

SEXUAL SEGREGATION IN WHITE-TAILED DEER: DENSITY-DEPENDENT CHANGES IN USE OF SPACE, HABITAT SELECTION, AND DIETARY NICHE

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Sexual segregation, defined as the exclusive use of different areas by males and females at specified spatial and temporal scales, is common among polygynous ruminants and in cervids in particular. Underlying mechanisms for such segregation are not understood fully, and reports have included female cervids segregating into habitats of both poorer and better quality than those used by males. Furthermore, two competing hypotheses of sexual segregation (body-size hypothesis, reproductive-strategy hypothesis) predict different responses to changes in population density; an increase in degree of sexual segregation with increasing density in the former and a decrease in segregation in the latter. We examined patterns of sexual segregation among white-tailed deer (*Odocoileus virginianus*) on the Welder Wildlife Refuge in south Texas at moderate (39 deer/km²) and high (77 deer/km²) population densities during 1974–1977. At moderate density, females with young made greater use of chaparral-mixed grass habitat with dense cover than did males, where preferred herbaceous forage was less abundant, presumably for reasons of predator avoidance. At high density, which was a result of predator control, sexual segregation among male and females decreased during all seasons ($P < 0.05$). Males that otherwise used more open habitats increased their use of the chaparral-mixed grass as levels of intraspecific competition increased. As spatial segregation between males and females decreased at the high population density, diets of both sexes shifted toward more graminoids and browse, and shifts were more pronounced among males. The result was decreased dietary overlap between sexes when measured by principal-component analysis. Measures of fat reserves suggested that although both females and males were in poorer condition at high density, females were affected to a greater extent than were males. This outcome suggested that females were not driving patterns of spatial segregation by being better able to compete with males for closely-cropped forages. Rather, predator avoidance by females with young related to the reproductive-strategy hypothesis best explained patterns we observed, and competition between sexes was rejected as a cause of sexual segregation.

Key words: *Odocoileus virginianus*, white-tailed deer, sexual segregation, social organization, competition, population density, niche, habitat selection, south Texas

Spatial separation of sexes outside the mating season is nearly ubiquitous among polygynous ruminants (Bleich et al., 1997; Main et al., 1996; Miquelle et al., 1992). The degree of spatial and temporal variation during sexual segregation for these large herbivores, however, is highly vari-

able (Bowyer et al., 1996). Moreover, despite numerous studies of sexual segregation, debate continues over causes of this phenomenon (Gross, 1998; Main, 1998; Main and Coblentz, 1990; Main et al., 1996).

Miquelle et al. (1992) and Bleich et al.

(1997) eliminated many of the hypotheses purported to explain segregation of sexes. We concur that these rejected ideas are unlikely to further our understanding of why sexes segregate. Nonetheless, several lines of inquiry remain viable and have been grouped into three broad categories by Main et al. (1996): reproductive-strategy, body-size, and social-factors hypotheses.

One problem in distinguishing among potential causes of sexual segregation is that the hypotheses that have been forwarded are not mutually exclusive (Bleich et al., 1997). In addition, only a relatively small number of studies have been designed specifically to test ideas about sexual segregation in ungulates (Beier, 1987; Bleich et al., 1997; Bowyer, 1984; Bowyer et al., 1996; Clutton-Brock et al., 1987; DuToit, 1995; Main and Coblenz, 1996; McCullough et al., 1989; Miquelle et al., 1992). Finally, difficulty in performing manipulative experiments with large mammals has led to correlative or inductive approaches even in those studies (Bleich et al., 1997; Main et al., 1996).

We realized that an existing data set on white-tailed deer (*Odocoileus virginianus*) offered the opportunity for a retrospective analysis of sexual segregation whereby critical tests of some hypotheses were possible because of a manipulative experiment. Although this experiment was originally designed to test ideas about predation on population density of white-tailed deer, data collected were likewise suitable for examining hypotheses concerning sexual segregation. We acknowledge that this approach is not ideal but believe it is worthwhile because this manipulative experiment allowed a critical test of why sexes segregate.

Density of white-tailed deer on the Welder Wildlife Refuge, Texas, fluctuated widely over the last 30 years (Fig. 1). Predator control within a 391-ha enclosure, begun in late 1972, resulted in an immediate increase in density of deer. Between 1974 and 1977, population density averaged 77 deer/km² inside the enclosure compared with 39 deer/

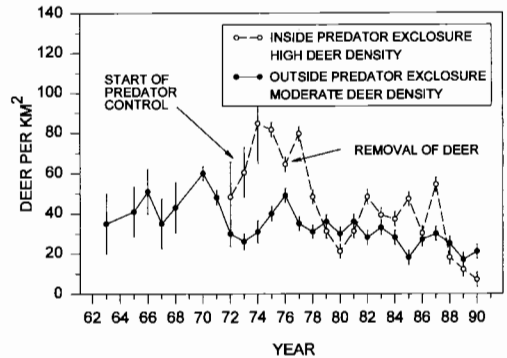


FIG. 1.—Estimated population densities of white-tailed deer inside and outside the predator enclosure on the Welder Wildlife Refuge, San Patricio Co., Texas, 1963–1990 (Kie and White, 1985; Teer et al., 1991). Error bars are 95% CI. Predator control began in late 1972, but some coyotes remained inside the enclosure throughout the experiment. The decline in density of deer within the predator enclosure in late 1975–1976 resulted from the removal of deer for study purposes.

km² outside the enclosure. Since the initial crash of the deer population inside the predator enclosure in 1978, numbers inside have fluctuated more widely than those outside the enclosure. In general, deer populations have declined somewhat since their peak during the late 1960s and early 1970s (Fig. 1). The difference in densities of deer between the predator enclosure and the remainder of the refuge in 1974–1977 allowed us to test the role of population density and, hence, intersexual competition and social factors in causing sexual segregation. We also gained insights into the reproductive-strategies hypothesis.

