

**SOCIAL INCOMPATIBILITY, ALARM STATE, AND SEXUAL
SEGREGATION IN URBAN WHITE-TAILED DEER**

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ABSTRACT

SOCIAL INCOMPATIBILITY, ALARM STATE, AND SEXUAL SEGREGATION
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Sexual segregation is prevalent among sexually dimorphic ruminants outside the mating season and no consensus has yet been reached to explain this phenomenon. Differential reactions to predation risk or sexual differences in aggression may be responsible for sexual segregation. I investigated how male and female white-tailed deer (*Odocoileus virginianus*) segregated in an urban environment. Two routes in San Marcos, Texas were surveyed from a vehicle at dawn and dusk for one year. Segregation was examined at the group level, at two spatial scales (groups within 300 or 600 m) and by amount of cover used ($\leq 50\%$, or $> 50\%$). Alarm response to the vehicle was measured for each group. Focal animal sampling was used to measure the time males and females spent within

one body length of each other and the number of aggressions within one body length. Males and females were segregated in winter and spring but segregation declined throughout the summer, a trend previously unrecorded. Spatial segregation followed a similar trend. Akaike information criterion model selection indicated that alarm response was related to group size and group composition. Larger groups were less alarmed and female groups were less alarmed when controlled for group size. Females generally used larger groups than males outside of parturition. Males were further apart and more aggressive than females. The difference in group sizes between the sexes indicated that males and females used different avoidance strategies, preventing aggregation of the sexes. This is likely due to the more aggressive nature of males. Predation risk and social incompatibility may both contribute to sexual segregation.

CHAPTER I

INTRODUCTION

In many mammals, males and females spatially segregate outside the mating season, often into same sex groups (Ruckstuhl and Neuhaus 2000). Although sexual segregation has been widely studied, especially in polygynous ruminants that are sexually dimorphic in body size, researchers have yet to reach a consensus about mechanisms that drive this phenomenon. Since sexual segregation occurs infrequently in sexually-monomorphic mammals (Ruckstuhl and Neuhaus 2002), investigations have centered on hypotheses that describe segregation as a result of sexual size dimorphism. Hypotheses founded in sexual size dimorphism include body size-forage selection, activity budget, predation-risk, and social preference hypotheses (Main et al. 1996, Ruckstuhl and Neuhaus 2000).

The body size-forage selection hypothesis maintains that differing male and female body sizes result in different energy needs and digestive capabilities (McCullough 1979a). Males, with their larger gut capacity, are presumably capable of longer retention of digesta, allowing microorganisms to break down more cellulose and release more nutrients (Gross et al. 1996, Barboza and Bowyer 2000). Males should then be able to take advantage of lower quality forage, leading to segregation of the sexes by habitat or forage availability (Clutton-Brock and Harvey 1983, Conradt et al. 1999, Barboza and Bowyer 2000). Some support has

been found for this hypothesis, as male white-tailed deer (*Odocoileus virginianus*) exhibit a wider dietary niche than females (Kie and Bowyer 1999). Bison (*Bison bison*) used the same meadows, but males produced less fecal nitrogen than females because they fed on low-quality grasses during summer, the period of greatest segregation for this species (Mooring et al. 2005). However, longer retention is not the only strategy ungulates can use to increase nutrient intake from low quality forage. For example, increasing oral processing in ruminants will increase digestibility, and forage digestibility can change significantly depending on the influence of past diet on the diversity of microorganisms in the gut (McCullough 1979b, Robbins 1987, Gross et al. 1995, Du Toit and Yetmen 2005). This may explain why sika deer (*Cervus nippon nippon*), white-tailed deer and mountain sheep (*Ovis canadensis*) males use a higher quality diet at least part of the time or the sexes have similar diet qualities (Kie et al. 1980, Weckerly and Nelson 1990, Koga and Ono 1994, Main and Coblentz 1996, Bleich et al. 1997). The body size-forage hypothesis has not been sufficient to explain the ubiquitous pattern of sexual segregation.

The activity budget hypothesis contends that due to intersexual differences in energy needs and digestive capabilities, males and females sexually dimorphic in body size need to spend different amounts of time foraging, the dominant active behavior, and resting, the dominant inactive behavior (Conradt 1998a, Ruckstuhl and Neuhaus 2000). This should lead to differences in active time between sexes, and assuming synchrony in activity is beneficial, result in passive segregation of animals by size (Conradt 1998a). Results of investigations measuring activity budgets have been mixed. Support for this hypothesis has been found in a bighorn sheep population (*O. canadensis*); where males were less active and spent less time foraging than females (Ruckstuhl 1998). In red deer (*Cervus elaphus*),

activity synchronization has been documented as less in mixed sex groups than same sex groups (Conradt 1998a, Bonenfant et al. 2004). However, no difference in active vs. passive activities was found between the sexes for Merino sheep (*O. aries*) (Michelena et al. 2006). In addition, the proportion of time desert bighorn sheep (*O. c. mexicana*) males and females foraged was not different, and consequently intersexual asynchrony was concluded to be a consequence of segregation, rather than a cause (Mooring et al. 2003, Mooring and Rominger 2004). A lack of synchronization between the sexes could be prompted by other factors including predation risk, intersexual aggression and social incompatibility (Ruckstuhl 1998, Conradt 1998a, Weckerly et al. 2001, Yearsley and Pérez-Barbería 2005).

Because the body size-forage selection and activity budget hypotheses have failed to consistently explain segregation, recent work has called for closer examination of possible behavioral causes (Weckerly et al. 2004, Yearsley and Pérez-Barbería 2005). Species with polygynous mating systems may have evolved adaptive behaviors as sexual dimorphism developed, leading to segregation (Pérez-Barbería et al. 2002). The predation-risk hypothesis suggests that the vulnerability of each sex differs due to life history and body size, thus males and females perceive risk from predators differently. Females with young should more likely choose foraging habitat with less risk of predation, because of the smaller size of themselves and neonatal offspring. Adult males should be less vigilant for predators because they are less vulnerable due to large size, or the demands of social interaction and nutrition preclude time for vigilance (Main et al. 1996, Weckerly 2001). For some species, avoiding conspecifics may also make females and young less conspicuous to predators (Main and Coblenz 1996, Corti and Shackleton 2002). For other species, increasing group size may be an effective strategy to mediate predation risk (Geist 1977, Roberts 1996). Evidence for the

predation-risk hypothesis, though evident, is correlative. Segregation often peaks in spring, when young are born and at the highest risk of predation (Bon et al. 2001, Bonenfant et al. 2004). In many species such as mule deer, mountain sheep, and Svalbard reindeer (*Rangifer tarandus platyrhynchus*), females use steeper sloped terrain than males, especially when young are present, which makes capture by coursing predators more difficult (Main and Coblenz 1996, Bleich et al. 1997, Loe et al. 2006). Female Masai giraffes (*Giraffa camelopardalis tippelskirchi*) with young at heel prefer areas with open habitat where less vigilance is required to detect predators (Ginnett and Demment 1999). Female fallow deer (*Dama dama*) avoid areas with high incidence of human disturbance, but return to these areas to feed when disturbance diminishes (Ciuti et al. 2004, Apollonio et al. 2005). In bighorn sheep, males use habitat with less cover than females, but males aggregate in larger groups as distance from cover increases, presumably because risk from predators increase (Mooring et al. 2003). More direct tests of the differences between male and female predator avoidance are needed to determine if the predation-risk hypothesis can explain sexual segregation.

