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2 **Sexual segregation of forage patch use: support for the social-factors and predation**

3 **hypotheses**

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17 **Abstract** Nearly all species of sexually dimorphic ungulates sexually segregate. Several
18 hypotheses have been proposed to explain this phenomenon, including the social-factors
19 hypothesis (SFH) and the predation hypothesis (PH). Interestingly, previous studies have
20 accepted and rejected each hypothesis within and across species but few studies have
21 simultaneously tested both hypotheses in the same population. In August 2011 and 2012
22 using 7,680 photographs taken with camera traps in standardized forage patches, we
23 tested two predictions of the SFH: 1) foraging efficiency of both sexes would decrease
24 when foraging rate in mixed-sex groups relative to single-sex groups, and 2) activity
25 patterns (i.e., the pattern of temporal use of forage patches on a diel scale) of the sexes
26 would decrease in temporal overlap at the forage patch level (i.e., social segregation)
27 compared to the overall temporal overlap of activity patterns of the population. Also, we
28 tested two predictions of the PH: 1) the relationship between feeding rates of each sex,
29 and 2) temporal activity overlap would change with changing risk level of forage patches
30 as a result of differing risk perception between sexes. In support of the SFH for temporal
31 segregation, when in mixed-sex groups, mature males and all females decreased feeding
32 rate 30% and 10%, respectively; further, the sexes had similar activity patterns overall
33 (94-95% overlap), though temporal overlap was lower in individual forage patches (68-
34 74% overlap). In multi-male mixed sex groups, at least one male exhibited aggressive
35 posture toward females during all foraging bouts suggesting intersex aggression was the
36 cause of the observed decrease in foraging rates. In support of the PH, the sexes adjusted
37 feeding rate differently in response to changing risk level of a forage patch, encouraging
38 spatial segregation; however, the PH was not supported for temporal segregation because
39 temporal activity pattern overlap did not vary as a function of predation risk. Coupling

40 our results with previous reports indicates that the SFH is supported for only temporal
41 segregation of forage patch use, and the PH may only be supported for spatial segregation
42 in forage patch use. Thus, both social factors and predation risk may interact to encourage
43 sexual segregation.

44 **Key words:** camera traps, feeding efficiency, *Odocoileus virginianus*, overlap analysis,
45 white-tailed deer

46 **Introduction**

47 Sexual segregation occurs in most sexually dimorphic ungulates and in cervids in
48 particular (Kie and Bowyer 1999, Bowyer 2004). Sexual segregation is a phenomenon
49 where sexes differentially use resources outside of the mating season (Bowyer 1984,
50 McCullough et al. 1989, Bleich et al. 1997, Kie and Bowyer 1999, Barboza and Bowyer
51 2000) and segregation can occur in space where the sexes use different areas altogether
52 (i.e., spatial segregation) or in time where the sexes use the same space at different times
53 (i.e., temporal segregation or social segregation; Ruckstuhl 2007). Though mechanisms
54 explaining sexual segregation are unclear, several hypotheses have been proposed. Two
55 commonly supported hypotheses are the social-factors hypothesis and the predation
56 hypothesis, but it is unclear whether either hypothesis necessitates spatial and temporal
57 segregation of forage patch use (Stewart et al. 2011).

58 The social-factors hypothesis postulates that social interactions between the sexes
59 can drive sexual segregation. However, the social-factors hypothesis cannot cause
60 consistent spatial segregation (Bowyer 2004, Stewart et al. 2011). For example, sexual
61 segregation may be the result of aggression between sexes (Weckerly 2001, Weckerly et
62 al. 2001) but the mechanisms proposed require animals to interact in space so the sexes

63 therefore cannot fully spatially segregate if social factors do indeed drive segregation.
64 This hypothesis could explain temporal segregation in the use of the same space if social
65 interactions encourage the sexes to avoid one another. Aggressive behavior in particular
66 should result in mutual avoidance of the sexes to forage together in a patch. Indeed,
67 fitness consequences could be mutual following aggressive interactions between the
68 sexes if defending a resource and avoiding a defender both detract from other activities
69 such as scanning for predators and foraging. In that case, the associated decreased fitness
70 in both sexes foraging together should be selected against over time yielding temporal or
71 social segregation (Weckerly 2001, Weckerly et al. 2001). Contrastingly, alternative
72 social factors such as intersexual affinity and social preferences may be the cause of
73 social segregation, but quantifying related factors are often difficult (Michelena et al.
74 2004, Pérez-Barbería et al. 2005). Few studies have examined whether the sexes foraging
75 together actually causes a fitness consequence. Feeding efficiency may provide a good
76 metric of relative fitness but it is often confounded by forage quality, availability, and
77 handling time (Stewart et al. 2011). Thus, an experiment evaluating the extent to which
78 social-factors can have fitness consequences for both sexes while also accounting for
79 confounding factors such as patch quality is needed.