Clutton-Brock et al. (1987) and Main and Coblenz (1996) suggested that indirect, or scramble, competition between sexes was the cause of sexual segregation. The competition hypothesis, included under the body-size hypothesis by Main et al. (1996), proposed that females competitively excluded males from some sites. Indeed, Clutton-Brock et al. (1987) postulated that male red deer (*Cervus elaphus*) were less tolerant of low plant biomass than were females,

and foraging by females excluded males from particular areas via passive competition. Those authors also reported that the degree of sexual segregation increased with increasing density. Main and Coblenz (1996) likewise provided supportive evidence for this hypothesis for mule deer (*Odocoileus hemionus*) by noting that the biomass of nutritious forage was lower on range occupied by females than for areas inhabited by males. In addition, Illius and Gordon (1987) suggested that metabolic requirements related to differences in body size between sexes might cause spatial separation of sexes for many ungulates.

Conversely, Miquelle et al. (1992) concluded that intersexual competition could not explain sexual segregation in moose (*Alce alces*), as did du Toit (1995) for greater kudu (*Tragelaphus strepsiceros*). Likewise, Weckerly (1993) noted little support for bite size as it relates to the body-size hypothesis in black-tailed deer (*O. hemionus columbianus*). Bleich et al. (1997) reported that female bighorn sheep (*Ovis canadensis*) occurred on poorer-quality ranges than males, making competitive exclusion of males an unlikely explanation for sexual segregation.

Predictions concerning the competition hypothesis are straightforward. Increasing density of white-tailed deer within the predator enclosure on the Welder Wildlife Refuge resulted in strong intraspecific competition with a concomitant reduction in body condition and rates of reproduction (Kie and White, 1985; Kie et al., 1983). Thus, if intersexual competition was the cause of sexual segregation, the degree of segregation should have been higher inside the enclosure where density of deer and, hence, competition was higher. Furthermore, with an increase in intersexual competition at the higher population density, males should have exhibited a greater proportional decrease in body condition compared with females.

Most components of the social-factors hypothesis were rejected by Miquelle et al.

(1992), Main et al. (1996), and Bleich et al. (1997) and will not be reiterated here. Nonetheless, one potential cause of sexual segregation related to social factors remains—males might avoid areas used by females because of behavioral interactions. Adult male ungulates typically are dominant over females (Main and Coblenz, 1990), but avoiding areas with females still could lower rates of aggressive interactions for males and, thereby, increase time for other activities such as foraging. Such an outcome would indicate direct, or interference, competition. Thus, if social factors were responsible for sexual segregation, we would predict changes in group size and composition with increased density, and the degree of segregation would be greater at high density because aggressive interactions would be intensified.

MATERIALS AND METHODS

Study area.—The Rob and Bessie Welder Wildlife Refuge was located 35 km N of Corpus Christi in San Patricio Co., Texas (28°06'N, 97°22'E). The refuge occurred in a transitional zone between gulf prairies and marshes and south Texas plains (Gould, 1975). Annual variation in rainfall was great, with a 16-year average of 90 cm and a range of 45–125 cm (Kie et al., 1980). Means for monthly rainfall showed peaks in May–June and September. Plant growth was depressed during the dry period in summer and again during the cool, dry winter (Box, 1960).

Two plant communities, mesquite–mixed grass and chaparral–mixed grass, were most common and comprised 41% and 34% of the Welder Refuge, respectively (Drawe et al., 1978; Main, 1994). A third community, bunchgrass–annual forb, was less common. The mesquite–mixed grass community contained honey mesquite (*Prosopis glandulosa*) and occasional stands of other shrubs. Mesquite comprised 12–27% of the canopy cover in that community (Drawe et al., 1978). The chaparral–mixed grass community consisted of several woody species including blackbrush acacia (*Acacia rigidula*), honey mesquite, and huisache (*A. farnesiana*). Shrubs accounted for 34–55% of the canopy cover in that community (Drawe et al., 1978).

Details of these and other plant communities on the Welder Refuge are available elsewhere (Drawe et al., 1978; Kie et al., 1980).

Sampling of deer.—Population densities of white-tailed deer on the Welder Refuge have been estimated with a variety of techniques, including mark-recapture and counts from fixed-wing aircraft prior to 1969, line-transect methods based on observations made from vehicles in 1972–1974, and counts from helicopters in 1970, 1971, and since 1975 (Kie and White, 1985; Teer et al., 1991). Between 1972 and 1990, density of deer was estimated separately for the 391-ha predator enclosure. Here we refer to that estimate as the high density to distinguish it from the moderate density on the remainder of the Welder Refuge.

Between June 1975 and May 1976, one of us (J. G. Kie) conducted regular counts of white-tailed deer from a vehicle on the Welder Refuge. Flat topography, a good system of roads, and habituation of deer to vehicles allowed collection of more data than would have been possible on foot (Kie et al., 1979). For all groups of deer observed, information recorded included group size and composition (numbers of adult males and females ≥ 12 months old and young < 12 months old), and location (to the nearest 0.16 km along the road). Social groups of deer were categorized according to Hirth (1977). Female groups consisted of adult females and could include other sex and age classes except adult males. Likewise, male groups could include other deer except adult females. Mixed-sex groups had at least one adult female and one adult male but could include other sex and age classes. Only groups of deer ≤ 91 m of either side of the road were recorded. Data were analyzed separately for the high-density population of deer within the predator enclosure.

We defined a sample quadrat as the area bounded by 91 m on either side of a single 0.16-km segment of road totaling 2.9 ha. Where the main road on the refuge followed the boundary of the predator enclosure, quadrats were defined as the 91 m on one side of the road (either inside or outside the enclosure) for a 0.32-segment of road, thereby maintaining a quadrat size of 2.9 ha. Each quadrat was assigned to a habitat based on existing maps (Drawe et al., 1978). We defined 13 quadrats for the high-density population within the predator enclosure and 139 quadrats for the moderate-density population on the re-

mainder of the refuge. Among the 139 quadrats sampled for the population of white-tailed deer at moderate density, 11% were mesquite-mixed grass habitat, 53% chaparral-mixed grass habitat, 21% some combination of mesquite-mixed grass and chaparral-mixed grass, and 15% bunchgrass-annual forb habitat. Among the 13 quadrats sampled for the population at high density, 74% were mesquite-mixed grass, and 26% chaparral-mixed grass habitat.