The social factors hypothesis proposes that there is a basic incompatibility between males and females of dimorphic species (Bon and Campan 1996). Males associate with other males to develop fighting skills and establish a rank in the dominance hierarchy (Bon 1991, Ruckstuhl and Neuhaus 2000). Consequently, male-male aggressions provide a benefit that male-female and female-female aggressions do not (McCullough 1979a, Main et al. 1996). Few studies have addressed this hypothesis, although there is some positive evidence. In mouflon (*O. gmelini*) sexual segregation increases as animals mature, probably due to an increase in sexual aggression (Cransac and Hewison 1997). In Roosevelt elk (*C. e. roosevelti*), males are more aggressive in close proximity than females. Females may choose

to avoid areas with males to maximize group cohesion and reduce aggressive encounters with males (Weckerly et al. 2001, 2004). In Soay sheep (*O. aries*), individuals consistently chose to associate with members of the same sex, rather than the opposite sex (Pérez-Barbería et al. 2005). Even when in mixed sex groups, sheep are closest to a same sex individual (Michelena et al. 2004). Female giraffes (*G. camelopardalis*) are more vigilant when an adult male is nearby than when alone, at the expense of foraging efficiency. Females may be trying to avoid sexual advances from males which may interrupt foraging (Cameron and Du Toit 2005). Although there is some support for the social factors hypothesis, more investigation is needed to determine if males are more aggressive than females, particularly in species where females are not strongly gregarious.

I examined the extent of sexual segregation in urban white-tailed deer to determine if behavioral hypotheses can explain this phenomenon. No studies have examined sexual segregation in urban environments. The urban environment provides an opportunity to study sexual segregation in abundant populations with fewer risks from natural predators but lethal hazards from automobiles (Romin and Bissonette 1996). In addition, social factors have not been examined in a less gregarious species such as white-tailed deer. Previous studies examining social factors and sexual segregation were conducted in elk and Alpine ibex (*Capra ibex ibex*), species that often associate in group sizes > 20 (Bon et al. 2001, Weckerly 2001). White-tailed deer in Texas mostly congregate with < 10 animals (Hirth 1977, Kie and Bowyer 1999).

If white-tailed deer are segregating due to intersexual differences in predation risk, I expect sexual segregation and female alarm state to be highest during parturition. During parturition females also should use more cover because of increased security. If white-tailed

deer are segregating due to social incompatibility owing to aggression among males, then the following predictions should be upheld. Males and females should segregate into separate groups (social segregation) outside the mating season. Social segregation should be extensive because males are more spaced apart in groups than females and display more aggression when close.

CHAPTER II

MATERIALS AND METHODS

Study area.— This study was conducted in San Marcos, Hays County, Texas. The climate was subhumid, mesothermal marked by hot summers and mild winters. Average daily temperature was 15°C in winter and 35°C in summer with a 30 year average rainfall of 94 cm. San Marcos covered 65 km² with a population of 44,769 in 2004. Located on the Edwards Plateau, the surrounding undeveloped land was a mosaic of Ashe juniper (*Juniperus ashei*) and live oak (*Quercus fusiformis*) with a woody understory comprised of many species including desert hackberry (*Celtis pallida*), agarita (*Berberis trifoliata*), and yaupon (*Ilex vomitoria*). Within the city, yards were well manicured with few shrubs and mostly comprised of St. Augustine grass (*Stenotaphrum secundatum*).

Sexual segregation.— Two survey routes in San Marcos were selected *a priori* to ensure inclusion of habitat representative of the urban landscape, such as homes, roadways and adjacent non-developed areas. The first route (8 km in length), located north of the town center was an established residential neighborhood where little development had occurred for at least twenty years. This route was composed of houses with small to medium sized (1/8-1/4 hectare) lawns interspersed with woody lots. The second route (11 km in length), southwest of town center was in a residential neighborhood that has had persistent development for at least the last five years. This route was composed of houses with medium

to large (1/4-1/2 hectare) lawn interspersed with shrubby, undeveloped lots. Deer were counted and classified during surveys from a vehicle along each route, traveling no faster than 24 kph. Surveys were conducted weekly between 1 January and 31 December 2005 excluding the period where males had no visible antlers (Feb. 20 – Mar. 31) and were difficult to identify. Counts began approximately fifteen minutes before sunrise and sunset. Night vision binoculars (5X) were used during nighttime surveys. The starting points of each route were reversed each week to reduce location bias. During surveys sex and age composition were recorded, as well as GPS location of each group. A group was defined as one or more animals synchronized in behavior and within 50 m each other (Frid, 1997). Size of a group was minimum group size because some animals may have been obstructed by anthropogenic structure and vegetation. Percent cover use of the animals was visually estimated as percentage of obstruction of observer's visual field and classified as open ($\leq 50\%$) or closed ($>50\%$). Antlerless deer were classified as female or juvenile based on size. When evidence of antlers was present, deer were classified as adult male. Any group where sex for each adult member could not be determined was recorded but not used in analyses. Density was calculated using the highest total count divided by total area covered during the route (Roberts et al. 2006).

Sexual segregation was calculated to examine whether males and nursery groups of juveniles and females were segregated into groups, across space, and in habitat that differed in cover. Segregation coefficients were calculated at the level of the group, at two spatial scales, and cover. Segregation coefficients were calculated at two spatial scales by dividing the routes into segments of 300 or 600 m and combining all groups within each segment for each route. These spatial scales were chosen because multiple groups were rarely observed

within 300 m of each other. Cover segregation was calculated by combining all the groups using open ($\leq 50\%$ cover) or closed ($> 50\%$ cover) habitats for each route. Sexual segregation was calculated according to Bonenfant et al. (2004).

$$\text{Modified Segregation Coefficient} = 1 - \frac{N}{MF} \sum_{i=1}^k \frac{m_i f_i}{n_i - 1}$$

N, M, and F were the respective totals for number of deer, number of males and number of females, m the number of males, f the number of females and n the number of deer counted in the *i*th group, or spatial quadrant. This coefficient provides a quantitative assessment of sexual segregation that was not influenced by population sex ratio, density, and group size (Conradt 1998b). Using this method, juvenile individuals were considered as females for calculation purposes, as they associate with females most often (Conradt 1998b). Solitary animals were removed from analysis (1.5 % of females and 6.1 % of males were solitary). Segregation coefficients range between -1 (indicating total aggregation) and 1 (indicating total segregation). Values close to 0 indicate random association of the sexes (Bonenfant et al. 2004).