80 The predation hypothesis predicts that predation risk encourages sexual
81 segregation because of differing risk associated with sexual dimorphism (Bleich et al.
82 1997, Kie and Bowyer 1999, Bowyer 2004). Unlike the social-factors hypothesis, the
83 predation hypothesis could cause temporal or spatial segregation because the larger male
84 body size allows them to forage in riskier patches and at riskier times than smaller
85 females (Bowyer 2004). There have been many studies that support the predation

86 hypothesis as a mechanistic explanation of sexual segregation in white-tailed deer
87 (*Odocoileus virginianus*; hereafter deer); only a few studies demonstrate lack of support,
88 but many of those may have been confounded by interactions between the quality of
89 escape cover and forage patch quality (Bowyer 2004, Stewart et al. 2011). Thus, an
90 experiment that holds either escape cover or forage patch quality constant is needed.

91 Explicit tests of multiple hypotheses in the same population may help clarify
92 support for some hypotheses over others. Moreover, an experiment that accounts for
93 confounding variables such as forage patch quality and dimorphism is needed. Also,
94 examination of spatial and temporal segregation simultaneously is rare but necessary to
95 fully understand mechanisms of sexual segregation. We addressed these issues by testing
96 two predictions of the social-factors hypothesis and 2 predictions of the predation
97 hypothesis using camera trap data of female and yearling and adult male deer collected at
98 standardized forage patches. The first prediction of the social-factors hypothesis
99 (Prediction 1) was that social interactions between males and females would negatively
100 affect feeding rates of both sexes as opposed to single sex groups when interacting in a
101 forage patch. The second prediction of the social-factors hypothesis (Prediction 2) was
102 that male and female activity patterns (i.e., the pattern of temporal use of forage patches
103 on a diel scale) would differ to a greater extent at the forage patch level than the overall
104 activity curves derived from pooled data from all patches. Prediction 1 is an explicit test
105 of the mechanism proposed by the social-factors hypothesis that a decrease in feeding
106 rate by each sex resulting from social interactions would mutually encourage the sexes to
107 temporally segregate the use of forage patches to maintain feeding efficiency. Prediction
108 2 is a behavioral test of the social-factors hypothesis to determine if interactions manifest

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

121 **Methods**

122 *Site Description*

123 We conducted our study at Fort Bragg Military Installation (Fort Bragg), located
124 (35°7' N, 79° 9' W) within the Sandhills physiographic region in the lower coastal plain
125 of North Carolina, USA. Longleaf pine (*Pinus palustris*) forests with wiregrass (*Aristida*
126 *beyrichiana*) understories were the dominant vegetation type (Lashley et al. 2014^a).
127 Forests were managed with growing-season prescribed fire on a 3-year fire-return
128 interval (Lashley et al. 2014^a). Potential predators of deer included coyotes (*Canis*
129 *latrans*; Chitwood et al. 2014), bobcats (*Lynx rufus*; Chitwood et al. 2015^a), and humans
130 (Chitwood et al. 2015^b). During the years of this study, deer were hunted in accordance

131 with North Carolina state hunting regulations from September to January each year
132 except that hunters were restricted to harvest of only males across much of the area.