We used a monthly temporal scale to define sexual segregation among adult deer (Bowyer et al., 1996). A quadrat was classified as segregated only if $\geq 90\%$ of the groups of deer observed in that quadrat for a particular month were either female groups or male groups. Quadrats without deer during a given month were excluded from analyses.

We grouped months into four seasons based on climate, plant phenology, and reproductive behavior of deer. Winter-spring (January–April) was cool and dry, cool-season C_3 grasses were growing actively, and large groups of deer commonly were seen foraging in open habitats. Young deer from the previous year were effectively recruited into the adult population by the end of that period (Kie and White, 1985). Parturition (May–July) occurred during warm weather when growth of forbs and warm-season C_4 grasses increased, and parturient females separated from other deer except for their female offspring from the previous year. Most young were born in June (Kie and White, 1985). Summer (August–September) was hot, growth of forbs slowed, and adult females were nursing young of the year. Rut (October–December) was cooler, all plant growth was depressed, and deer were mating.

Dietary and nutritional analyses.—Changes in diets of deer and nutritional levels as a result of differences in population density have been reported previously for samples collected during 1975–1976 (Kie et al., 1980). We report dietary differences between adult males and females at both moderate and high densities based on data collected in 1977, because raw data for 1975–1976 were no longer available. Collection and analytical techniques were similar to Kie et al. (1980); 75 deer were shot with a rifle in January–July 1977 as part of ongoing efforts to monitor health, condition, and reproduction of deer on the Welder Refuge (Kie et al., 1983; Teer et al., 1991). One-half liter samples were removed

from the rumen of each deer and frozen for later analysis. All study protocols met the field methods subsequently adopted by the American Society of Mammalogists (Animal Use and Care Committee, 1998), although data reported in this analysis were collected prior to the passage of the Animal Welfare Act (7 U.S.C. 2131, et seq.) in 1985, and no formal Institutional Animal Care and Use Committee existed to review the study plan.

Botanical composition of deer diets were obtained by microscopic analysis of plant fragments at the Forage Analysis Laboratory at Texas Tech University (Sparks and Malechek, 1968). Three slides were made from each rumen sample, and each of those slides was examined until 30 fields of view were recorded with identifiable plant fragments. Frequency for plant species or forage class was converted to particle density per field and then expressed as a relative density for each species (Sparks and Malechek, 1968). Seven individual species of plants were reported as separate items because they met the following criteria; those species were: 1) eaten by $\geq 20\%$ of the deer; 2) comprised $\geq 30\%$ of the diet in at least one deer; and 3) comprised $\geq 5\%$ of diets averaged over all deer. Those seven plant species included one graminoid, Texas wintergrass (*Stipa leucotricha*), a cool-season C_3 grass; and six forbs: western ragweed (*Ambrosia psilostachya*), bladderpod (*Lesquerella argyraea*), falsemallow (*Malvastrum aurantiacum*), largefoot pepperwort (*Marsilea macropoda*), Texas frogfruit (*Phyla incisa*), and prairie coneflower (*Ratibida columnaris*). Other plant species detected in diets were grouped into other graminoids, other forbs, and browse.

Changes in physical condition.—To assess the relative role of intersexual versus intrasexual competition relative to density of deer, we examined patterns of kidney-fat index and femur-marrow fat among adult males and females at both densities. Ninety-six adult deer were collected between July 1975 and May 1976, and differences in body weights, fat reserves, and blood values were reported previously (Kie et al. 1983). We re-examined those data for only those adult deer ≥ 2 years old (moderate density, $n = 47$; high density, $n = 42$). We chose kidney-fat index and femur-marrow fat as measures of condition because they were sensitive to changes in population density but were not affected by age in adult deer as were bled car-

cass weight and eviscerated carcass weight (Kie et al.; 1983). Details of methods of data collection and analysis are given by Kie et al. (1983).

Statistical analyses.—We used a Z-test to evaluate changes in the proportion of deer in group types between high and low density and among seasons, and one-way analysis of variance (ANOVA) for similar tests for group size (Zar, 1996). We examined differences in the proportion of males and females by calculating 95% CI based on a binomial distribution (Bowyer, 1991). Diets of deer were examined using principal component analysis (PCA—SAS Institute, Inc., 1988). Ten dietary categories were used (7 individual species of plants plus other graminoids, other forbs, and browse in this analysis). We used square-root arcsine transformations to insure additivity of treatment effects (Gilbert, 1973). We plotted the mean and 95% CI as bivariate ellipses ($n = 75$ deer) for the first three principal components to examine differences between adult males and females at moderate and high densities during winter–spring and parturition. Insufficient numbers of samples existed to examine dietary differences during summer and rut. We used eigenvectors of those 10 dietary categories along the first three principal-component axes to explain patterns of dietary separation. Principal-component analysis reorganizes data along separate, uncorrelated axes (SAS Institute, Inc., 1988); however, when considering subsets of original data, significant correlations between axes can occur (Lenart, 1997). Therefore, using simple linear regression, we examined relationships among subsets of data between the first three principal-component axes (PC2 versus PC1 and PC3 versus PC1; for males versus females, moderate versus high density, and winter–spring versus parturition). Following a sequential Bonferroni correction for multiple comparisons (Holm, 1979; Rice, 1989), none of those regressions were significant ($P > 0.05$). Consequently, we plotted bivariate ellipses with their axes parallel to the ordinate and abscissa.

To test for differences in proportional changes between males and females at moderate and high densities in kidney-fat index and percent femur-marrow fat, we first transformed data using the square-root, arcsin transformation to insure additivity of treatment effects (Gilbert, 1973). Population means were then compared using Welch's approximate t for samples with unequal variances (Zar, 1996).

RESULTS

A total of 5,201 deer in 1,490 groups was recorded during 1975–1976. Sex ratios for white-tailed deer during different seasons did not vary significantly ($P > 0.10$, Table 1). There was a greater proportion of males at high density (0.45 on a year-round basis) than in the population at moderate density (0.29); 95% CI for these estimates overlapped only during winter-spring (Table 1).