Variation in segregation coefficients between months, diel period, and routes was estimated using mixed-effect models (Pinheiro and Bates 2000). Because myriad routes were possible, route was set as a random variable. To assess temporal serial correlation in weekly segregation coefficients, two models were constructed and likelihood ratio tests were used to compare models (Draper and Smith, 1998). The first model contained week as a fixed variable and route as a random variable but had no correlation structure. The second model had the same fixed and random variables and temporal correlation structure. No serial correlation was present in segregation data at level of the group, 300 m or 600 m increments,

or cover ($\chi^2 \geq 0.0001$, *d.f.* 1, $P \geq 0.6654$). Therefore the segregation coefficients calculated each week were treated as independent. Intraclass correlation coefficients evaluated whether separate regressions were helpful for each route (Pineiro and Bates 2000). An intraclass correlation coefficient near 0 indicated little variation among routes, whereas an intraclass correlation coefficient near 1 suggested separate regressions for each route would be helpful. Percent of animals using cover classes was examined between sexes, months, diel period, and routes using mixed-effect models (Pineiro and Bates 2000).

Alarm state.— During surveys we also measured alarm state to the surveyors.

Distance from vehicle to an animal in the center of the group was measured with a rangefinder. Activity was classified as feeding, bedded, reproductive, or loafing (unable to specify) depending on the behavior of the majority of the animals in the group. Alarm state was classified as none (1 - no ostensible reaction), orientation (2 - attention focused on the observer <15 sec), hold (3 - attention focused on observer for > 15 sec), walk (4 - animals move away at a walk), and run (5 - animals flee). Alarm state was classified based on both adult and juvenile reactions, but not for neonatal animals. Groups where a majority of animals were bedded were not used for alarm state analysis.

Twelve models were constructed to evaluate sources of variation that influenced alarm state. We divided alarm state by distance from vehicle to transform alarm state from a discrete to a continuous variable. This ratio was then log transformed to meet the assumption of homoscedasticity. The group or solitary animal was treated as the replicate ($n=1963$). Possible predictors of variation included group composition (male only, female only and mixed sex), group size, percent cover used, month, and diel period as well as interactions between the predictors. Group composition, month and diel period were coded as dummy

variables. Route was a random-effect predictor and the remaining were fixed-effect predictors. Regression coefficients were estimated using maximum likelihood estimation in the Linear Mixed Effect program of S-PLUS (Insightful Corporation, Seattle, Wash.). An information-theoretic model selection approach was used to assess which model fit the data considering the number of parameters estimated (Burnham and Anderson 1998). For each model, the Akaike's Information Criterion (AIC) was calculated from its log-likelihood, number of parameter estimates, and sample size. Akaike weights were calculated to compare AIC among models. A high Akaike weight (range 0-1) indicated increased probability that the given model fit the data relative to other considered models. A model was selected when its Akaike weight was higher than other models and it was parsimonious (Burnham and Anderson 1998). Means were then calculated for each group type using the predicted model. To assess temporal serial correlation in alarm data, a model was tested where week was a fixed variable and route was a random variable but had no correlation structure against a model with the same random and fixed variables with temporal correlation structure (Pinheiro and Bates 2000). Likelihood ratio tests were used to compare models (Draper and Smith, 1998). No serial correlation was detected ($\chi^2 = 1.426335$, df 1, $P = 0.2324$).

Social interaction.— Social interaction measurements were recorded from 15 April 2005 to 15 October 2005 and 1 to 31 January 2006 to avoid sampling animals displaying mating behavior. No groups at a distance of more than 60 m from observer, behind more than 25% cover, or with a “walk” or “run” response were used for social measurements to reduce errors in determining numbers of aggressions. For mixed sex groups, an adult male or adult female was selected haphazardly. In same sex groups, a focal adult was selected haphazardly and observed for two to ten minutes (mean = 3.2 minutes), depending on

behavior and movement of the group. Percent time the focal animal was within one body length (percent BL) of any other animal was measured to determine degree of sociality. Number of aggressions between focal animal and any other animal were also counted. Types of aggression were classified as hard look (stare from individual with ears flattened along neck), head threat (head is lowered and extended toward aggressor), kick (one or more blows with forefoot), chase, and rear (rising on hind legs to kick with pedaling movement of forelegs). These are the most commonly viewed types of aggressions (adapted from Hirth 1977).

For the response variable percent BL, an ANOVA was conducted in S-PLUS (Insightful Corporation, Seattle, Wash.). Because animals consistently use the same areas, it is likely that my observations included repeated measurements on the same groups. However, because all observations were more than three days apart, I still considered them to be independent (Weckerly et al. 2004). For the response variable number of aggressions within one body length divided by percent BL, a Wilcoxon-signed rank test was performed.

CHAPTER III

RESULTS

Mean total counts were lowest during the season of parturition and highest in late summer (Fig. 1). Few males were observed compared with observed numbers of females. Generally, more animals were observed during sunset surveys than sunrise surveys. The highest total count for any route was 131 animals, indicating a minimum white-tailed deer density of one per 10 hectares. The interaction between month and group composition (male-only, female-only and mixed sex) was significant for group size ($F=2.1292$, *d.f.* 1,18, $P=0.0038$). Mixed sex groups (except in November) were largest, followed by female-only groups and male-only groups (Fig. 2).

Sexual segregation.— Segregation was dependent on month at the level of the group ($F=6.79$, *d.f.* 10,157, $P<0.0001$), and at 300m ($F=5.17$, *d.f.* 10,157, $P<0.0001$) and 600m spatial increments ($F=4.95$, *d.f.* 10,157, $P<0.0001$). Segregation was lowest (< 0.3) during the mating season, lasting from August through November. Outside the mating season, segregation was consistent regardless of group or scale until May when it began to decline (Fig. 3). Diel period was not significant for the level of the group ($F=0.58$, *d.f.* 1,157, $P=0.4476$) or at 300m ($F=0.38$, *d.f.* 1,157, $P=0.5397$) and 600m spatial scales ($F=0.93$, *d.f.* 1,157, $P=0.3408$). Also, no interaction was detected between diel period and month for group segregation coefficients ($F=1.55$, *d.f.* 10,157, $P=0.1257$) or 300m ($F=1.26$, *d.f.* 10,157,

$P=0.2600$) and 600m spatial increments ($F=1.5$, $d.f. 10,157$, $P=0.1317$). Intraclass correlation coefficients were low for segregation coefficients by group (<0.01), and at spatial scales of 300m (0.01) and 600m (0.01), indicating little variation in segregation between routes. Cover segregation also differed among months ($F=6.13$, $d.f. 10,157$, $P<0.0001$). Unlike other measures of segregation, cover segregation differed between diel periods ($F=3.68$, $d.f. 2,157$, $P=0.0569$). No interaction between month and diel period was detected ($F=1.62$, $d.f. 10,157$, $P=0.1042$). Cover segregation was lowest during late summer and the mating season (August- November). Outside of this period, cover segregation was higher during morning surveys than evening surveys (Fig. 4). Intraclass correlation coefficients were low for cover segregation (0.02), indicating little variation in segregation between routes.

Percent animals using cover was dependent on sex ($F=16.44$, $d.f. =1, 315$, $P=0.0001$). Females (mean monthly animals using cover 2.756 ± 0.205 SE) used more cover than males (0.291 ± 0.022). Percent of animals using cover was not dependent on month ($F=0.78$, $d.f. 10,315$, $P=0.6453$) or diel period ($F=1.94$, $d.f. 1, 315$, $P=0.1651$). No interactions were present between month, diel period or sex (month x diel $F=0.63$, $d.f. 10,315$, $P=0.7844$, month x sex $F=0.46$, $d.f. 10, 315$, $P=0.9125$, diel x sex $F=0.46$, $d.f. 1, 315$, $P=0.4968$, month x diel x sex $F=0.66$, $d.f. 10, 315$, $P=0.7656$).

