CAUSES AND CONSEQUENCES OF SOCIALITY IN MULE DEER

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ABSTRACT: We tested hypotheses concerning evolution of sociality in mule deer (*Odocoileus hemionus*) by examining effects of resources and risk of predation on group size of these large herbivores. Groups of deer were largest during rut and smallest at parturition. Likewise, habitat had a profound effect on group size with groups being largest in open meadows and smallest in densely vegetated chaparral. Patch size of habitats, however, was unrelated to group size. Availability of preferred forage correlated with number of deer but not their group size. Limited and concentrated sources of free water affected distribution but not group size of deer. Group size increased, however, with distance from concealment cover. Steepness and ruggedness of terrain was not correlated with mean size of deer groups, but maximum group size was related inversely to both variables. With increasing group size, deer increased percentage of time spent feeding and decreased alert and alarm behaviors. Feeding and alert-alarm behaviors of deer also were affected by the likelihood of encountering a predator. Feeding was reduced and alert-alarm postures increased near concealment cover, where deer would encounter stalking predators such as bobcats (*Lynx rufus*) and mountain lions (*Puma concolor*), and also far from cover, where coursing predators such as coyotes (*Canis latrans*) were more effective hunters. Overall rate of aggressive interactions increased with group size, but per capita rate for deer declined as groups increased in size. That outcome ostensibly was a result of larger groups of deer spacing themselves farther apart, perhaps because individuals in larger groups were less vulnerable to predators than deer in smaller groups. Resources likely constrained the upper limits to group size by regulating the number of deer available to form groups. Deer balanced the need to acquire food against risk of predation and altered feeding and alert-alarm behaviors accordingly. Groups of deer formed as an adaptation against predation while trying to acquire necessary resources: the evolution of sociality in mule deer is best explained as a tradeoff between those life-history strategies.

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Some animals are gregarious and others are solitary. This phenomenon has perplexed and intrigued biologists for over a century (Galton 1871) and has resulted in a myriad of hypotheses that attempt to explain why animals live in groups (Wilson 1975, Bertram 1978, Pulliam and Caraco 1984, Slobodchikoff 1984, Elgar 1989, Lima and Dill 1990, Mangel 1990 for reviews). An understanding of this enigma is important. Group living may influence the mating system and social behavior that ultimately evolves and, thereby, help modify the degree of sociality (Alexander 1974, Van Ballenberghe and Miquelle 1993, Molvar and Bowyer 1994). Thus, gaining knowledge about why animals are gregarious may provide insights into the evolution of many aspects of sociality.

Associations among animals include passive aggregations drawn together by favorable conditions. These passive collections of individuals typically are not connected by social signals and obtain no selective advantages from aggregating over those conferred on lone animals (Schoener 1971, Brown 1975). Conversely, social groups are composed of individuals that actively associate with each other. Group members engage in social interactions and often exhibit synchronous movements and feeding activities. Permanence of social groupings may vary, but these assemblages should provide some selective advantage over that conferred by a solitary existence (Brown 1975, Wilson 1975, Morse 1980).

Sociality means group living (Alexander 1974). Degree of sociality exhibited by a species reflects interplay among selection pressures, some promoting grouping and others favoring solitude. The social organization that ultimately evolves is a summation of individual adaptations to a particular environment (Williams 1966). There has been considerable debate, however, over which selection pressures are responsible for group formation.

Theoretical models concerning group living (Rubenstein 1978) have focused attention on how natural selection might favor the evolution of gregariousness. Nevertheless, applicability of generalized mathematical treatments and hypothetical examples to free-living species is extremely limited and serves primarily to point to a general direction for empirical research (Treisman 1975a).

Origin and evolution of social grouping in most species may be explained without invoking kin or group selection. Although kinship may play a role in the formation of some groups (Brown 1975), kin selection clearly is not a prerequisite for sociality (Hirth and McCullough 1977). Likewise, Williams (1966) argued convincingly that group selection offers an unlikely explanation of gregariousness for most species. Studies of the ecological benefits that accrue to social groups have been conducted on a large number of species (Wilson 1975, Bertram 1978, Morse 1980, Krebs and Davies 1981). One ultimate factor, however, may not explain sociality for all animals. Species with divergent evolutionary histories and differences between environments may preclude a single explanation for sociality.