133 *Data Collection*

134 In August of 2011 and 2012, we established 100 standardized forage patches with
135 ~20 kg of corn (*Zea mays*) and monitored each with a single camera trap (i.e., 50 sites
136 established August 1 and 50 sites established August 8) and cameras were able to detect
137 researchers consistently out to a maximum distance of 21m with the maximum width of
138 8m (see Lashley et al. 2014^b for study design details). Each forage patch was established
139 for 14 days to allow deer to adopt the new forage patch into their daily foraging activity
140 and then we refreshed the corn and activated cameras to take pictures for 14 days and as
141 our frequently as every 3 minutes (Jacobson et al. 1997). After the 14 days of camera
142 trapping, we collected all pictures and tallied the group size, sex, age of the oldest male,
143 group type (mixed- or single-sex), group feeding rate by sex, time and date of the picture,
144 and distance of the forage patch to escape cover. Distance to escape cover is known to
145 affect the perception of risk (Crowell et al. 2016) and should change in relative
146 importance to animals with differing vulnerability to predators (Camp et al. 2012). We
147 considered a deer to be in a feeding posture if its head was below its stomach line and
148 appeared to be actually feeding or approaching the food source (i.e., feeding; Lashley et
149 al. 2014^b). We determined sex based on the presence or absence of antlers; if the head
150 was not visible the picture was discarded. Also, we discarded pictures containing a
151 spotted fawn and other taxa to reduce their influence on individual deer feeding rates
152 (Lashley et al. 2014^b). We discarded pictures of single deer to analyze the effects of
153 foraging in mixed- versus single-sex groups on individual feeding rates of males and

154 females because we were interested in conspecific interactions. However, photographs of
155 single deer were used to generate activity curves to avoid biases associated with
156 excluding solitary individuals (Monteith et al. 2007). We classified males into one of two
157 age classes, yearling ($<2\text{yr}$) and adult ($\geq 2\text{yr}$), based on the number of antler points. We
158 derived this classification from 10 years of hunter harvest data at Fort Bragg, whereby
159 ~90% of yearling males had ≤ 4 antler points (3.18 ± 0.05 antler points [mean;SE],
160 $n=1,014$) and 90% of mature males had ≥ 5 antler points (7.07 ± 0.04 antler points
161 [mean;SE], $n=1,266$). Based on hunter harvest data, the majority of inaccuracy in this
162 method at Fort Bragg was associated with broken antlers. Therefore, we discarded any
163 pictures where antler points could not be tallied or antlers were broken.

164 *Data Analysis*

165 To test Prediction 1 (that feeding rate would be lower when sexes foraged
166 together), we used linear mixed models in program R (R Development Core Team 2011)
167 to examine the effects of group type on feeding rate of each sex. Feeding rate was the
168 response variable and group type was the explanatory variable. Based on our criteria, four
169 group types were possible: 1) Single-sex female, 2) Single-sex male, 3) Mixed-sex with
170 adult male, and 4) Mixed-sex with yearling male. We compared feeding rates of females
171 when feeding with a mature male and when feeding with a yearling male to female
172 feeding rates when feeding in single sex groups. Also, we compared feeding rates of
173 mature males foraging in mixed-sex groups to males foraging in single-sex groups.
174 Group size was reported previously as the most important variable affecting white-tailed
175 deer feeding rate (Lashley et al. 2014^b), so we controlled for group size in the model by
176 including group size as a random effect. We assumed that forage patches were

177 independent because uniquely marked males and females were never observed in
178 multiple forage patches.

179 To test prediction 2 (that male and female activity patterns would differ to a
180 greater extent at the forage patch level than the overall activity curves derived from
181 pooled data from all patches), we used a temporal overlap analysis in the Overlap
182 Package within program R. Specifically, we fit kernel density functions to camera trap
183 pictures of male and female deer (Ridout and Linkie 2009). First, to avoid biases
184 associated with small sample sizes, we selected only camera trap locations that contained
185 ≥ 100 detections of males and ≥ 100 detections of females during 2011 which was
186 determined to produce robust activity curves (Lashley unpublished data) and repeated the
187 selection of sites for 2012. This yielded fourteen camera trap locations in 2011 and 17
188 locations in 2012 (5 camera trap locations common to both years) for which we estimated
189 the coefficient of overlap, a quantitative measure of temporal overlap ranging from 0 to 1,
190 with 1 representing identical activity pattern curves of males and females. The forage
191 patch was the experimental unit for this analysis producing one unique coefficient of
192 overlap value per forage patch per year. Further, we calculated the overall coefficient of
193 overlap based on the pooled activity pattern for males and females producing one unique
194 coefficient of overlap value in 2011 and one in 2012 from all one hundred forage patches.
195 This allowed us to compare the average coefficient of overlap at the forage patch level to
196 the overall coefficient of overlap from all camera locations. A lower coefficient of
197 overlap at the forage patch level compared to the coefficient of overlap from all camera
198 locations would indicate temporal segregation of forage patch use to a greater degree than
199 expected by the population-level temporal segregation.