Alarm state.— I selected models 3 and 5 to summarize the log of the ratio of alarm state: distance to vehicle (Table 1). I selected these models because of relatively high Akaike weights (0.12, 0.15, respectively) and the fewer number of parameters estimated in these models compared to other models with similar Akaike weights. Model 3 had a fixed predictor for group size. The between route variance component was small (intraclass

coefficient = 0.01), indicating that a single model for both routes was sufficient. The parameter estimates (with standard error in parentheses) for model 3 were:

$$\text{alarm:distance} = -2.606 (0.211) + 0.45(0.008) \text{ group size.}$$

This estimate suggests that as group size increases alarm state:distance to vehicle increased. However, group size declined at further distances from vehicle (Fig. 5). Consequently, animals in smaller groups were more alarmed but further from the vehicle.

Model 5 had fixed predictors of group size and group composition. The between route variance component was small (intraclass coefficient = 0.01), again indicating that a single model for both routes was sufficient. The parameter estimates for model 5 were:

$$\text{alarm:distance} = -2.643 (0.211) + 0.446 + (0.008) \text{ group size} + 0.318(0.117) \text{ male-only groups} \\ + 0.097(0.073) \text{ mixed-sex groups.}$$

Similar to model 3, group size was positively associated with alarm:distance. The group type coefficients estimated the deviation of that group type from the Y-intercept. For example, the deviation of male-only groups from the mean of all groups was -2.325 (-2.643+0.318) on the logarithmic scale. To control for group size I used mean group size (4) and estimated the response variable using model 5. Mean alarm/distance was 0.1181 for male-only groups, 0.0947 for mixed sex groups, and 0.0949 for female-only groups. Males may have a greater alarm state than females, when group size was controlled. Yet, none of the examined models fits the data well. There was little change in residual standard deviation between the

null model and any other model (Table 1). During the season of parturition (April – July) mixed-effect linear models indicate an interaction between group size and group composition ($F= 2.60, d.f. 5, 752, P= 0.0241$). During this period, mean alarm/distance at group size 4 was 1.415 for female-only groups, 1.309 for female-only groups with fawns, 1.383 for mixed-sex groups, 1.486 for mixed-sex groups with fawns, and 1.187 for male-only groups. At a group size of 9 mean alarm/distance was 2.004 for female-only groups, 1.701 for female-only groups with fawns, 1.592 for mixed-sex groups, 1.972 for mixed-sex groups with fawns, and 1.089 for male-only groups.

Social interaction.– Percent time a focal animal spent within one body length (1 BL) was dependent on group type (females in same-sex groups, females in mixed-sex groups, males in same-sex groups, males in mixed-sex groups) ($F=3.75, d.f. 3, 32, P=0.0203$). Females spent more time within 1 BL of other animals than males regardless of group type (same-sex or mixed-sex, Fig. 6). Percent time within 1 BL was independent of group size ($F=0.79, d.f. 1, P= 0.3804$). Wilcoxon signed-rank test indicated a difference in the number of aggressions within 1 BL divided by percent time within 1 BL ($Z=1.9396, P=0.0262$). Males had a greater percentage of aggression within 1 BL ($0.3894 \pm 0.3587, n=20$) than females ($0.0007 \pm 0.0007, n=17$).

CHAPTER IV

DISCUSSION

Sexual segregation.— Sexual segregation was evident in this population of urban white-tailed deer from December to April. During this time males and females were socially segregated and male and female groups were not close in proximity because segregation was large at 300 and 600 m scales, except in February. At dawn in April and dusk in November the extent of segregation of males and females into open and closed cover habitat was also extensive. A trend of declining sexual segregation, regardless of the measure of segregation, began in May. By August, males and females were randomly associating with each other. Random association of males and females persisted until October and sexual segregation became evident again in December. In central Texas, most fawns are born from May to July (Thomas et al. 1965, Hirth 1977, Kie and Bowyer 1999). I observed neonatal fawns as early as mid-April. Segregation was therefore not most extensive during the season of parturition. These findings do not support the predation risk hypothesis.

The trend of sexual segregation declining through-out the summer (previous to the mating season) has not been previously reported. Two trends have been reported. The most common is ubiquitous segregation year-round, excluding the mating season (Bowyer 1984, Bleich et al. 1997, Conradt 1999, Mooring et al. 2003, Loe et al. 2006). The second features

segregation year-round, with a noticeable peak in segregation at parturition, and absence during the mating season (Kie and Bowyer 1999, Bon et al. 2001, Bonenfant et al. 2004).

The decline of sexual segregation through-out the summer in this population has several possible explanations. The classification system used may have contributed to this trend. Many juvenile males remain with nursery groups for up to two years of age and perhaps should not be classified as adult males (Apollonio et al. 2005). I was unable to determine age of males ≥ 1 years, and therefore classified any males with evident antler growth as adults from May to August. The study areas may have also affected the sexual segregation trend. San Marcos is home to a large university, with approximately 27,000 students enrolled in 2005. Many students leave the area during the summer months. The number of total animals observed increased during the period of decreasing segregation. This trend could then be the result of a change in behavior due to changes in perceived predation risk. In addition, many homeowners water their lawns during summer and the animals could have congregated to take advantage of this higher quality food source. I often observed mixed-sex congregations when homeowners provided corn to feed deer. Male and female ungulates have been known to tolerate each other for short periods of time in order to exploit a particularly rich resource (Ruckstuhl and Neuhaus 2005).

Alarm state.— Female alarm state was not greatest from April to July because month was not a variable in either model selected to predict alarm state. During this period, female groups with fawns did not have the highest alarm state. Also, there was some evidence supporting lower female alarm state, controlling for group size, than male alarm state. Males also used more cover at dusk in November than females. Males may be more sensitive to

anthropogenic predation in this population because they are more likely to be poached than females (Ginsberg and Milner-Gulland 1994).

These results do not support the predation risk hypothesis. In spite of these findings about alarm state, it should be noted that alarm state was not strongly related to any variable measured. Still, females may have been less alarmed if they were in large group sizes. Female-only groups were 12 to 80 % larger on average than male groups, dependent on month. This has been observed not only in white-tailed deer but other species including mountain sheep, desert bighorn sheep and bison (Hirth 1977, Kie and Bowyer 1999, Bleich et al. 1997, Mooring et al. 2003, 2005). From April through June, however, female and mixed sex groups tended to be smaller than found in other months. At dawn in April females frequented closed habitat and segregated from males. This behavior is likely a predator avoidance behavior. White-tailed deer females hide their newborn young, and solitary does visit only to nurse (Halls 1984). During the season of parturition, large group sizes would attract predators to vulnerable young. Females are likely using a solitary strategy during parturition and then mediating predation risk the remainder of the year by increasing group size.