Mixed-sexed groups of deer were larger than female groups or male groups across all seasons ($P < 0.05$); mixed groups also were larger in winter-spring than in other seasons ($P < 0.05$; Fig. 2). No significant difference occurred in the size of mixed groups ($P > 0.10$), female groups ($P > 0.10$), or male groups ($P > 0.10$) between high and moderate densities of deer (Fig. 2).

Few differences in the composition of deer groups occurred between high and moderate densities (Fig. 3). Mixed-sex groups exhibited no difference in any season, female groups differed only in summer, but male groups comprised a larger proportion of deer groups at high density in all seasons except winter-spring, because males were more abundant at high density (Table 1). Thus, population density had little effect on group size or patterns of male-female associations.

Spatial segregation of sexes was most pronounced at parturition at both moderate and high densities of deer (Fig. 4). Differences between the percentage of quadrats categorized as segregated on a monthly basis at moderate density ranged from 47 to 61% and at high density from 0 to 35%, depending upon season (Fig. 4). Degree of sexual segregation was significantly higher at moderate than at high density during all seasons (Fig. 4).

The mean absolute value ($\pm 95\%$ CI) of the deviation between the proportion of males in the population at the moderate density and the proportion of males among all quadrats observed on a monthly basis at

TABLE 1.—Sex ratios in white-tailed deer observed at moderate and high population densities on the Welder Wildlife Refuge, San Patricio Co., Texas, 1975–1976.

| Period | Sex ratio (males : female) | | | Proportion males | | | 95% CI for proportion males | | | Deer observed (n) | | |
|-------------------------------|----------------------------|--------------|--|------------------|--------------|--|-----------------------------|--------------|--|-----------------------|--------------|--|
| | Moderate density | High density | | Moderate density | High density | | Moderate density | High density | | Moderate density | High density | |
| Winter-spring (January–April) | 0.45 | 0.50 | | 0.31 | 0.34 | | 0.29–0.33 | 0.28–0.39 | | 2,050 | 278 | |
| Parturition (May–July) | 0.36 | 1.00 | | 0.27 | 0.50 | | 0.23–0.30 | 0.44–0.56 | | 547 | 256 | |
| Summer (August–September) | 0.36 | 1.09 | | 0.27 | 0.52 | | 0.24–0.30 | 0.47–0.57 | | 887 | 391 | |
| Rut (October–December) | 0.39 | 0.74 | | 0.28 | 0.42 | | 0.24–0.32 | 0.36–0.49 | | 568 | 224 | |
| Year-round | 0.41 | 0.83 | | 0.29 | 0.45 | | 0.28–0.30 | 0.42–0.48 | | 4,052 | 1,149 | |

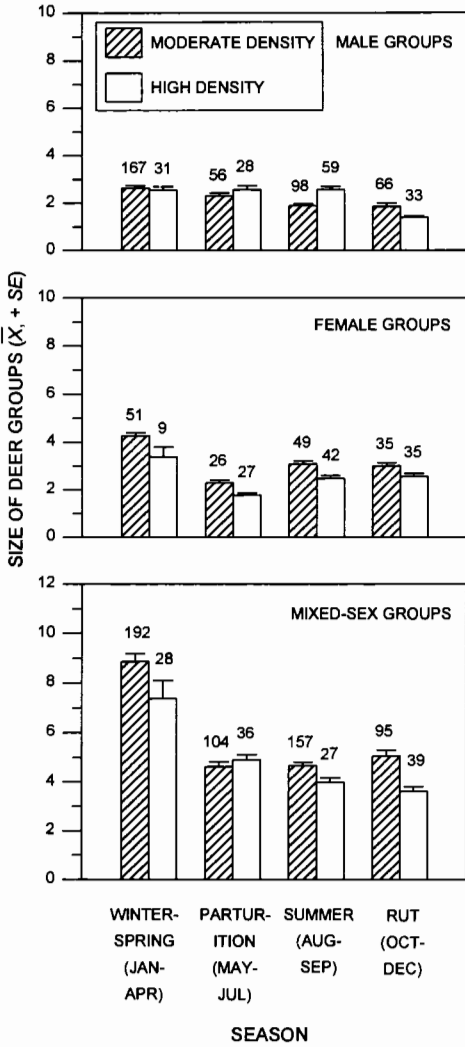


FIG. 2.—Mean ($\pm SE$) group size for males-only, females-only, and mixed-sex groups of white-tailed deer at moderate and high densities on the Welder Wildlife Refuge, San Patricio Co., Texas, 1975–1976. Number of groups are shown above each bar.

the moderate density was 0.26 (± 0.01), which differed significantly ($P \leq 0.01$) from the overall mean of 0.29 male (Table 1). The mean absolute value of the deviation between the proportion of males in the population at the high density and the proportion of males observed among all quadrats at the high density was 0.23 (± 0.02), which differed significantly ($P \leq 0.01$)

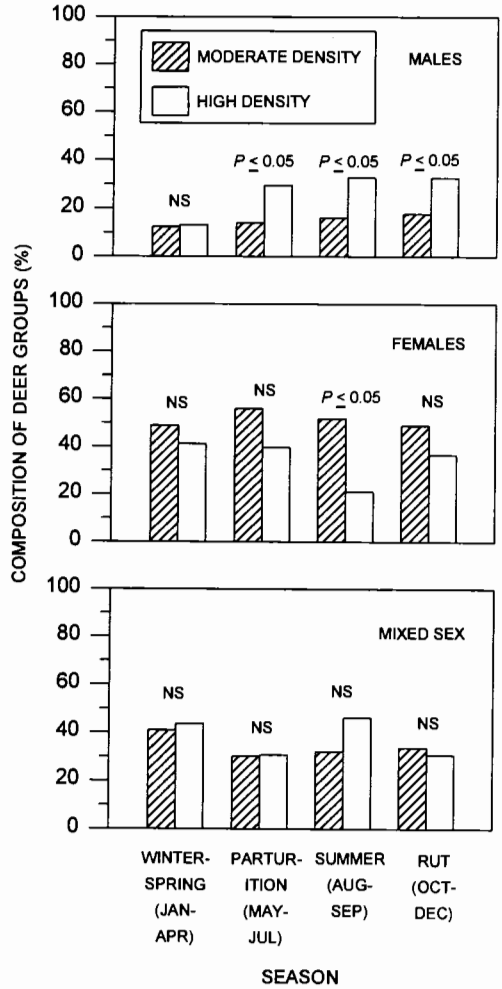


FIG. 3.—Percentage of total groups classified as male, female, and mixed-sex for white-tailed deer at moderate and high densities on the Welder Wildlife Refuge, San Patricio Co., Texas, 1975–1976. P -values for differences between moderate and high densities, where significant, are shown above each set of bars; NS = not significant ($P > 0.10$).

from the overall mean of 0.45 male (Table 1). Those data indicate that changes in the degree of sexual segregation between high and moderate densities of deer (Fig. 4) were not simply artifacts of the skewed sex ratios (Table 1).