200 To test Prediction 3 (that the relationship in feeding rates between the sexes
201 changes as a function of predation risk), we modeled the difference in male and female
202 feeding rate (i.e., male feeding rate – female feeding rate) at a forage patch as a function
203 of distance to escape cover, which served as a proxy for predation risk. The forage patch
204 served as the experimental unit, the difference in feeding rate was the response variable,
205 and the distance of the patch to escape cover was the explanatory variable. In this study
206 area, because of the unique land management practices, the majority of high quality cover
207 is relegated to drainages where moisture prevents fire from consuming understory plants,
208 and deer heavily select those areas for escape cover (Lashley et al. 2014^a, 2015^a, 2015^b).
209 If the relationship between feeding rates is altered by distance to escape cover, that would
210 indicate the sexes are perceiving predation risk differently.

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

217 **Results**

218 We collected 40,540 photos of deer that were used to generate activity curves and
219 analyzed 7,680 photos meeting our criteria to determine the effect of foraging in single
220 verses mixed-sex groups on individual foraging rates of males and females. We recorded
221 4,390 pictures of females, 2,338 of mature males, and 952 of yearling males. Mixed-sex
222 and single-sex groups comprised 1,715 and 5,965 photos, respectively. Thus, single sex

223 groups were almost 3.5 times more likely to be encountered than mixed-sex groups.
224 Single-sex female groups had a mean group size of 2.2 (SD=0.51), single-sex male
225 groups had a mean group size of 2.2 (SD=0.41), mixed-sex mature male groups had a
226 mean group size of 2.1 (SD=0.29), and mixed-sex yearling male groups had a mean
227 group size of 2.7 (SD=1.1). The percentage of detections of males in forage patches
228 ranged from a minimum of 11% to a maximum of 77%, with a median of 48% and a
229 mean of 45%. Thus, on average, the sex ratio across cameras was slightly skewed
230 towards females. Also, males appeared to have high intersex aggression as aggressive
231 posture was observed in all foraging bouts when multiple males were in the group (Figure
232 S1).

233 *Social Factor Hypothesis*

234 Prediction 1

235 Mature males spent 30.2% less time feeding ($T=4.6$, $P<0.001$) when females were
236 present than when foraging in single-sex groups (Figure 1). Females spent 9.6% less time
237 feeding ($T=2.1$, $P=0.03$) when mature males were present than when either yearling
238 males or no males were present (Figure 1). Yearling males spent 12% more time ($T=4.9$,
239 $P<0.001$) feeding when females were present than in single-sex groups (Figure 1). Also,
240 males and females both had lower feeding rates in mixed-sex groups than single-sex
241 groups at a given group size. However, males were still able to increase feeding
242 efficiency with increasing group size when feeding in mixed-sex groups and females
243 were not able to do so (Figure S2).

244 Prediction 2

245 The coefficient of overlap between male and female activity patterns at the forage
246 patch level ranged from 0.38 to 0.91 with a median of 0.71. Female and male overall
247 activity patterns had a high coefficient of overlap in both years (2011=0.95 and
248 2012=0.94; Figure 2). However, the coefficient of overlap at the patch level averaged
249 0.74 (± 0.03 ; SE) in 2011 and 0.68 (± 0.04 ; SE) in 2012 (Figure 3, Figure S3).

250 *Predation Hypothesis*

251 Prediction 3

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

255 Prediction 4

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

259 **Discussion**

260 Our results support the social-factors hypothesis, demonstrating that mechanisms
261 related to social interactions may result in reduced feeding efficiency of both sexes and
262 encourage mutually-driven temporal sexual segregation in deer. Further, the substantial
263 decrease in activity pattern overlap between males and females at the forage patch level
264 may indicate that social interactions could encourage temporal sexual segregation. Other
265 studies have reported similar coefficients of overlap in species commonly considered to
266 have differing modes of activity (Farris et al. 2015). Because male and female
267 interactions decreased the feeding rate of both mature males and females in our study,

268 social interactions between the sexes may outweigh the increased feeding efficiency of
269 larger groups and explain some the decrease in activity pattern temporal overlap of the
270 sexes at the forage patch level. Interestingly, although males and females had greater
271 feeding rates in single-sex groups of a given group size, only males increased feeding
272 efficiency when foraging in mixed-sex groups. Thus, the cost of foraging in mixed-sex
273 groups may be much greater for females than males.