The lack of strong effects of alarm state is possibly due to two factors: limitations of alarm state as a measure of predation risk, lack of predation risk in the urban environment for white-tailed deer. I was unable to measure the reaction of deer to actual predators, and instead measured reaction to disturbance caused by my vehicle. The reaction exhibited in response to disturbance are likely less intense than reactions to an actual predator. Although natural predators are probably less abundant in urban environments, it is likely that the deer perceived risks. Deer-vehicle collisions occur frequently in abundant populations and are

often lethal to the deer (Romin and Bissonette 1996). I observed five does with unique leg injuries likely caused by motor vehicles and two road-kill neonates. The deer respond to perceived risks of proximity to roads by aggregating; larger group sizes generally occurred closer to the survey vehicle than smaller groups. Increasing group size is a behavior widely accepted to mediate predation risk by diluting the possibility of predation (Molvar and Bowyer 1994, Apollonio et al. 1998).

Social interaction.— The findings of this study were equivocal in support of the social factors hypothesis. As expected, females were more likely to be in close proximity than males, and males had a higher level of aggression when in close proximity. Males are more spaced apart in groups because the probability of aggression is much higher when males are close to one another (Weckerly 2001, Weckerly et al. 2001). When a male enters close proximity to another male may signal a desire to interact or a lack of submission. Because female status is not strongly related to reproductive success and coexistence may benefit food exploitation and reduce predation, females in close proximity do not often interact aggressively (Weckerly 2001, Weckerly et al. 2001, Creel et al. 2005). The resulting social incompatibility may help explain why males do not frequently associate with females in mixed-sex groups.

The decline in social segregation from May to August cannot readily be explained by social factors. Males in Texas begin displaying reproductive behavior in October and the bulk of the mating season occurs mid-October to mid-December (Thomas et al. 1965, Hirth 1977). The sexes generally aggregate only during this period (Main et al. 1996, Ruckstuhl and Neuhaus 2002). During this study, males and females randomly associated beginning in August, possibly signaling an early start to the mating season. Also, extensive cover

segregation at dusk in November and dawn in April is difficult to explain in light of only social compatibility.

Conclusion.— This study reveals differences between the sexes of white-tailed deer in response to disturbance and social behavior. The literature contains many examples of how females may mediate predation risk (Roberts 1996, Main and Coblentz 1996, Bleich et al. 1997, Mooring et al. 2003, Ciuti et al. 2004, Bonenfant et al. 2004). In this study, females appeared to alter predation risk strategies dependent on their life history. Since predation risk varies greatly with different species and environments, it is logical that behaviors evolved to mediate predation risk are site-specific and time sensitive. This would mean that predation risk is a proximal factor in sexual segregation as it would evolve depending on each species' life history. This may explain why predation risk is not universally accepted as a cause of sexual segregation. Anti-predator behaviors are likely reinforcing segregation in conjunction with other factors.

Social incompatibility as a factor in the explanation of sexual segregation has only been addressed in more gregarious species (Weckerly et al. 2001). Detecting social incompatibility in a less gregarious species suggests that social incompatibility may help explain why males and females segregate in more than just gregarious ruminants. However, we were unable to document the role of inter-sexual aggression in segregation. The role of aggression in social incompatibility may be important in determining its impact on sexual segregation. Sexual dimorphism likely evolved as a mechanism to increase reproductive success in polygynous species and is often linked to aggression (Geist 1977, Pérez-Barbería et al. 2002). It is becoming evident that social factors may have a larger role in explaining

sexual segregation than previously realized (Bon et al. 2001, Weckerly et al. 2001, Michelena et al. 2004, Pérez-Barbería et al. 2005).

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Table 1. Fixed-effect predictors, log-likelihoods (LL), residual standard deviation (RSTD), number of parameters estimated (K), Akaike Information Criterion (AIC), and Akaike weights (w) of models chosen to estimate relationships of group composition, group size and alarm state/distance of white-tailed deer. Each model had a random effect predictor for route.

Model	Fixed predictors	LL	R STD	K	AIC	w
1	Null (y-intercept only)	-3154.983	1.205572	2	6315.967	0.022352
2	GC	-3147.568	1.201037	4	6305.136	0.038415
3	GS	-3137.148	1.194738	3	6282.297	0.120349
4	C	-3151.848	1.203656	3	6311.695	0.027674
5	GC + GS	-3132.763	1.192078	5	6277.525	0.15278
6	GC*GS	-3132.494	1.191914	7	6280.989	0.128483
7	C+GC	-3144.275	1.199032	5	6300.549	0.048318
8	C*GC	-3144.266	1.199027	7	6304.532	0.039593
9	M+D+GC+GS	-3121.204	1.185061	16	6276.409	0.161547
10	M+D+GC*GS	-3120.899	1.184876	18	6279.799	0.13636
11	M+D+C+GC	-3129.846	1.190232	16	6293.692	0.068077
12	M+D+C*GC	-3129.790	1.190196	18	6297.579	0.056053

¹GC= group composition (male-only, female-only, mixed sex) GS= group size, C= percent cover used ($\leq 50\%$, or $> 50\%$),

M= month, D=diel period surveyed (morning or night).

Fig. 1. Mean total counts of males and females for the year 2005.

