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SEXUAL SEGREGATION IN SOUTHERN MULE DEER

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ABSTRACT.—Sexual segregation in southern mule deer (*Odocoileus hemionus fuliginatus*) was studied on East Mesa, Cuyamaca Rancho State Park, San Diego Co., California, from June 1977–January 1979. Spatial separation of the sexes occurred throughout the dry portion of the year (May–October), but was most pronounced during and immediately following the fawning period (June–August). Bucks occurred most frequently on dry meadows during sexual segregation, and does and fawns primarily in moister meadows. Bucks occurred farther from summer sources of water than did other sex and age classes of deer. Sexual segregation was not attributable to food habits or selection of vegetative types. However, the percent cover of *Sisymbrium altissimum*, a preferred food, was higher and in earlier phenological stages on ranges occupied primarily by does than in meadows where bucks predominated. The proportion does and fawns comprised of all deer in eight meadow systems was correlated positively with overall population density; an inverse relationship existed between the proportion of bucks and deer density. Consequently, the availability of forage per individual did not vary between ranges inhabited by bucks and does. Sexual segregation in southern mule deer may occur as a result of the greater needs for water of lactating does. Larger body size and rumen to body volume ratio of bucks reduce rates of water loss and may allow males to subsist on vegetation in drier phenological states.

The role of sexual dimorphism in niche separation has been investigated for birds (Selander, 1966, 1972), fish (Keast, 1977), and plants (Freeman et al., 1976). Current theory suggests that morphological differences between the sexes of some species allow individuals to occupy different niches. The resulting resource-partitioning is thought to lessen intersexual competition and ultimately enhance reproductive success. Although the origin and evolution of sexual dimorphism is explained most convincingly by sexual selection, morphological or behavioral differences between the sexes still might lead to differential use of resources (McCullough, 1979). Similar theories also may hold for mammals, but until recently few studies existed (McCullough, 1979).

Spatial segregation of the sexes is known to occur outside rut for a number of polygynous ungulates (McCullough, 1979). The extreme sexual dimorphism exhibited by these mammals (Ralls, 1977) makes them ideal for studying niche separation between the sexes.

This study investigated niche separation by sex in southern mule deer (*Odocoileus hemionus fuliginatus*). Variables considered to assess resource-partitioning were: 1) the timing of sexual segregation; 2) differential use of the study area by the sexes; 3) deer density and group composition on different portions of the area; 4) sexual differences in the use of vegetative types and distance from free water; 5) the occurrence of preferred forage on deer ranges; and 6) social interactions.

METHODS

Study Area

Location and climate.—Research was conducted at an elevation of 1,520 m on 1,250 ha of East Mesa, Cuyamaca Rancho State Park, San Diego Co., California (32°59'N, 116°35'W). The Park is located 65 km E of San Diego, and 40 km N of the Mexican border in the Cuyamaca Mountains of California's Peninsular Range.

The mean annual temperature is 12°C, and precipitation averages 88 cm per year. Most precipitation falls between November and April; snow is common during winter but usually melts within several weeks.

Description of vegetative types.—Four major plant communities occur on East Mesa. The area is dom-

inated by extensive upland meadows (619 ha) composed primarily of introduced annual forbs and grasses. Most common are *Bromus tectorum, B. diandrus, Festuca octoflora, Avena barbata, Erodium cicutarium,* and *Sisymbrium altissimum.* The oak community (149 ha) is typified by *Quercus kelloggii, Q. agrifolia, Q. wislizenii,* and *Pinus jeffreyi.* Trees of the pine community (241 ha) include *Pinus jeffreyi, P. ponderosa, P. coulteri, Quercus kelloggii,* and *Q. agrifolia.* The chaparral community (241 ha) is composed primarily of *Cercocarpus betuloides, Adenostoma fasciculatum,* and *Quercus wislizenii.*

Deer made extensive use of meadows; consequently this plant community was divided further into seven vegetative types which were distinguished easily in the field. These types were dominated by the species for which they were named and included: cheat grass (*Bromus tectorum*) (509 ha), wild oat (*Avena barbata*) (37 ha), deer grass (*Mulenbergia ridgens*) (36 ha), buckwheat (*Eriogonum fasciculatum*) (15 ha), rose (*Rosa californica*) (11 ha), mustard (*Sisymbrium altissimum*) (7 ha), and chokecherry (*Prunus virginiana*) (5 ha). Plant nomenclature is according to Munz (1974). A more complete description of vegetation on East Mesa is provided by Bowyer and Bleich (1980).