274 We should expect males and females to be temporally sympatric in patch use
275 because their overall activity across all camera locations was similar. However, deer
276 clearly temporally segregated their use of forage patches. Notably, Bowyer et al. (1996)
277 warned that the degree of sexual segregation measured depended on the scale of
278 measurements and that improper scale of measurements may result in improper
279 conclusions. The scale-dependent differentiation in the degree of sexual segregation may,
280 at least in part, be a result of one potential mechanism causing temporal sexual
281 segregation (i.e., mutually antagonistic social interactions). Therefore, this scale
282 dependency provides evidence that other hypotheses (e.g., predation or gastrocentric
283 hypotheses; Barboza and Bowyer 2000) that do not require male and female interaction
284 may not fully explain the observed temporal segregation of patch use. Moreover,
285 different scales may be required to address different hypotheses with the same data. For
286 example, although possible, we did not attempt to test predictions of the activity-budget
287 hypothesis proposed by Conradt (1998) and Ruckstuhl (1998) primarily because many
288 studies have rejected this hypothesis as a mechanistic explanation of spatial segregation
289 (Bowyer and Kie 2004, Mooring and Rominger 2004, Mooring et al. 2005, Yearsley and
290 Pérez-Barbería 2005, Michelena et al. 2006). However, unlike the social-factors

291 hypothesis tested, data at our largest scale of inference (i.e., pooled data of all forage
292 patches) was sufficient to reject the activity-budget hypothesis for temporal segregation
293 because males and females overall shared a similar activity pattern. In this case, the scale
294 of inference was an important consideration given that we may have had a different
295 interpretation of the data if we had only considered the forage patch scale to make
296 inferences about the activity-budget hypothesis.

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

312 Our results support the predation hypothesis in that males and females adjusted
313 feeding rate differently as the distance to escape cover increased, which suggests that

314 males and females have a different perception of risk. Thus, the observed differential risk
315 perception between sexes demonstrates the proposed mechanism of the predation
316 hypothesis (Bowyer 2004, Stewart et al. 2003). However, if females were more
317 vulnerable to predation than males, male feeding rates should have been greater relative
318 to female feeding rates as risk level of the patch increased. The fact that we observed the
319 counterintuitive opposite relationship suggest that males may have perceived a greater
320 predation risk than females as distance from escape cover increased even though smaller
321 females should be at greater risk to predators (Kotler et al. 1994). We suggest that even
322 though males are larger, they may perceive greater risk than females in this population
323 because only males were allowed to be harvested by human hunters. So, because fear
324 induced by humans supersedes that of cursorial predators (Proffitt et al. 2009), humans
325 targeted males in this population, and coyotes were a primary source of mortality for
326 females and their young on the study site (Chitwood et al. 2014, 2015^a, 2015^b), it is
327 plausible that the sexes may have perceived differing risk by their respective primary
328 predator. Interestingly, that would indicate that human hunting could generate dissimilar
329 patterns in sexual segregation than would be expected from other predators if the largest
330 individuals are at greatest risk. However, whether predators could cause differences in
331 fear perception between individuals in high and low risk portions of a population have
332 not been well examined, especially in this context. An alternative explanation of the
333 observed changes in relative fear perception could be that distance to escape cover was a
334 poor proxy for perceived risk of a patch; however, we believe that is unlikely given the
335 hide-and-flee antipredator strategy of white-tailed deer that is dependent on escape cover
336 (DeYoung and Miller 2011) and the fact risk perception is related to distance to escape

337 cover in many ungulates (Mysterud and Østbye 1999, Burger et al. 2000). Additional
338 research is needed to disentangle how different types of predators may affect sexual
339 segregation.