Chaparral–mixed grass habitat occurred both inside and outside the enclosure and was selected (use greater than availability)

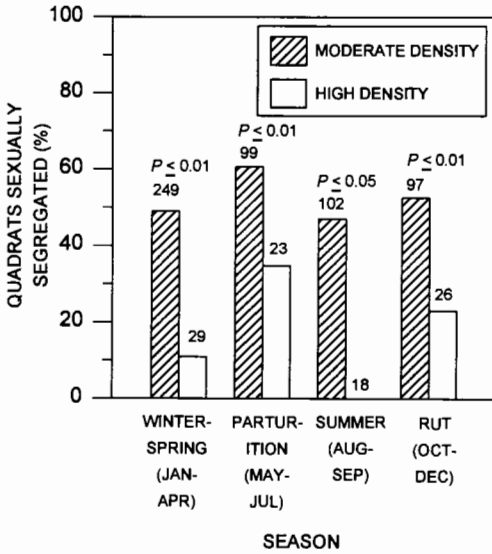


FIG. 4.—Percentages of quadrats that were sexually segregated on a monthly basis at moderate and high densities deer on the Welder Wildlife Refuge, San Patricio Co., Texas, 1975–1976. Number of quadrats in each month containing deer summed within seasons are shown above each histogram; P-values are for differences between moderate and high densities; percentages of quadrats at moderate density are significantly different from zero ($P \leq 0.01$); percentages of quadrats at high density are significantly different from zero ($P \leq 0.01$) only during parturition and rut.

by males and females in all seasons; consequently, we used that vegetation association to evaluate the role of population density on habitat selection (Fig. 5). Adult females showed strong site fidelity and were relatively consistent in their preference for chaparral-mixed grass habitat during parturition, summer, and rut at both moderate and high densities, with selection values (percent use minus percent available) ranging between 25% and 37% (Fig. 5).

During winter-spring, females reduced their preference for chaparral-mixed grass habitats at moderate density but increased their preference for that habitat at high density (Fig. 5). Adult males selected chaparral-mixed grass habitat less strongly than did adult females during all seasons at mod-

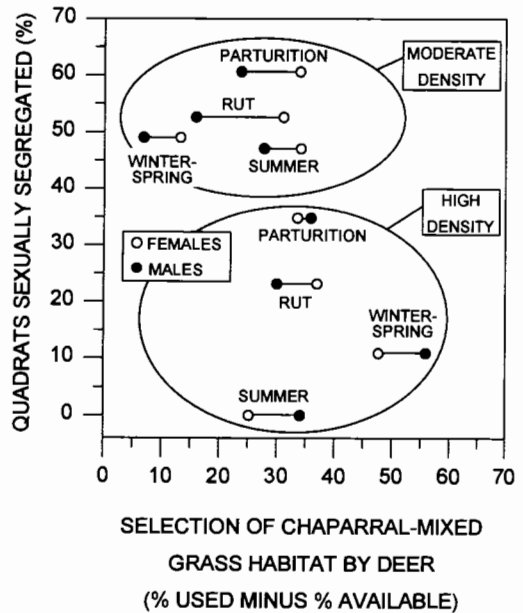


FIG. 5.—Selection for chaparral-mixed grass habitat (percent used minus percent available) by adult male and female white-tailed deer and percentages of quadrats that were sexually segregated at moderate and high densities on the Welder Wildlife Refuge, San Patricio Co., Texas, 1975–1976. Ellipses group moderate and high densities of deer but have no statistical meaning.

erate density (Fig. 5). At high density, however, selection for chaparral-mixed grass was stronger in males than in females during winter-spring, parturition, and summer (Fig. 5).

In general, diets of deer consisted primarily of forbs during winter-spring and parturition, with a limited amounts of grasses and browse (Table 2). Differences in diets between winter-spring and parturition as shown by 95% CI ellipses were strongly represented along PC1, which explained 40% of the total variation (Fig. 6). *Stipa leucotricha* and other graminoids loaded with large positive eigenvectors (0.315, 0.395, respectively), whereas *Malvastrum aurantiacum* (−0.385), *Marsilea macropoda* (−0.317), and other forbs (−0.382) loaded with large negative eigenvectors along PC1, representing a shift from cool-

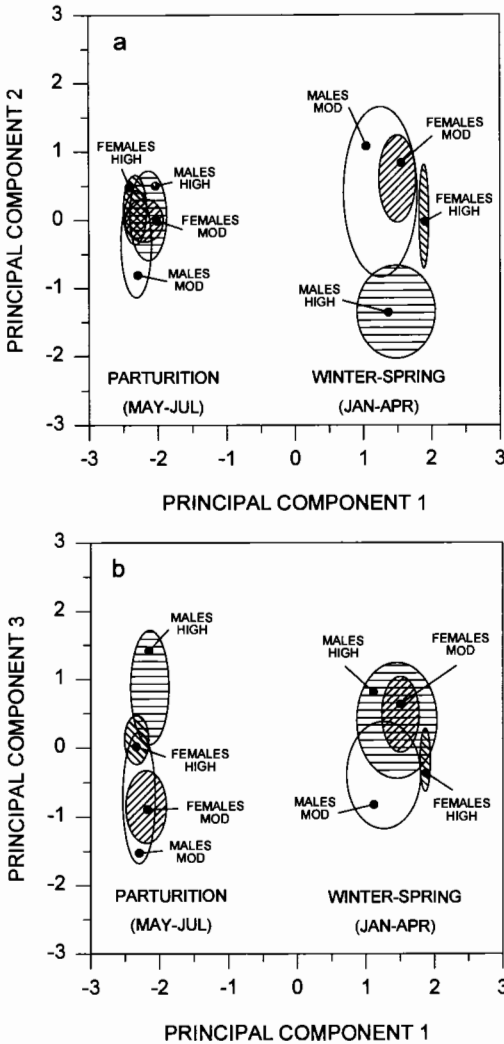


FIG. 6.—a) Principal components 1 and 2 and b) principal components 1 and 3 for diets of white-tailed deer at moderate and high densities during winter-spring and parturition on the Welder Wildlife Refuge, San Patricio Co., Texas, 1977. Ellipses are 95% CI. The first three principal components (PC) explained 66% of the variation in diets (PC1 = 40%, PC2 = 15%, and PC3 = 11%).