Sampling Procedures

Direct observations.—The deer population on East Mesa was nonmigratory and totaled approximately 250 individuals. Deer were observed on 268 days from June 1977–January 1979 with the unaided eye, 7× binoculars, or a 20–45× spotting scope from a vehicle or on foot over distances of 5–800 m. Observations were made primarily during the 3 to 4 h around sunrise and sunset when deer were most active.

When roads on East Mesa were passable, a fixed transect of 8.2 km typically was driven once each morning and evening. A 7.5-km fixed transect was walked once daily when snow or mud prevented driving on East Mesa. Data were collected only for undisturbed deer. If deer exhibited alert or alarm postures upon my approach, data collection was terminated. Care was taken to obtain a complete count and accurate classification of sex and age classes of deer, especially those in dense vegetation.

Sex and age classes recognized were buck (adult males older than 2 years), male yearling, doe (adult female older than 2 years), female yearling, and fawn (deer of either sex less than 1 year). Fawns were considered yearlings on June 1 following their birth. All categories were easily distinguished by body size and form or antler development for most of the year.

Deer social groupings were defined according to Hirth (1977). Doe groups contained does, but also could include yearlings and fawns. Buck groups also could include yearlings and fawns. Mixed groups included at least one buck and doe, but could contain other deer. Yearling groups contained yearlings and rarely fawns. Fawn groups contained only fawns.

Locations of deer were plotted on an aerial photograph divided into grids equivalent to 25 m^2. Sources of free water also were located on the aerial photograph; the status of ephemeral creeks and seeps was monitored weekly during the dry season. Number of deer, their sex and age class, the vegetative type in which they occurred, and their distance from free water during summer were recorded for each sighting. Focal-group and scan procedures (Altmann, 1974) were used to record deer grazing (feeding on herbaceous plants) or browsing (feeding on plants with woody stems), and when possible which plant species were consumed. Social behavior was recorded using an all-occurrences log (Altmann, 1974).

Sexual segregation of deer was examined by dividing East Mesa into eight areas ($\bar{X}$ = 78 ha, SD = 56 ha, range = 7–124 ha) based around similar meadows and bounded by natural breaks in topography and vegetation. The year was divided into dry (May–October) and wet (November–April) seasons. Deer density and the proportion of each sex and age class were determined for the eight areas. A Kruskal-Wallis test showed no significant difference ($P > 0.40$) in the use of these areas by deer occurred between years, thus data were pooled for analyses.

Vegetation sampling.—A slight modification (Bowyer and Bleich, in press) of the step-point method (Evens and Love, 1957) was used to determine the percent cover of plant species. Samples (N = 20,631 step-points) were stratified by vegetative type; starting points were determined with a random numbers table. The proportion of times a species was "hit" by a thin line (<1 mm) drawn on the toe of a boot corresponded to percent cover. If a step-point did not

strike a plant, either bare ground or litter was recorded. Although this technique may slightly overestimate percent cover, it provides a reliable index for comparing vegetative cover in different plant communities or areas (Kershaw, 1964). Adequate sample sizes for important forage species were determined by arranging the step-points into groups of 36 and stabilizing the means (Kershaw, 1964).

Each plant encountered during vegetation sampling was placed into a phenological category (green-up, midgrowth, seeding, or dormant) and examined for signs of deer use. Percent utilization was estimated by noting the amount of forage available on unutilized plants and the amount removed on plants where deer had fed (Mackie, 1970). Wallmo et al. (1973) reported that estimates of forage intake from hand-plucked samples varied little from measurements of bites removed by feeding deer. Selected plant species were measured, clipped, and weighed to compare with estimates of forage removal and to determine their moisture content.