340 The apparent change in fear perception we observed with feeding rates did not
341 manifest in temporal segregation in forage patch use. This suggests that the sexes
342 accommodate the different risk associated with a patch with an avoidance strategy rather
343 than by adjusting use to safer times of the day. Thus, for sexes to fully segregate spatially
344 and temporally, we propose that the predation hypothesis and the social-factors
345 hypothesis could interact to encourage the full extent of sexual segregation commonly
346 observed in ungulates, with the predation risk potentially explaining the overall spatial
347 segregation and the social-factors potentially explaining the temporal segregation in
348 patches used by both sexes. However, we were unable to test for changes in the degree of
349 segregation over time which is an important consideration when evaluating mechanisms
350 of sexual segregation. Thus, future research is needed to address changes in the degree of
351 sexual segregation over longer term experiments to determine the relative importance of
352 social interactions, predation risk, and other hypotheses as mechanisms of segregation.

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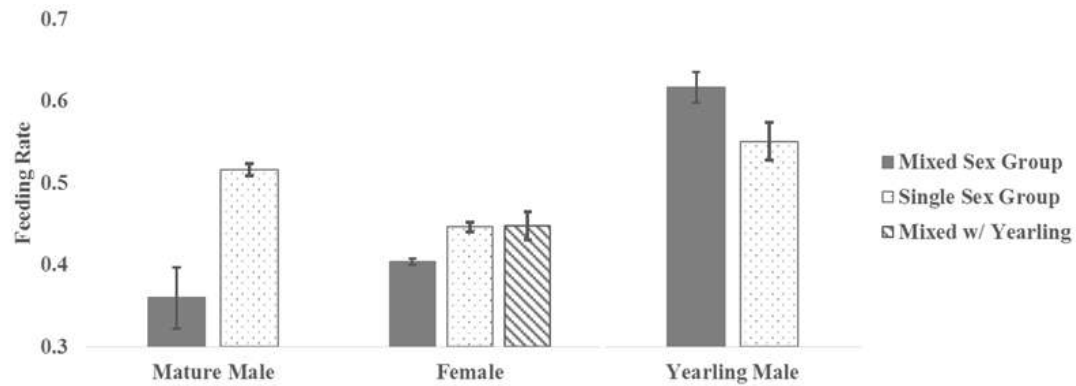
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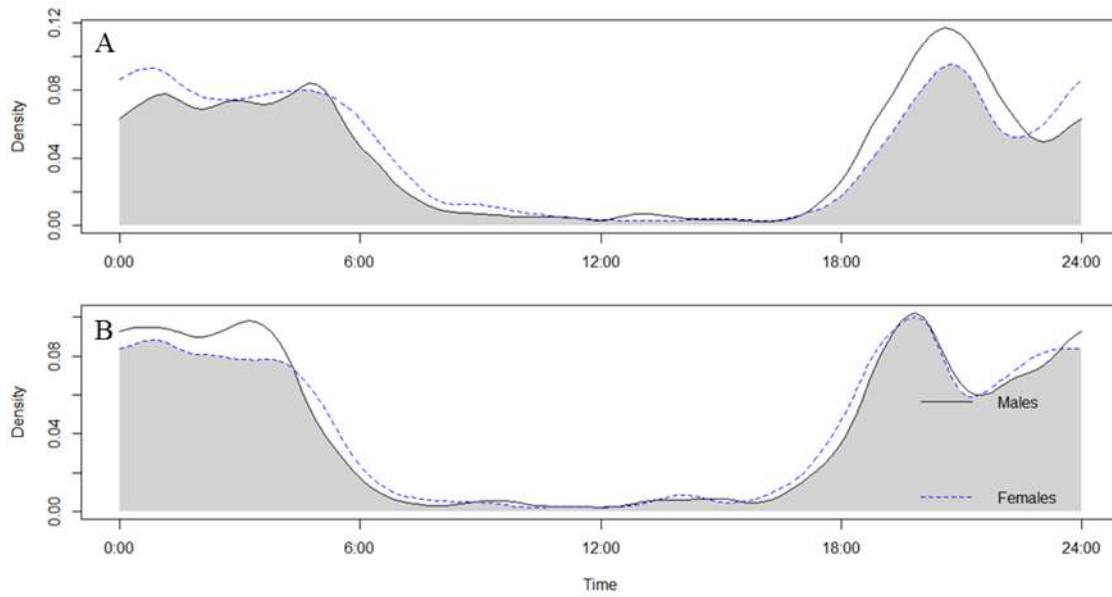