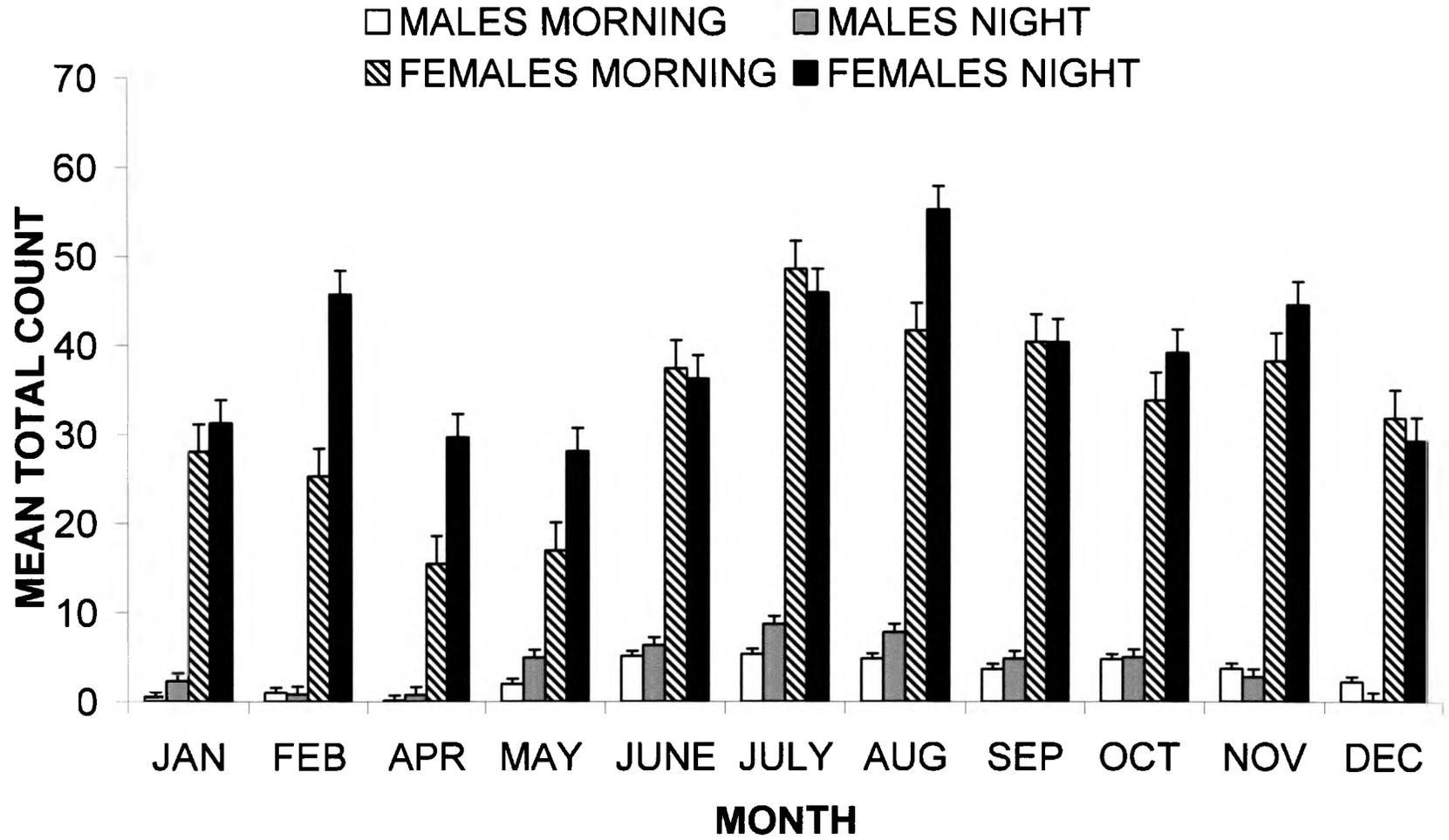


Fig. 2. Mean group size for male-only, female-only and mixed sex groups.