McCullough (1969) and Anderson et al. (1972) found strong relationships between the location of mule deer feces and the occurrence and utilization of preferred foods. Thus, the area (ca. 1 m radius) immediately surrounding each deer fecal group encountered during vegetation sampling was searched for plants on which deer had fed.

Statistical analyses.—Most data were analyzed using the MIDAS statistical package at the University of Michigan. Assumptions of statistical inference were evaluated for each variable and the most appropriate test applied. Statistical tests used included the Spearman rank correlation, Kruskal-Wallis analysis of variance, Mann-Whitney *U*-test (Seigel, 1956), *G*-test (Sokal and Rohlf, 1969), *t*-test, and two-sample Z-test for proportions (Remington and Schork, 1970).

Results

Timing of sexual segregation.—The spatial separation of bucks and does on East Mesa was reflected in the lower percentages of mixed groups and higher percentages of buck groups from May–October; this was most pronounced during and immediately following the fawning period in June–August (Fig. 1). A Z-test showed the proportions of mixed groups ($P < 0.001$) and buck groups ($P < 0.001$) in June–August differed significantly from those in the peak of rut in November–December. These data alone, however, do not demonstrate spatial separation of the sexes, but rather a shift in the types of groups with which bucks and does associated.

Distribution and density of deer.—During the dry season, bucks predominated on three drier areas on the eastern half of the Mesa, whereas a Z-test indicated does occurred with a significantly higher frequency in five moister western meadows with some free water (Table 1). The lack of significant differences for yearlings may have resulted from small sample sizes. Although the percent of fawns did not differ significantly between eastern and western meadows, fawns rarely were observed on eastern ranges (Table 1).

A *t*-test showed deer densities (deer/10 ha/mo) on eastern portions of the study area during dry ($\bar{X} = 5.2$, SD = 2.8) and wet ($\bar{X} = 11.4$, SD = 1.0) seasons were significantly lower ($P < 0.001$) than means for western meadows (dry, $\bar{X} = 18.3$, SD = 10.0; wet, $\bar{X} = 25.0$, SD = 12.0). Positive correlations between deer density and the percent of does ($r_s = 0.762$, d.f. = 6, $P < 0.01$) and fawns ($r_s = 0.571$, d.f. = 6, $P < 0.10$) occurred for all eight meadow systems during the dry season, whereas an inverse relationship was found between the percent of bucks and density ($r_s = -0.738$, d.f. = 6, $P < 0.02$). For the wet season, the correlation between percent of bucks and population density was also significant ($r_s = -0.691$, d.f. = 6, $P < 0.05$), but correlations for does ($r_s = 0.515$, d.f. = 6, $P > 0.10$) and fawns ($r_s = 0.371$, d.f. = 6, $P > 0.20$) were not. Thus, during the period of sexual segregation, bucks occurred primarily in areas of lower population density and does in areas of higher deer abundance.

Food habits and range quality.—Scans of feeding deer revealed that 9.5% of 389 bucks, 8.5% of 1372 does, and 4.4% of 159 fawns were observed browsing rather than grazing during the dry season. A Z-test showed significant differences in the use of these forage classes occurred between fawns and bucks ($P = 0.02$) and fawns and does ($P = 0.02$), but not between bucks and does ($P = 0.55$). Deer fed more often ($P < 0.001$) on herbaceous plants than on those with