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476 **Figure 1.** Feeding rates (mean and SE) of mature male, female, and yearling male white-
 477 tailed deer in mixed- and single-sex groups based on camera trap detections at Fort Bragg
 478 Military Installation, North Carolina, USA, August 2011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

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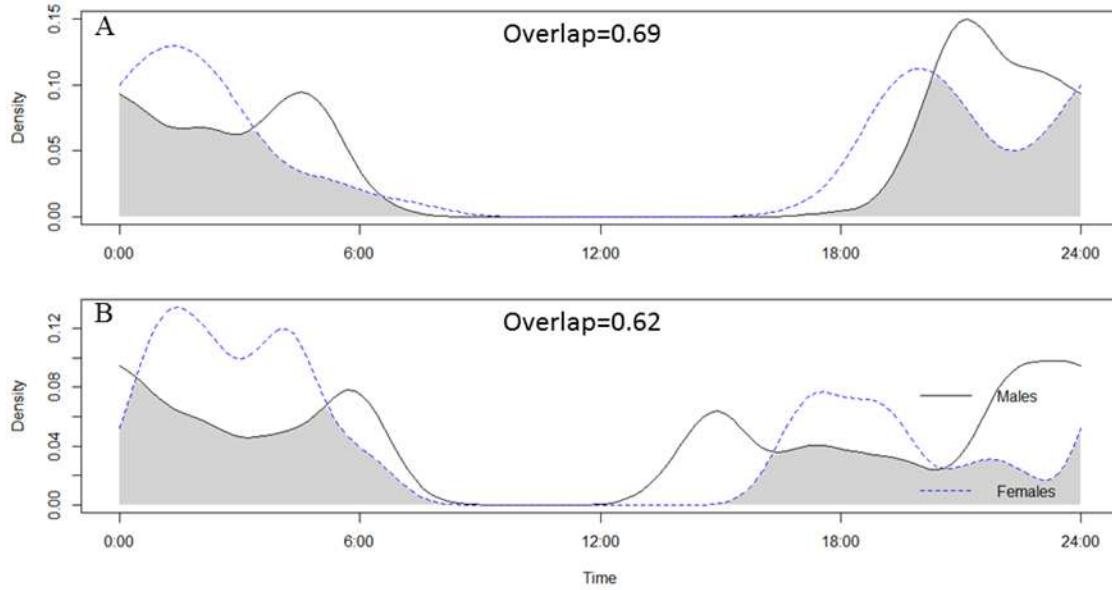
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486 **Figure 2.** Overall temporal overlap of male and female deer activity patterns in August
487 2011 (Overlap=0.95; A) and 2012 (Overlap=0.94; B) at Fort Bragg Military Installation,
488 North Carolina, USA. Males and females have similar activity patterns when considering
489 activity from all forage patches.

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492 Figure 3. Forage patch level temporal overlap of male and female deer activity patterns in

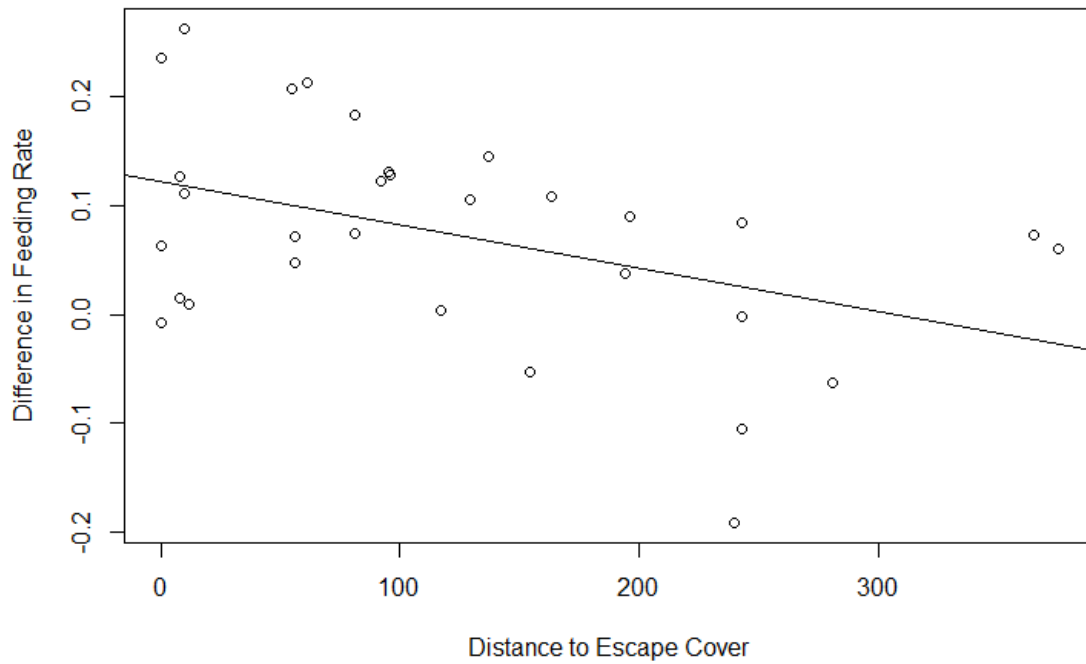
493 August 2011 (A) and 2012 (B) at Fort Bragg Military Installation, North Carolina, USA.