Experimental data demonstrating the adaptive significance of groups are few, and their relevance to natural groupings of large mammals are questionable because of the difficulty of duplicating natural conditions in the laboratory (Morse 1980). Field research has implicated mating, rearing of young, thermal advantages from being close together, hydrodynamic benefits in swimming, success in foraging, reduced risk of predation, and a host of other factors as being responsible for living in groups (Alexander 1974, Bertram 1978, Morse 1980, Krebs and Davies 1981, Rita et al. 1997). Although numerous factors may be responsible for group living, an assortment of proposed advantages and disadvantages provides no clear understanding of why animals live in groups. Even studies that were designed to consider sociality often examined only one potential cause of group living. Indeed, social groups probably offer individuals more than one benefit, and studies that test for a single advantage may be open to criticism (Morse 1980).

Alexander (1974) suggested that predation, highly localized and limited resources (including mates), and enhanced foraging efficiency might be the only factors necessary to explain why animals live in groups. Moreover, he proposed that advantages that accrued to individual group members might be offset by detriments of gregariousness including intensified competition for resources, increased risk of parasite and disease transmission, misdirected parental investment in unrelated young, and increased conspicuousness to predators.

Our purpose was to obtain empirical data to test hypotheses concerning group living and assess costs and benefits of sociality for a large herbivore, the mule deer (*Odocoileus hemionus*). Factors that are likely to influence gregariousness in deer comprise 2 general categories: resources and predation. Hypotheses concerning distribution of resources tested in our study were that social groups of deer actively congregated in and around clumped resources, and that resource quality and patch size were related to group size of deer. Hypotheses that considered the role of predation in group formation of deer included that deer altered group size with respect to amount of concealment cover, and that surveillance for predators and rates of feeding were related to group size. The hypothesis considering costs of group living and, thereby, limits to sociality, was that larger groups of deer would have higher rates of aggressive encounters than smaller ones.

STUDY AREA

Location and Climate

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

Mean annual temperature is 12° C; summer maxima rarely exceed 35° C and winter minima seldom fall below -10° C. The climate is Mediterranean with most precipitation falling between November and April, but thundershowers of tropical origin produce limited rainfall during summer (Bowyer 1991). The area averages 88 cm of annual precipitation. Mean annual snowfall is 92 cm, but snow rarely accumulates and normally melts within several weeks after falling. The first year of this study was the last of a 3-year drought; flow of many streams and creeks ceased or was reduced substantially during that summer. The second year had exceptionally high precipitation that approached recorded maxima (Bowyer 1991).

Prevailing winds came from the southwest, but Santa Ana winds (hot, dry winds originating in the Great Basin) were predominantly from the northeast. Seasons were defined by climate and phenological changes in vegetation: spring (April-June); summer (July-September): autumn (October-December); and winter (January-March). Meadows, which dominated vegetation communities on East Mesa, tended to be dry from May to October, and wet from November to April (Bowyer 1984, 1991).

Flora and Fauna

East Mesa consisted of extensive upland meadows (619 ha) interspersed with stands of oak (149 ha) or pine (241 ha), and surrounded by dense brush-fields of chaparral (241 ha). The meadow plant community was composed primarily of introduced annual forbs and grasses including *Bromus tectorum*, *B. diandrus*, *Festuca octoflora*, *Avena barbata*, *Erodium cicutarium*, and *Sisymbrium altissimum*. The oak community was typified by *Quercus kelloggii*, *Q. agrifolia*, *Q. wislizenii*, and *Pinus jeffreyi*. Trees of the pine community included *P. jeffreyi*, *P. ponderosa*, *P. coulteri*, *Quercus kelloggii*, and *Q. agrifolia*. The chaparral community was characterized by *Cercocarpus betuloides*, *Adenostoma fasciculatum*, and *Quercus wislizenii* (Bowyer 1986a). Plant nomenclature was according to Munz (1974).