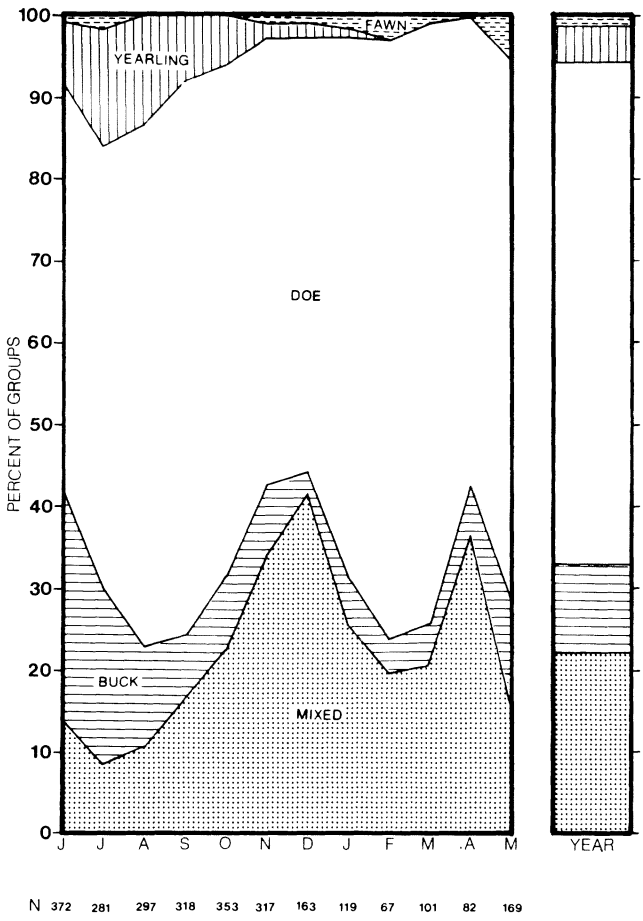

FIG. 1.—Monthly percent of southern mule deer occurring in different social groups on East Mesa, Cuyamaca Rancho State Park, San Diego Co., California, 1977–1979.

woody stems during the dry season. However, difficulty in observing which herbaceous species were ingested by deer, and too few rumen samples from periods of sexual segregation, prevented meaningful tests for further differences in the diets of bucks and does.

Sisymbrium altissimum provided a reliable measure of range quality for deer, and this plant was used to evaluate buck and doe ranges on East Mesa. An examination of plants for signs of deer use near 343 deer fecal groups showed that *Sisymbrium altissimum* was grazed upon more often (29%) than any other species during the dry season. An additional 83 *S. altissimum* were examined during vegetation sampling in June; 54% exhibited some deer use, and of those, an average of 45% of each plant was removed by deer. The importance of *S. altissimum* in the diet of southern mule deer was substantiated further by the significant correlation between the percent cover of *S. altissimum* and deer densities on the eight meadow systems of East Mesa ($r_s = 0.720$, d.f. = 6, $P < 0.02$).

A Z-test indicated the percent cover of *S. altissimum* on eastern ranges where bucks predominated ($\bar{X} = 0.4\%$, SD = 0.4%, $n = 1269$ step-points) was significantly ($P < 0.001$) lower than on western areas ($\bar{X} = 3.2\%$, SD = 2.1%, $n = 2160$ step-points) where does occurred most frequently during the dry season. Twenty-one percent of *S. altissimum* on western meadows in June were

TABLE 1.—*Percent of southern mule deer in sex and age classes during the dry (May–October) and wet (November–April) seasons on eastern (170.7 ha) and western (451.4 ha) meadows of East Mesa, Cuyamaca Rancho State Park, San Diego Co., California, 1977–1979.*

Sex and age class	Dry season			Wet season		
	Eastern meadows	Western meadows	*P*	Eastern meadows	Western meadows	*P*
Bucks						
% ($\bar{X}$ ± SD)	53 ± 13	15 ± 9	<0.001	23 ± 10	17 ± 8	0.16
N	163	575		105	454	
Male yearlings						
% ($\bar{X}$ ± SD)	11 ± 2	12 ± 5	0.86	1 ± 1	5 ± 2	0.28
N	34	383		10	121	
Does						
% ($\bar{X}$ ± SD)	32 ± 9	60 ± 8	<0.001	62 ± 11	65 ± 8	0.23
N	103	2,744		448	2,569	
Female yearlings						
% ($\bar{X}$ ± SD)	2 ± 1	5 ± 2	0.67	<1 ± 1	2 ± 1	0.62
N	4	198		7	40	
Fawns						
% ($\bar{X}$ ± SD)	2 ± 2	9 ± 5	0.27	14 ± 3	12 ± 4	0.63
N	5	497		79	531	

in green-up, 56% in midgrowth, 8% in seed, and 15% dormant. On eastern meadows, no plants were in green-up, 57% were in midgrowth, 14% were in seed, and 29% were dormant. A clear tendency existed for *S. altissimum* to be in drier condition on eastern ranges, but the only significant difference between areas was for the percent of plants in green-up ($P < 0.01$). The moisture content of 100 *S. altissimum* in each phenological stage was: green-up 66%, midgrowth 86%, seeding 74%, and dormant 5%.