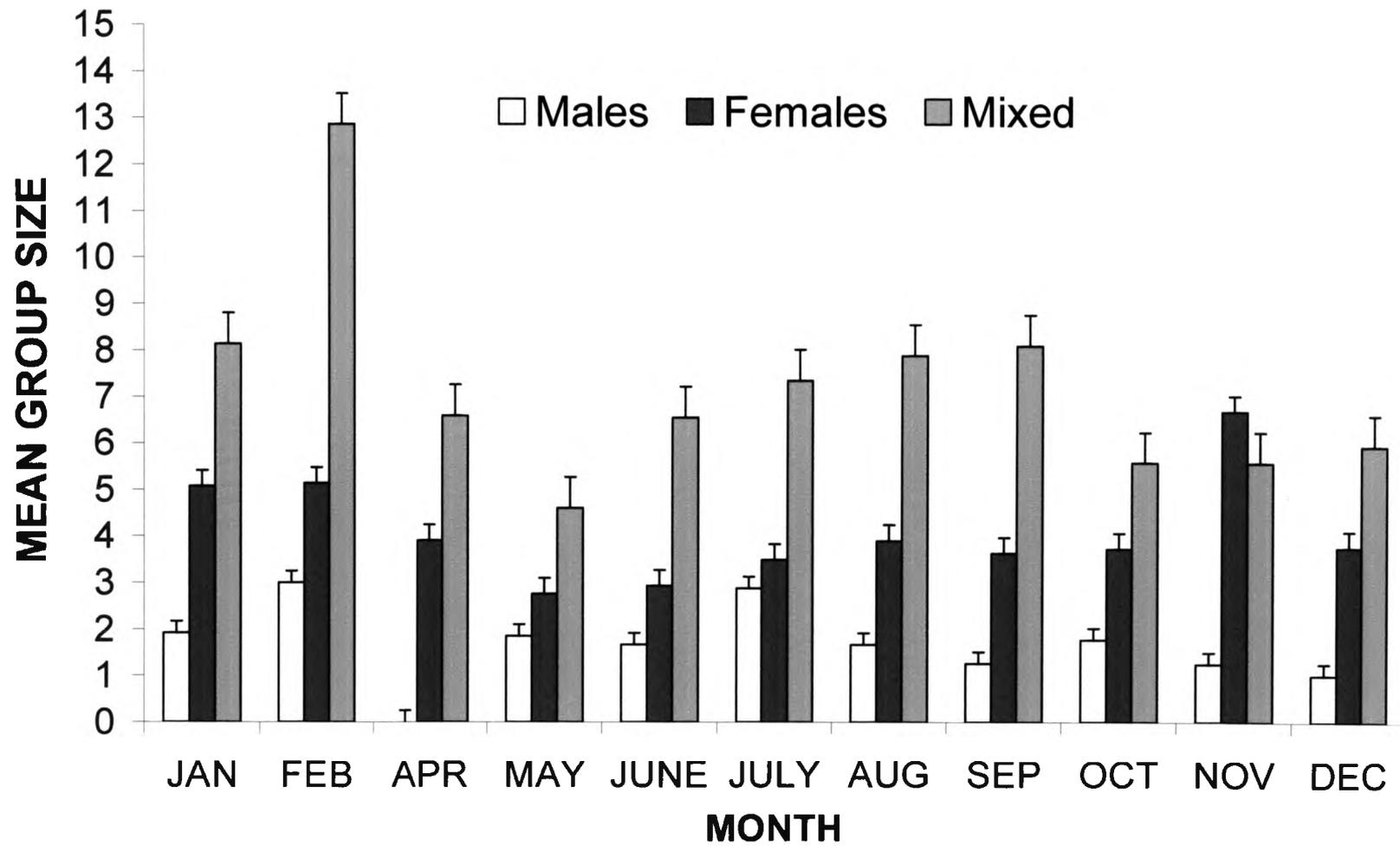


Fig. 3. Segregation coefficients at group, 300 and 600m spatial scales

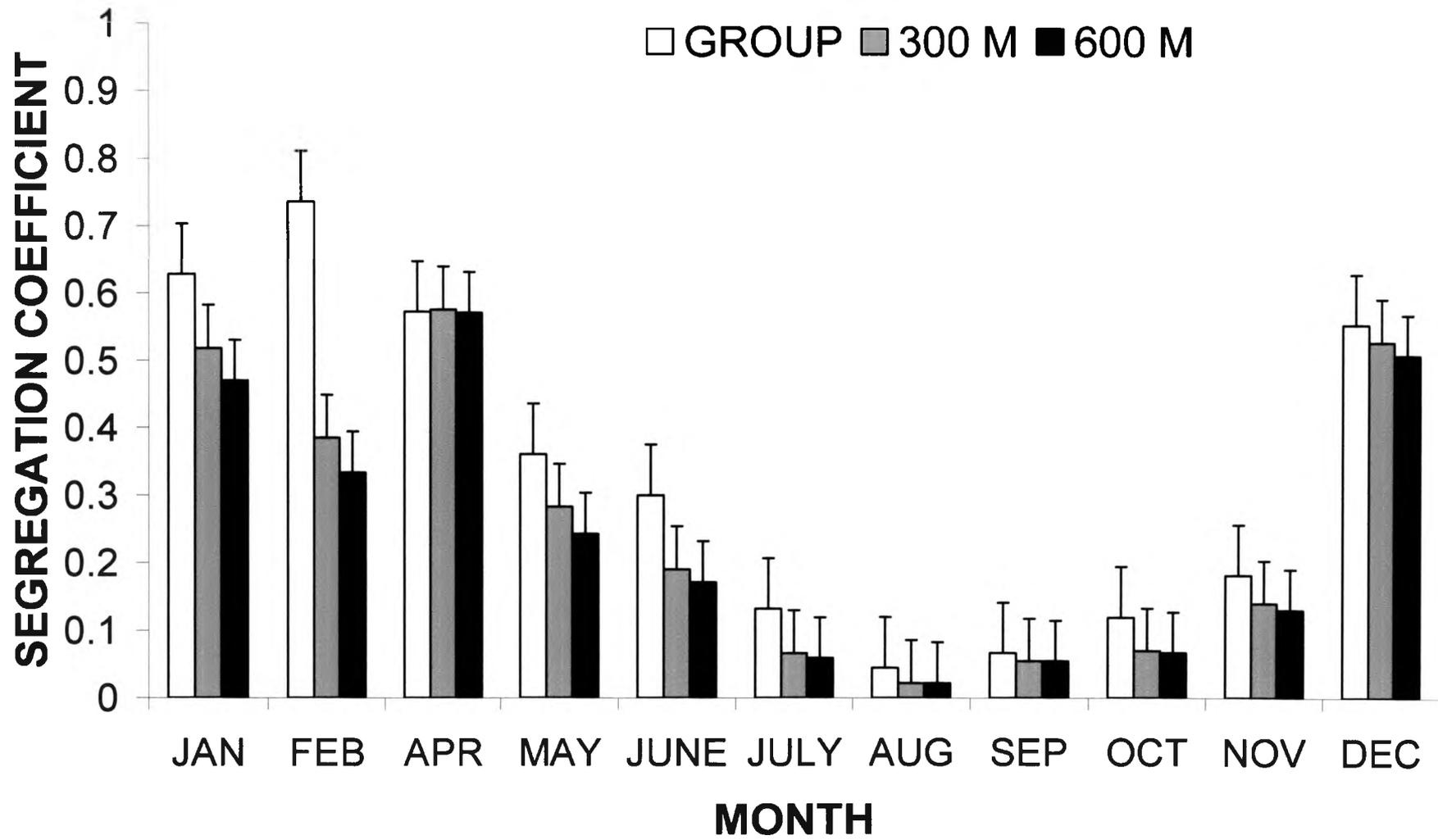


Fig. 4. Segregation coefficient at morning and night for % cover used.

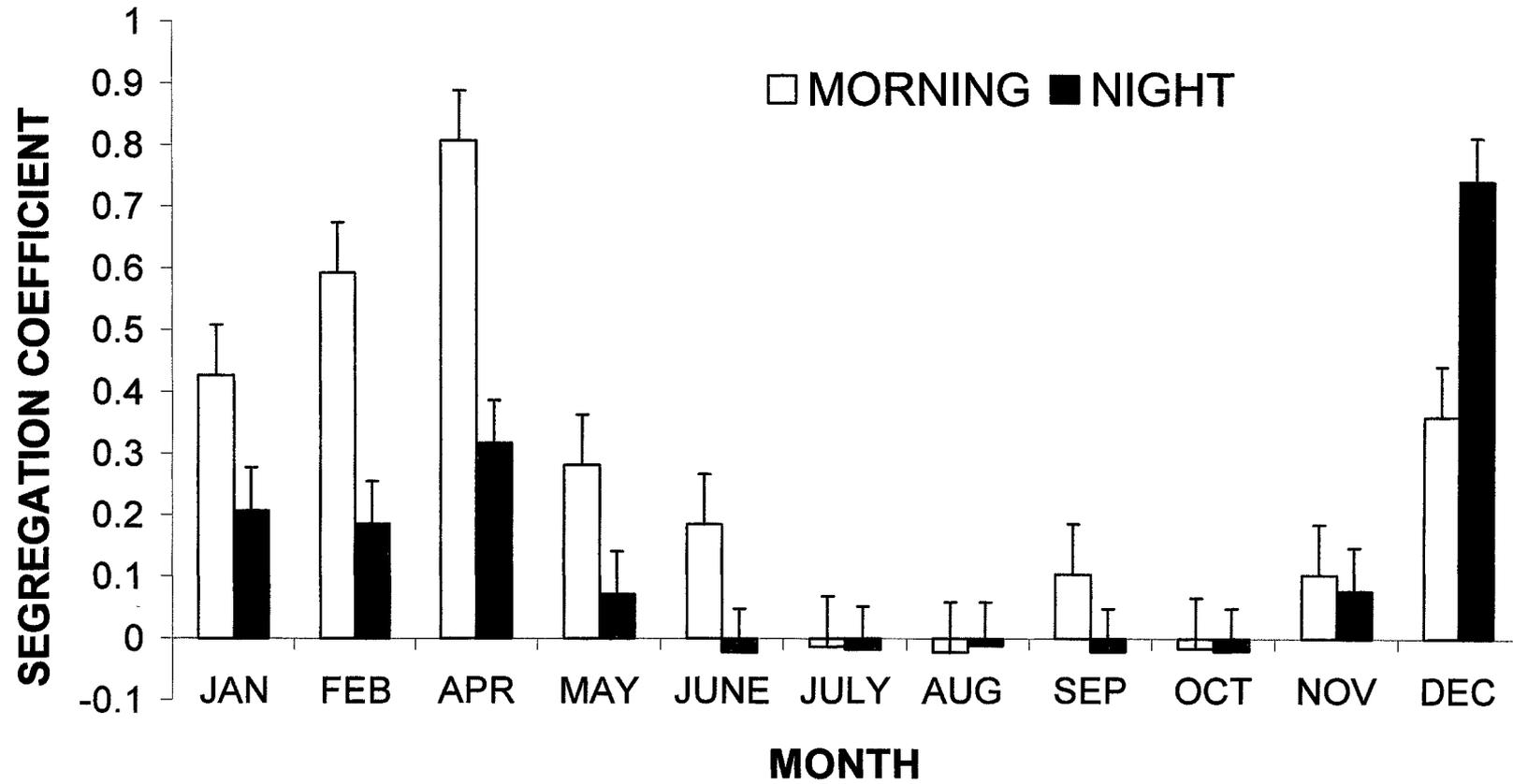


Fig. 5. Average distance from roadway for male-only, female-only, and mixed sex groups.