season C₃ grasses during winter-spring to a diet richer in forbs during parturition (Table 2).

Principal component 2 explained an additional 15% of the variation and was related to dietary differences between males

and females at high density during winter-spring (Fig. 6a). At moderate density, diets of males were broad and encompassed the niche breadth of females completely (when defined along PC2; Fig. 6a). At high density, however, diets for both males and females diverged; furthermore, there was no overlap along PC2 between males and females (Fig. 6a). *Stipa leucotricha* (-0.256), other graminoids (-0.288), and browse (-0.521) loaded with large negative eigenvectors along PC2, suggesting that at high density during winter-spring, deer ate more grasses and browse and fewer forbs (Table 2). That pattern was most pronounced among males at the high population density (Fig. 6a).

Principal component 3 explained an additional 11% of the variation (for a cumulative total of 66% for the first three principal components) and reflected dietary differences between males and females at high density during parturition (Fig. 6b). At moderate density, diets of males were diverse and encompassed the niche breadth of females to a large extent (Fig. 6b), similar to diets in winter-spring as indicated by PC2 (Fig. 6a). At high density, however, diets for both males and females changed, and there was little overlap along PC3 between sexes (Fig. 6b). *Ratibida columnaris* (0.485) and browse (0.536) loaded with large positive eigenvectors along PC3, suggesting greater reliance on those items during parturition at high density (Table 2).

In the moderate-density population, kidney fat among females averaged 16.8% (*SD* = 15.9%, *n* = 32) and femur-marrow fat averaged 56.0% (*SD* = 17.5%). In the high-density population, adults of both sexes had lower amounts of kidney and femur-marrow fat. Among females at high density, kidney fat averaged 6.3% (*SD* = 3.7%) and femur-marrow fat averaged 35.0% (*SD* = 20.0%). Proportional reductions in kidney fat and femur-marrow fat among females at the high density were 0.62 and 0.38, respectively.

In the moderate-density population, kid-

ney fat among males averaged 20.8% ($SD = 12.3\%$, $n = 15$), and femur-marrow fat averaged 54.4% ($SD = 18.2\%$). Comparable data for males in at high density were mean kidney fat = 12.6% ($SD = 11.2\%$) and mean femur-marrow fat = 44.3% ($SD = 20.6\%$). Proportional reductions in kidney fat and femur-marrow fat among males at the high density were 0.40 and 0.18, respectively. The difference in the proportional reduction in femur-marrow fat between females and males (0.38 versus 0.18) was significant ($t = 2.71$, $P < 0.01$). The difference in the proportional reduction in kidney fat between females and males (0.62 versus 0.40) was not significant ($t = 1.02$, $P > 0.10$).

DISCUSSION

Spatial separation of sexes outside the mating season is widespread among polygynous ruminants (Bleich et al., 1997; Main et al., 1996). Although there may be no single explanation for sexual segregation (Miquelle et al., 1992), the near ubiquitous nature of this phenomenon among polygynous bovids and cervids suggests some common cause. The most likely reasons for segregation of sexes are intersexual competition or other aspects of differential body size between sexes, social factors, and predation (Bleich et al., 1997; Main et al., 1996). One long-standing difficulty in gaining insights into the way sexes segregate has been the lack of manipulative experiments that allowed critical tests of hypotheses. Our retrospective study overcame that limitation.

Sexual segregation requires that sexes be spatially separated and is not merely a difference in the manner in which sexes associate with one another (Bleich et al., 1997; Bowyer, 1984; Main et al., 1996). Indeed, there can be substantial variation in the degree of segregation (Fig. 4) without changes in the proportion of single-sex and mixed-sex groups (Fig. 3). Moreover, testing ideas about sexual segregation requires a spatial component. If sexes continue to use the same area but at different times,

competitive exclusion of one sex by the other through passive competition for preferred forage (sensu Clutton-Brock et al., 1987) is not possible. Sexual segregation also might appear as an artifact of a skewed sex ratio among adults (Bowyer et al., 1996). Although the stress of raising more fawns to older ages likely added to the mortality of adult females at high densities within the predator enclosure and resulted in a relative increase in the proportion of adult males (Kie and White, 1985), we demonstrated that the degree of observed segregation was not biased by differences in the ratio of adult male and female deer.

In addition to demonstrating spatial separation of sexes, sexual segregation must be measured at the proper scale (Bowyer et al., 1996). Female and male white-tailed deer partition use of space on a very fine scale (1 ha—McCullough et al., 1989). Likewise, our 2.9-ha quadrats were sufficiently small to detect segregation on the Welder Refuge (Fig. 4). Main (1994), however, reported little sexual segregation among white-tailed deer on the Welder Refuge using 25-ha quadrats. Clearly, scale has a profound effect on the ability to detect sexual segregation.

If males and females avoided each other because of social factors, we predicted that increased density, and hence, increased levels of social interactions, would lead to greater segregation of sexes. Such an outcome would be similar to results from interference competition, irrespective of the social behaviors involved. Our data, however, clearly indicate that sexual segregation decreased with increased density (Fig. 4). Moreover, no difference occurred in the proportion of mixed-sex groups between moderate and high-density populations of deer (Fig. 3), although we expected a decline in mixed-sex groups at high density if social factors were responsible for sexual segregation. Consequently, we rejected the social-factors hypothesis as an explanation for spatial separation of sexes.