The percent cover of *S. altissimum* in each of the eight meadow systems on East Mesa was multiplied by the size of the area and divided by the number of deer on that area to provide a measure of forage availability per individual. Areas with the greatest percentage of bucks (eastern meadows) were compared with areas where does predominated (western meadows) using a Mann-Whitney *U*-test, and no significant differences in forage abundance per individual occurred between those areas for the dry season ($P > 0.70$) or during the height of sexual segregation in June–August ($P > 0.25$).

Spatial segregation of the sexes may be related to differential use of vegetative types. During the dry season, 53% of 742 bucks, 66% of 359 male yearlings, 64% of 2,399 does, 59% of 182 female yearlings, and 60% of 383 fawns were found in cheat grass. A Z-test showed bucks occurred in cheat grass significantly ($P < 0.02$) less often than all sex and age classes except female yearlings ($P = 0.16$). Sex and age class differences in the use of the other nine vegetative types during the dry season were not significant ($P > 0.10$). However, 68% of 511 bucks and 75% of 2,411 does occurred in cheat grass during autumn when the sexes often associated; this difference was highly significant ($P < 0.004$).

Free water.—The distribution of southern mule deer was influenced greatly by the availability of free water. During the wet season, water was ubiquitous on East Mesa; even meadows that were extremely dry in summer abounded with springs and seeps during this period. However, by mid-June, intermittent water sources were dry and remained so until autumn.

A significant inverse correlation ($r_s = -0.967$, d.f. = 8, $P < 0.001$) existed between the percent of all deer observed and their respective distances from water during the extremely dry months of June–September. During this dry period, 77% of all deer were found within 500 m of free water; the mean distance deer occurred from water was 380 m (SD = 256 m, range =

0–2,500 m, $n = 3{,}053$ deer). A G-test showed the distance from water was significantly ($P < 0.001$) less than would have occurred if deer had been distributed randomly over East Mesa. Different sex and age classes of deer exhibited considerable variation in the distances they were found from water during June–September. Bucks occurred the greatest distance from water ($\bar{X} = 578$ m, SD = 346 m, $n = 596$), followed by male yearlings ($\bar{X} = 393$ m, SD = 258 m, $n = 3{,}359$), does ($\bar{X} = 351$ m, SD = 243 m, $n = 1{,}663$), female yearlings ($\bar{X} = 310$ m, SD = 242, $n = 182$), and fawns ($\bar{X} = 245$ m, SD = 168, $n = 253$). A t-test showed all sex and age classes differed significantly ($P < 0.02$) in their distance from water. Additionally, does with fawns ($\bar{X} = 267$ m, SD = 199 m) occurred significantly ($P < 0.001$) closer to dry season water than does without fawns ($\bar{X} = 371$ m, SD = 265). Indeed, areas on East Mesa without summer water sources typically were devoid of fawns. I observed known does and their fawns move to areas with water as intermittent springs dried out. Otherwise suitable habitat without water was not used by fawns in 1977. However, they began using this area in 1978 after Park personnel refurbished a spring which had ceased flowing during summer.

Social behavior.—Sexual segregation may be the result of social antagonism between bucks and does. I observed does chase small bucks away from fawns on three occasions. Agonistic encounters with bucks comprised 3.0% of 503 social interactions by does during the dry season, whereas a Z-test showed these aggressive interactions declined significantly ($P < 0.001$) to 0.4% of 455 interactions in the wet season.