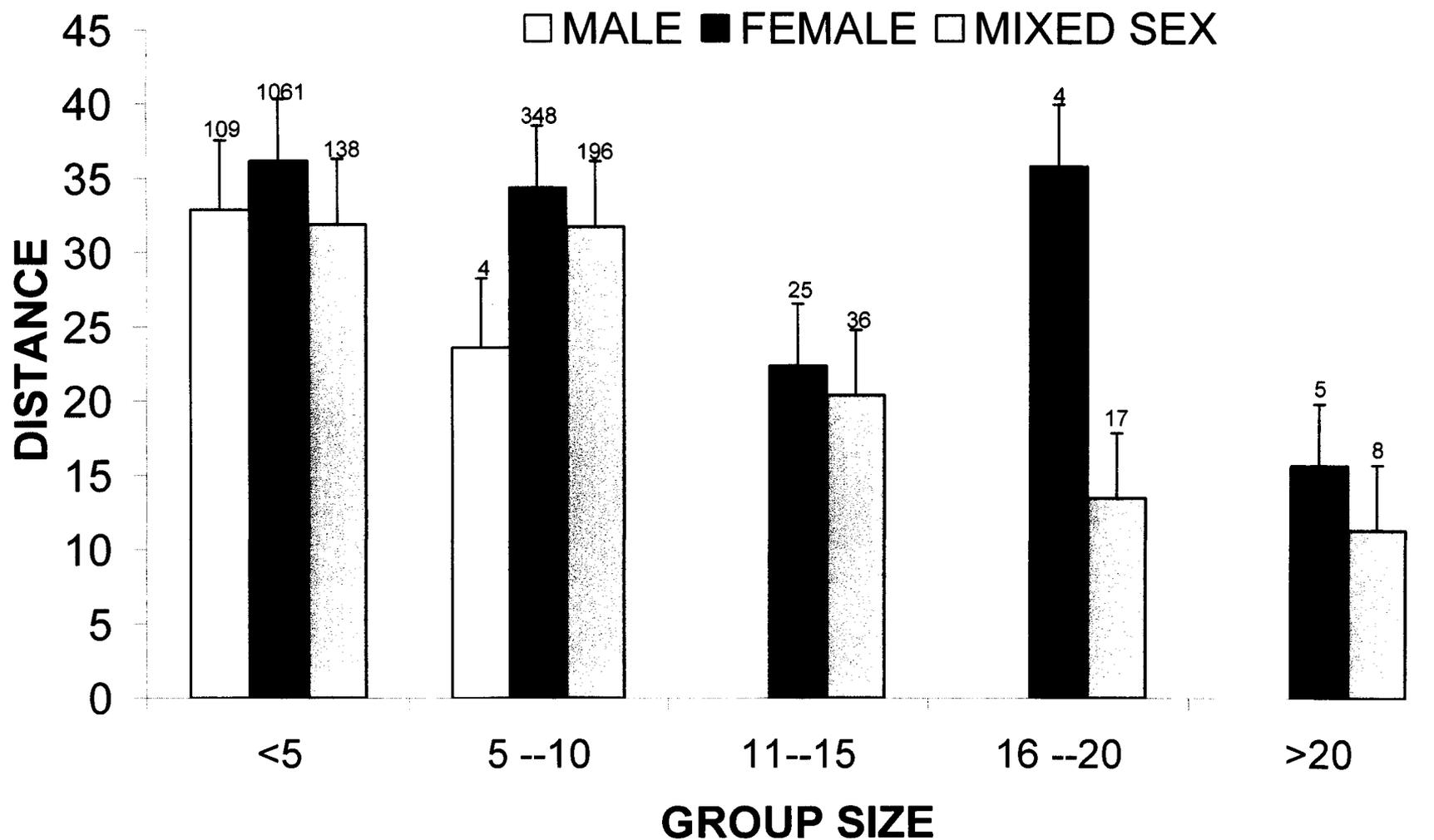
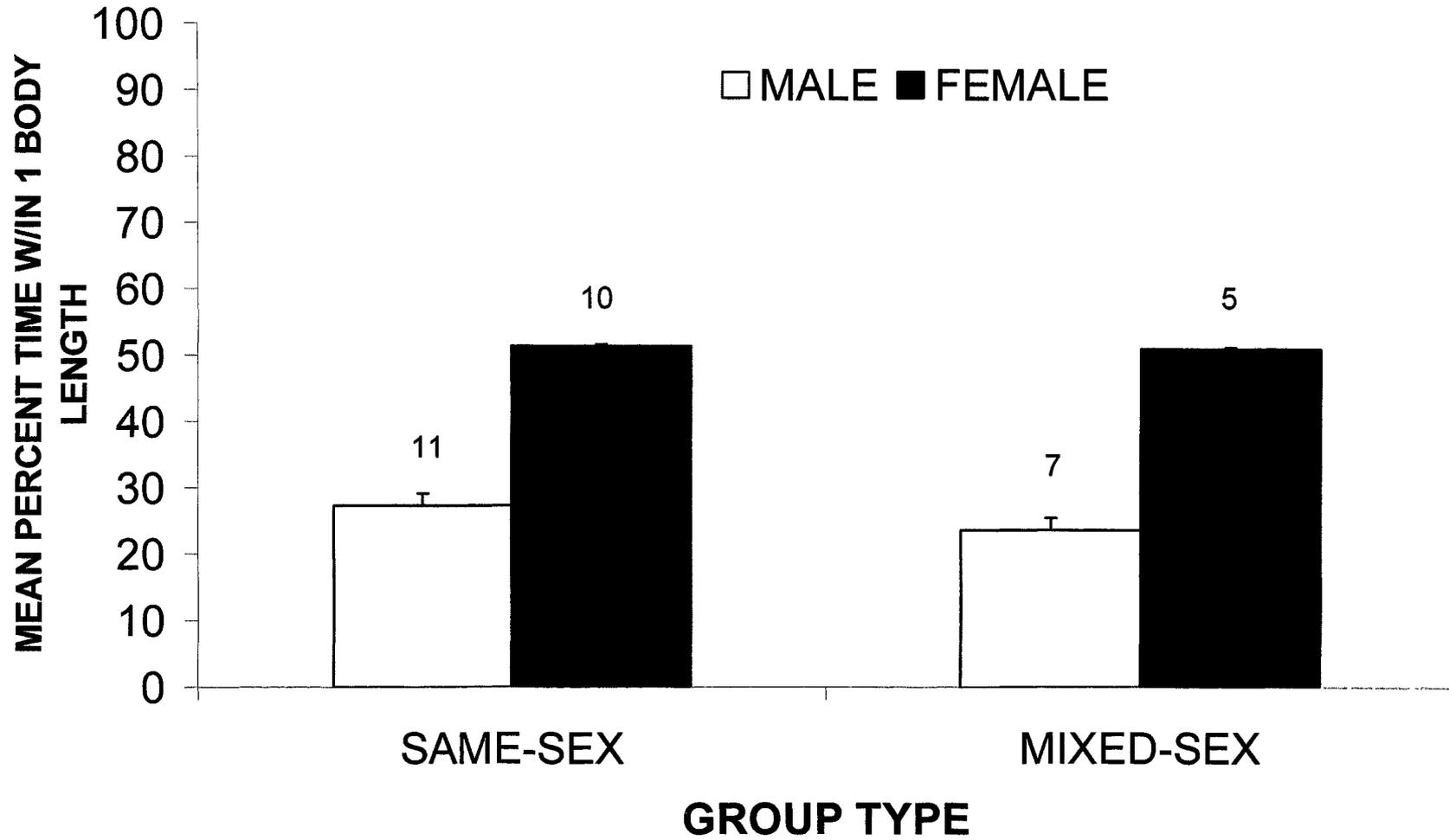


Fig. 6. Mean percent time within one body length for males and females.



VITA

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