Males and females also might segregate

because of passive intersexual competition. Support for this hypothesis comes from Clutton-Brock et al. (1987), who reported that red deer living in a relatively homogeneous environment exhibited increased levels of sexual segregation with increasing population density. Those authors postulated such an outcome resulted from smaller females competitively excluding larger males from higher-quality sites by reducing forage biomass below levels on which males could feed effectively. Supportive data are available elsewhere (Gross, 1998; Main and Coblenz, 1996). Illius and Gordon (1987) also argued that allometric differences between sexes may explain segregation in ruminants. Subtle differences in the diets of male and female deer have been reported (Beier, 1987; Bowyer, 1984), but whether such variation in diet is sufficient to explain sexual segregation is uncertain.

Miquelle et al. (1992) questioned the role of population density, and hence competition, on sexual segregation in Alaskan moose, because sexes showed strong spatial separation at low population levels where intense competition was unlikely. Du Toit (1995) likewise doubted the importance of intersexual competition in causing sexes of greater kudu to segregate. Bleich et al. (1997) reasoned that female mountain sheep were unlikely to have competitively excluded males, because males occupied better-quality ranges than did females at the peak of sexual segregation. Clearly, considerable difference of opinion exists regarding the role of competition in causing sexual segregation among these large herbivores.

Our experiment greatly increased levels of competition for both female and male white-tailed deer as a result of increased population density. When removal of coyotes (*Canis latrans*) started in 1973 within the predator enclosure, deer numbers began increasing immediately, resulting in a mean density of 77 deer/km² compared with 39 deer/km² elsewhere on the refuge 1974–1977 (Fig. 1). Some coyotes, however, re-

mained within the enclosure during our experiment. Those coyotes exhibited a functional response and were likely the cause of cessation in population growth in deer through increased predation on fawns 3–12 months of age (Kie and White, 1985). Within the predator enclosure, body weights and fat reserves of deer were significantly lower (Kie et al., 1983), reproductive rates declined, reproduction was delayed and became less synchronous (Kie, 1977; Kie and White, 1985), and males retained their antler velvet longer but shed their hardened antlers earlier (Kie et al., 1979). All of these outcomes are consistent with a lower level of nutrition caused by increased competition. Such a relationship has been well documented for other populations of white-tailed deer (McCullough, 1979).

At moderate density, males were able to make greater use of open mesquite–mixed grass habitat (Fig. 5), where canopy cover of shrubs was lower (Drawe et al., 1978) and forbs were more abundant. As a result, kidney-fat index, a measure appropriate at the upper end of the condition scale, was higher in males than females but femur-marrow fat, a measure appropriate at the lower end, did not differ between males and females at moderate density (Kie et al., 1983). Adult deer of both sexes in the high-density population had lower amounts of kidney and femur-marrow fat than those in the moderate-density population. The proportional reductions in kidney fat and femur-marrow fat for females at high density were 0.62 and 0.38, respectively, but those for males were only 0.40 and 0.18. Those differences were significant ($P < 0.01$) for femur-marrow fat, but not for kidney fat, the latter of which is indicative of physical condition only at the upper end of the scale (Kie et al., 1983). That outcome suggests that females exhibited greater proportional reductions in fat reserves at the high-population density than did males. Although both sexes were in poorer condition at high density (Kie et al., 1983), based on kidney

fat and femur-marrow fat, females suffered proportionally more than males. If intersexual competition had been the most important factor in the dietary differences between sexes at high density and males were being forced to subsist on poorer-quality forages, we should have seen greater reductions in kidney fat and femur-marrow fat among males. Males, however, appeared to suffer less than females, suggesting that intrasexual competition was stronger than was intersexual competition at high density.

Data reported herein are consistent with previously published information. The increased proportion of adult males at high density was comparable with those previously reported for 1974–1997 with 0.37 males at moderate density and 0.24 males at high density (Kie and White, 1985). Diets also were consistent with those reported for 1975–1976 (Kie et al., 1980), with one exception. In this data set collected during 1977, we noted the frequent occurrence of *Marsilea macropoda*, a plant common in aquatic and other wet habitats such as swales, particularly during parturition (Table 2). That species likely was not present in detectable amounts in the previous data because of differences in annual patterns of rainfall.

Despite a dramatic increase in population density and competition inside the enclosure that resulted from predator control, the degree of sexual segregation did not increase but declined significantly at high density (Fig. 4). Consequently, we rejected intersexual competition as a cause of sexual segregation in white-tailed deer on the Welder Wildlife Refuge. We cannot rule out that differences in density of predators inside and outside the enclosure may have affected our results, even though some predators remained inside the enclosure. Nonetheless, ungulates typically respond to habitat characteristics in a manner that reflects risk of predation (Bleich, 1999; Hirth, 1977; McNamara and Houston, 1987; Sinclair and Arcese, 1995). We cannot critically test ideas about how predation directly

relates to sexual segregation with our experiment because reduction of coyotes inside the enclosure was responsible for increasing survivorship of deer fawns ≤ 3 months of age and ultimately changes in population density of deer (Kie, 1977; Kie and White, 1985; Kie et al., 1979; Fig. 1). Nonetheless, our data are consistent with predation playing an important role in segregation by sex; population density alone is not sufficient to explain patterns of habitat selection and spatial separation we observed at moderate and high densities.

Our data may differ from those of previous authors studying sexual segregation for several reasons. Others have been forced to use induction to resolve questions about how competition affected segregation of sexes by simply noting if their data were consistent with that hypothesis. Even the long-term data set of Clutton-Brock et al. (1987) is correlative rather than manipulative in design. We do not believe, however, that design alone explains the difference between our data and those obtained by Clutton-Brock (1987) for red deer in the open, treeless habitats on the Isle of Rhum, Scotland. Red deer have existed there since the end of the Pleistocene but in heavily forested habitats for most of that time (Clutton-Brock et al., 1982). Miquelle et al. (1992) and Bleich et al. (1997) have argued convincingly that habitat heterogeneity plays a role in sexual segregation. Red deer on Rhum may have responded to loss of forested habitats and the corresponding reduction in habitat heterogeneity by intensifying competition for the limited number of remaining habitat types thereby resulting in competitive exclusion of males by females. The question cannot be resolved without further manipulative tests, but we believe conclusions from the study of red deer on Rhum are not likely to hold for areas with a more heterogeneous environment.