Feeding deer regularly occurred in

meadows (Bowyer 1986a); consequently that plant community was subdivided into 7 vegetation types that were distinguished readily in the field. Those types were composed largely of species for which they were named and included: cheat grass (*Bromus tectorum*—509 ha); wild oat (*Avena barbata*—37 ha); deer grass (*Muhlenbergia ridgens*—36 ha); buckwheat (*Eriogonum fasciculatum*—15 ha); rose (*Rosa californica*—11 ha); mustard (*Sisymbrium altissimum*—7 ha); and chokecherry (*Prunus virginiana*—1 ha).

Deer in the Park were nonmigratory and had not been hunted legally in decades. With the exception of grizzly bears (*Ursus arctos*), which were extirpated in the early 1900s (Abbott 1935), a full complement of large mammalian carnivores occurred on East Mesa. Relatively high densities of coyotes (*Canis latrans*), and bobcats (*Lynx rufus*) inhabited East Mesa, and mountain lions (*Puma concolor*) also frequented the area (Bowyer 1987). The historical distribution of gray wolves (*Canis lupus*) did not encompass extreme southern California (Mech 1970). More complete descriptions of the flora and fauna of East Mesa are available elsewhere (Bowyer and Bleich 1980; Bowyer et al. 1983; Bowyer 1984; Bowyer and Bleich 1984; Bowyer 1986a, 1986b, 1987, 1991).

METHODS

Sampling of Deer

We observed mule deer over 268 days from June 1977 to January 1979 with the unaided eye, 7 x binoculars, or a 20-45 x spotting scope at distances of 5-800 m. Observations were made from a vehicle or on foot primarily during the 3-4 h around sunrise and sunset when deer were most active; some observations also were made at midday. Weather permitting, observation periods of 24 h were undertaken at monthly intervals; nighttime observations were dependent upon clear, moonlit conditions. A fixed transect of 8.2 km typically was driven once each morning and evening when roads were passable; a fixed transect of 7.5 km was walked once daily when snow or mud prevented driving.

For purposes of data analyses, and to include the complete spectrum of sociality (i.e., from solitary to highly gregarious), we defined a group as ≥ 1 deer that were ≤ 50 m from their nearest neighbor (Siegfried 1979), and apparently aware of each other as evidenced by staring at other group members. If questions arose as to whether a deer was part of a particular group, that individual was watched until it clearly joined the group or moved away. In practice, we had little difficulty distinguishing deer groups using those criteria because groups tended to move as cohesive units.

Because group composition was relatively unstable, we evaluated 141 groups in October 1977 to determine if our criteria provided a reasonable definition of a group. Mean (±SD) nearest-neighbor distance between 106 groups of deer encountered during the same observation period was 367±280 m, whereas mean distance across each group (solitary deer excluded) was only 38±32 m. Their wide spacing indicated individuals categorized as a group formed discrete clumps. Moreover, proportion of deer feeding showed greater synchrony within groups (75%) than between groups (58%) sampled within the same observation period (~ 3 h), indicating that our definition of a group was reasonable.

We collected data only from groups that were undisturbed by our presence. If any member of a group exhibited alert or alarm postures at our approach, data collection was terminated, except where it was our purpose to evaluate that disturbance. Care was taken to assure a complete count and accurate identification of deer in each group. No data were recorded unless we were confident that hills, gullies, or vegetation did not hide deer. We spent extra time with groups in dense vegetation to assure all deer were counted. Interdependence between observations was minimized by sampling a deer group only once during an observation period, which allowed group members an opportunity to join different groups before we resampled. No significant difference occurred among direct observations, spotlight transects, and track counts in preference ratings of deer for vegetation types (Bowyer 1986a), indicating that direct observations provided a reliable measure of deer use of habitats.