Discussion

Most studies of niche separation between male and female ungulates have concluded that males occurred on areas that were of poorer quality (Charles et al., 1977; Geist and Petocz, 1977; McCullough, 1979; Staines et al., 1982; Watson and Staines, 1978). However, Wehausen (1980) and Shank (1982) found bighorn sheep (*Ovis canadensis*) rams on better ranges than ewes. Based solely on the percent cover of a highly preferred forage (*Sisymbrium altissimum*), southern mule deer bucks also appeared to inhabit inferior ranges during the period of sexual segregation. It would seem maladaptive for bucks to occupy areas of lower resource quality when better ranges were nearby. However, bucks occurred on ranges with significantly lower population densities than did does, and consequently, the availability of forage per individual deer did not differ significantly between areas. This finding, however, does not offer an explanation for spatial separation of the sexes.

Sexual segregation in southern mule deer may be related to differences in the use of vegetative types. Does were found significantly more often in cheat grass than bucks. A similar pattern also occurred in autumn when the sexes were more closely associated. Thus, differences in the use of cheat grass or other vegetative types holds little promise as an explanation for spatial separation of the sexes.

Southern mule deer bucks ingested more browse than does or fawns. However, browse composed such a small percentage of the overall diet during the dry season (Bowyer and Bleich, 1980) that it is questionable if this alone would have been sufficient to produce sexual segregation. McCullough (1979) found little difference in the diets of white-tailed deer (*O. virginianus*) bucks and does during spatial separation. Although Shank (1982) detected a difference in the food habits of wintering bighorn sheep rams and ewes, he concluded that spatial segregation probably was not related to differences in the energy content of their diets.

McCullough (1979) suggested that one factor influencing sexual segregation in white-tailed deer may relate to the buck's ability to subsist on a lower quality diet than that of does. Bucks possess a larger rumen in relation to body size than do does; consequently they can utilize a lower quality of forage than can females (Short, 1963). Moreover, the larger body size of bucks produces a lower metabolic rate per unit of body weight. Thus, larger males on a lower quality diet could do as well as smaller females feeding on higher quality forage (McCullough, 1979). McCullough's (1979) finding that bucks had a higher dry weight rumen fill relative to body size than did does supports this hypothesis. Forage quality on ranges occupied by southern mule deer bucks probably was lower than on areas where does occurred because *Sisymbrium altis-*

simum was in drier condition on buck ranges. Plant succulence is indicative of nutritional value for many forages (Klein, 1965). But, the larger rumen to body volume ratio of bucks may allow them to obtain a diet of equal quality to that of does consuming forage in earlier phenological stages.

Geist and Petocz (1977) speculated that males may avoid areas with females and young to minimize competition with their offspring or potential mates. However, McCullough (1979) pointed out that among highly polygynous ungulates, where sexual segregation is most pronounced, large dominant males do most of the breeding. Thus, unless group selection is invoked, it is difficult to explain why males that do not breed should avoid competing for resources with the mates and young of unrelated dominant males.

McCullough (1979) suggested that social antagonism between the sexes was not the cause of spatial segregation. He noted that although females may drive males away from fawns, they could not move more dominant bucks from prime areas. Likewise, social antagonism probably had little influence on segregation in southern mule deer; it was primarily females that changed their distribution to ranges with water and more succulent forage. Rates of agonistic interactions between bucks and does were significantly higher in the dry season, but it is unlikely that bucks drove does from lower quality to better ranges.

Does and fawns occurred significantly closer to water than bucks during sexual segregation. Larger-bodied mammals have lower rates of water loss than smaller-bodied ones (Gordon, 1977). Moreover, the water requirements of lactating mule deer are quite high (Short, 1981). Thus, females and young probably have higher water requirements than males. This hypothesis was supported by the movement of does and their fawns to new sources of water as intermittent springs became dry. Further, does with fawns were found significantly closer to water than does without young. It is probable that differences in water requirements were the primary cause of sexual segregation and niche differentiation in southern mule deer.

Whether differences in water requirements will explain sexual segregation in other ungulates is questionable. Sexual separation in many ungulates occurs during winter, and it is primarily males that alter their distribution (Charles et al., 1977; Geist and Petocz, 1977; McCullough, 1979; Shank, 1982). The finding that lower population density on buck ranges allowed males to occupy apparently inferior areas, yet obtain a diet equal to that of females may be more applicable to other species.

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