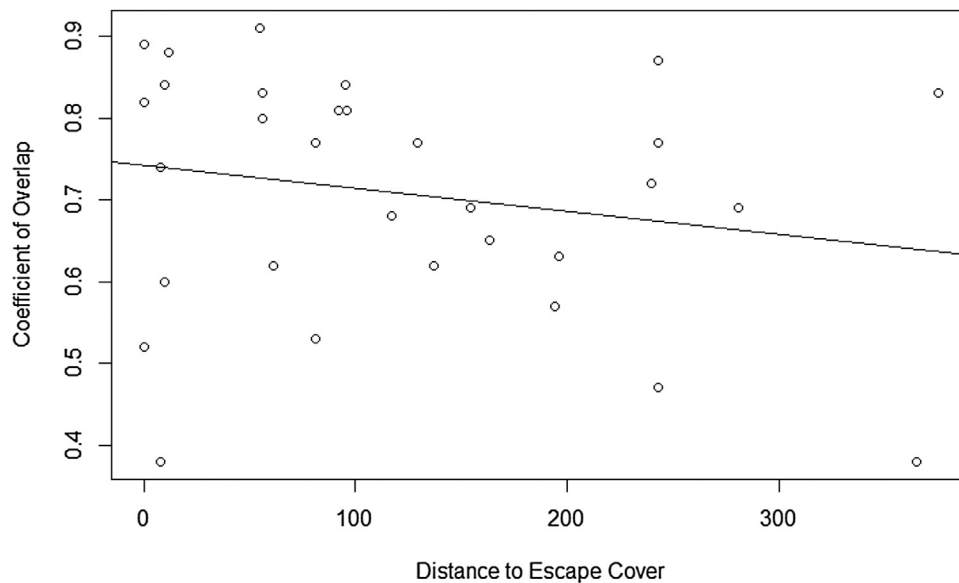


Fig. 5. The relationship between the temporal overlap in activity patterns between male and female deer in a forage patch and the distance of the forage patch to escape cover. The overlap did not change as a function of distance to escape cover, indicating the sexes did not temporally segregate because of difference in risk perception ($R^2 = 0.04$, $F_{29} = 1.32$, $P = 0.26$).

tion (Bowyer and Kie, 2004; Mooring and Rominger, 2004; Mooring et al., 2005; Yearsley and Pérez-Barbería, 2005; Michelena et al., 2004). However, unlike the social-factors hypothesis tested, data at our largest scale of inference (i.e., pooled data of all forage patches) was sufficient to reject the activity-budget hypothesis for temporal segregation because males and females overall shared a similar activity pattern. In this case, the scale of inference was an important consideration given that we may have had a different interpretation of the data if we had only considered the forage patch scale to make inferences about the activity-budget hypothesis.

Sexual segregation is more prominent among species that are more dimorphic potentially because of the associated intersexual aggression (Mysterud, 2000). In agreement with this notion, our data demonstrate that both females and similar-sized young males decrease feeding rates when in groups with larger males. Also, mature males commonly appeared to have aggressive posture toward the smaller individuals in the group likely causing the relationships we observed. Similarly, Weckerly (2001) reported larger male Roosevelt elk (*Cervus elaphus roosevelti*) showed more aggressive behavior toward young smaller males and females. And, Donohue et al. (2013) reported that large white-tailed deer males commonly defended concentrated forage patches from smaller conspecifics in their study. Interestingly, in our study, we determined that social interactions, whether aggressive or not, decreased foraging efficiency of both sexes, which likely encourages mutual avoidance of the opposite sex. Whether antagonistic social interactions will result in long-term segregation in space use and diet still warrants further investigation, but social-factors are unlikely to do so given that it requires the animals to interact to some degree in space (Bowyer, 2004).

Our results support the predation hypothesis in that males and females adjusted feeding rate differently as the distance to escape cover increased, which suggests that males and females have a different perception of risk. Thus, the observed differential risk perception between sexes demonstrates the proposed mechanism of the predation hypothesis (Bowyer, 2004; Stewart et al., 2003). However, if females were more vulnerable to predation than males, male feeding rates should have been greater relative to female feeding rates as risk level of the patch increased. The fact that we observed the counterintuitive opposite relationship suggest that

males may have perceived a greater predation risk than females as distance from escape cover increased even though smaller females should be at greater risk to predators (Kotler et al., 1994). We suggest that even though males are larger, they may perceive greater risk than females in this population because only males were allowed to be harvested by human hunters. So, because fear induced by humans supersedes that of cursorial predators (Proffitt et al., 2009), humans targeted males in this population, and coyotes were a primary source of mortality for females and their young on the study site (Chitwood et al., 2014, 2015a,b), it is plausible that the sexes may have perceived differing risk by their respective primary predator. Interestingly, that would indicate that human hunting could generate dissimilar patterns in sexual segregation than would be expected from other predators if the largest individuals are at greatest risk. However, whether predators could cause differences in fear perception between individuals in high and low risk portions of a population have not been well examined, especially in this context. An alternative explanation of the observed changes in relative fear perception could be that distance to escape cover was a poor proxy for perceived risk of a patch; however, we believe that is unlikely given the hide-and-flee antipredator strategy of white-tailed deer that is dependent on escape cover (DeYoung and Miller, 2011) and the fact that risk perception is related to distance to escape cover in many ungulates (Mysterud and Østbye, 1999; Burger et al., 2000). Additional research is needed to disentangle how different types of predators may affect sexual segregation.

The apparent change in fear perception we observed with feeding rates did not manifest in temporal segregation in forage patch use. This suggests that the sexes accommodate the different risk associated with a patch with an avoidance strategy rather than by adjusting use to safer times of the day. Thus, for sexes to fully segregate spatially and temporally, we propose that the predation hypothesis and the social-factors hypothesis could interact to encourage the full extent of sexual segregation commonly observed in ungulates, with the predation risk potentially explaining the overall spatial segregation and the social-factors potentially explaining the temporal segregation in patches used by both sexes. However, we were unable to test for changes in the degree of segregation over time which is an important consideration when evaluating mechanisms of sexual segregation. Thus, future research

is needed to address changes in the degree of sexual segregation over longer term experiments to determine the relative importance of social interactions, predation risk, and other hypotheses as mechanisms of segregation.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.beproc.2017.01.003>.

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