494 Males and females temporally segregate the use of single forage patches indicating that

495 interactions between the sexes encourage mutual avoidance of foraging together in

496 support of the social-factors hypothesis.

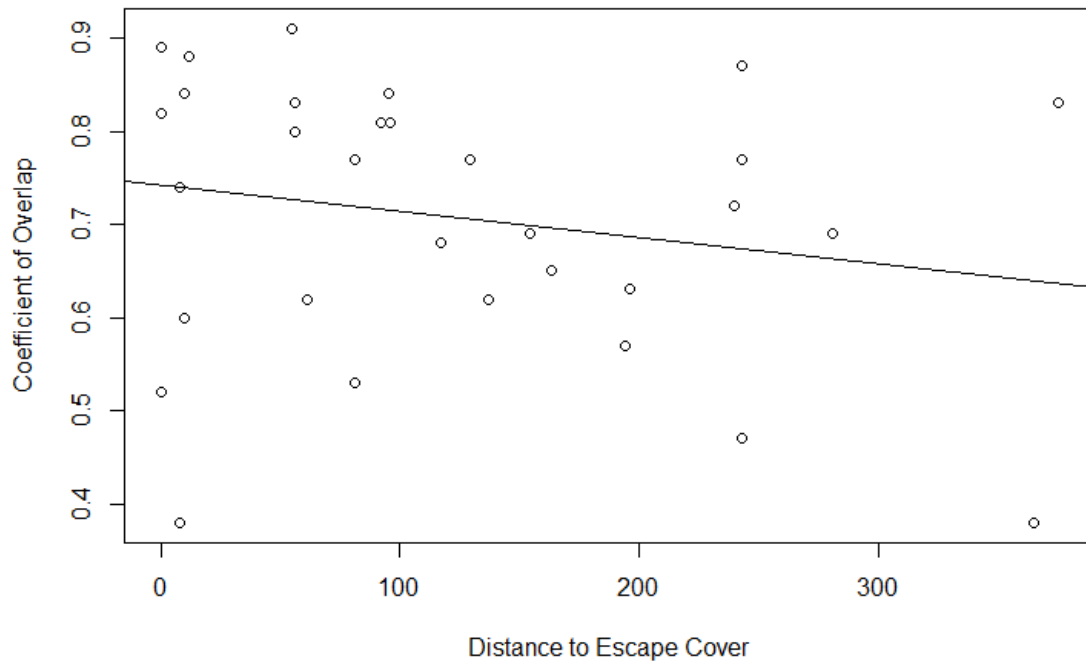
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499 **Figure 4.** The difference in feeding rates of male and female deer as a function of
500 distance of the forage patch to escape cover. The change in values from positive to
501 negative indicates that the feeding rate of males is decreasing relative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

503



504
505 **Figure 5.** The relationship between the temporal overlap in activity patterns between
506 male and female deer in a forage patch and the distance of the forage patch to escape
507 cover. The overlap did not change as a function of distance to escape cover, indicating
508 the sexes did not temporally segregate because of difference in risk perception ($R^2 = 0.04$,
509 $F_{29} = 1.32$, $P = 0.26$).