Although not strongly heterogeneous, habitats on the Welder Refuge exhibited sufficient differences to contribute to seg-

regation of sexes in white-tailed deer. Indeed, white-tailed deer segregate sexually on a fine scale compared with other ungulates (Bowyer et al., 1996). Canopy cover of shrubs on the Welder Refuge differed between the two most common habitat types: 12–27% in mesquite–mixed grass, and 34–55% in chaparral–mixed grass (Drawe et al., 1978). Cover of graminoids and forbs was related inversely to the canopy cover of shrubs (Drawe et al., 1978). Habitats were sufficiently heterogeneous for us to detect sex-related differences in selection for particular types. All deer on the Welder Refuge showed preferences for chaparral–mixed grass habitats, but such preferences were stronger among females than males at moderate densities during all seasons, and weakest in both sexes during winter–spring (Fig. 5). During winter–spring, cool season C₃ grasses were growing rapidly, and males and females made use of the more open mesquite–mixed grass habitats where they ate substantial amounts of *Stipa leucotricha* and other graminoids (Table 2). During parturition, summer, and even into rut, females in particular showed increased selection for chaparral–mixed grass habitats (Fig. 5).

The manner in which spatial separation of sexes, diet, and habitat selection are interrelated is complex. At moderate density when competition was lower, there was broad overlap in dietary niches of females and males during both winter–spring (Fig. 6a) and parturition (Fig. 6b). At high density, where competition was intense, there were marked differences in the dietary niches of sexes during the same periods (Fig. 6). Thus, the greatest differences in diet between sexes occurred at high density when males and females reduced their degree of spatial separation (Fig. 4). We conclude from that analysis that dietary differences between sexes were not the cause of sexual segregation but rather a consequence of that behavior. These outcomes (Fig. 6) are consistent with niche theory (Pianka, 1988); increasing population density and competition should lead to a broadening of

niche width for a species, whereas reduced competition should narrow niche breadth. Ungulates exhibit extreme sexual dimorphism (Ralls, 1977; Weckerly, 1998), and consideration of niche dynamics of sexes as if they were separate species has merits for understanding sexual segregation.

A comparison of habitat selection between moderate and high density (Fig. 5) also can be interpreted using niche theory. Male white-tailed deer selected chaparral–mixed grass habitat more strongly at high density than at moderate density. Thus, high density resulted in more spatial overlap between sexes (less sexual segregation; Fig. 4), at least in part, because males broadened their niche to include more chaparral–mixed grass habitat (Fig. 5). That increased overlap on the habitat–niche axis likely resulted in more partitioning (avoidance) on the dietary–niche axis; diets of females and males were more dissimilar at high density (Fig. 6). Ungulate species that coexist in complex assemblages often partition one niche axis if overlap occurs on another important axis. For example, bison (*Bison bison*) and pronghorn (*Antilocapra americana*) exhibited substantial overlap in use of space, but had diets that were extremely divergent, with bison consuming mostly grasses and pronghorns eating primarily forbs (McCullough, 1980).

One aspect of habitat selection, especially by female deer, cannot be explained solely as a result of increased competition at high population density. Females exhibited few changes in their preference for chaparral–mixed grass habitat between moderate and high density in all seasons except winter–spring. Males, however, showed increasing selection for chaparral–mixed grass habitat at high density (Fig. 5). The chaparral–mixed grass community provided more hiding and escape cover than the more open mesquite–mixed grass type. Because predation, especially by coyotes, is a major source of neonatal mortality among white-tailed deer on the Welder Refuge (Cook et al., 1971), we hypothesize that females with

young at heel preferred chaparral-mixed grass habitat in most seasons because risk of predation to young was greater in more open habitats. Consistent with this interpretation was the shift in habitat selection by females toward more open mesquite-mixed grass habitats during winter-spring when young deer were becoming less reliant on adult females for maternal care and were less susceptible to predation.

Risk of predation is thought to be a major factor regulating habitat selection (Berger, 1991; Rachlow and Bowyer, 1998) and thus sexual segregation in many ungulates (Bleich et al., 1997). For example, female huemuls (*Hippocamelus bisulcus*) in Chile occurred mainly on bluff habitats, newborns were seen only on bluff habitats, and males were seen most commonly on periglacial grasslands (Frid, 1994). Frid (1994) suggested that females were using more rugged habitats to minimize risk of predation. King and Smith (1980) also invoked predator avoidance as one cause of segregation between male and female mule deer in Utah, with large groups of males occupying open habitats where they could detect predators at a distance and females with young using closed habitats with better hiding cover. Similarly, the greatest degree of sexual segregation in alpine ibex (*Capra ibex ibex*) in the French Alps occurred during parturition when females made extensive use of cliffs (Villaret et al., 1997). Female Nubian ibex (*C. ibex nubiana*) in Israel that did not have young at heel also selected richer feeding habitats and foraged further away from escape terrain than those with young (Kohlmann et al., 1996). In both instances, female ibex with young appeared to choose habitats of lower quality for reasons associated with avoidance of predators. Gross et al. (1995), however, provided data that suggest nutritional factors also influenced how male and female ibexes segregated.

Miquelle et al. (1992), Main et al. (1996), and Bleich et al. (1997) attempted to reduce the large number of hypotheses proposed to

explain sexual segregation in ungulates, so that research could be concentrated on ideas that would likely yield fruitful results. Our study resulted in rejection of the social-factors hypothesis and the idea that differences in intersexual competition leads to sexual segregation, at least in areas where habitats are somewhat heterogeneous. Moreover, our data indicate that dietary differences between sexes are not the cause of sexual segregation but are instead a consequence of spatial separation. Our study indicates that risk of predation is involved in sexual segregation, but more manipulative experiments are necessary to elucidate its role. Finally, we suggest that there is merit in considering male and female ungulates as separate species for purposes of management.

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