We recorded sex and age of deer in each group. Categories recognized were adult males (≥ 2 years old), yearling males, adult females (≥ 2 years old), yearling females, and young (deer of either sex < 1 year old). All categories were distinguished easily based on body size and form or antler development for most of the year. Number of tines on both antlers (excluding brow tines) was noted for adult males when they possessed antlers.

We recognized 5 major types of social groups for deer (Hirth 1977, Bowyer 1984, Kie and Bowyer 1999). Adult female groups consisted of adult females but could include yearlings and young. Adult male groups contained ≥ 1 adult male and, likewise, could include yearlings and young. Mixed-sex groups were composed of ≥ 1 adult male and ≥ 1 adult female and also could contain other sex and age classes. Yearling groups included ≥ 1 yearling and rarely young, but no adult deer. Groups of young contained only young deer.

We recorded environmental data (time, temperature, relative humidity, wind speed, vegetation type, slope aspect, and steepness and brokenness of terrain) each time a group was sighted. A dial hydrometer, thermometer, and wind meter were used to gather climatic information. We obtained data on terrain from a topographic map by noting the number of contour lines in a 50-m zone around each group of deer. We determined locations of deer groups using an aerial photograph divided into grids equivalent to 25 m^2. Sources of free water also were plotted on the aerial photograph; we monitored status of intermittent sources of water weekly during summer.

Deer activity (number standing, feeding, and bedding), the area encompassed by a group, its distance from concealment cover (cover sufficient to conceal a standing deer from view at a distance of 50 m), distance from summer water, and number of individuals alerted or alarmed were recorded with focal-group and scan sampling (Altmann 1974). We obtained estimates of the area encompassed by groups by multiplying the maximum length across each group by an approximation of the average width for that group. Average spacing between group members was estimated by dividing number of individuals in a group into the area they encompassed. Estimates of group areas were compared with areas from 30 groups plotted on an aerial photograph and measured with a compensating polar planimeter; values generated by those 2 techniques did not differ by > 10%.

We sampled behavioral interactions using an all-occurrences log (Altmann 1974). Behavioral acts per active hour (A/AH; McCullough 1969, Rachlow and Bowyer 1994) were defined as any distinguishable, relatively stereotyped display that occurred in a social context (Bowyer 1981). Those acts included sexual, maternal, and aggressive interactions.

Vegetation Sampling

We used a modification of the step-point method (Evens and Love 1957) to determine percent cover and percent relative frequency of plant species (Bowyer and Bleich 1984). Step-point samples (*n* =

20,631) were collected along randomly located transects and were stratified by vegetation type and season. We determined adequate sample sizes for important forage species by arranging step points into groups of 36 and examining reduction in variance of the mean as sample size increased (Kershaw 1964). Bowyer and Bleich (1984) provide a more detailed description of this procedure.

Each plant encountered during vegetation sampling was placed into a phenological category (green-up, mid-growth, seeding, or dormant—Bowyer 1991). Additionally, percent utilization by deer was estimated by noting the amount of forage available on unused plants and the amount remaining on plants where deer had fed (Mackie 1970). Distribution of mule deer was influenced greatly by availability of succulent forbs, especially *Sisymbrium altissimum* (Bowyer and Bleich 1980; Bowyer 1986a, 1991), and we concentrated much of our sampling effort on that species.

Preference ratings were calculated according to Petrides (1975). A preference rating > 1 indicated deer occurred in a plant community more often than expected from its availability, values < 1 indicated a community was used less often than expected, and values = 1 indicate a community was used in proportion to its availability. Availability of acorns to deer was determined with 20 plots, each 0.22 m^2, which protected acorns from wildlife, and 80 unprotected plots of the same size; plots were randomly located in oak habitat. Removal of acorns by deer was determined by sampling a 49-m^2 enclosure that allowed the entry of all wildlife except deer. Data on use and availability of plant communities by deer were from Bowyer (1986a), and data on timing of acorn drop and abundance of acorns (*Quercus kelloggii*) from Bowyer and Bleich (1980).

Measurements of concealment cover were made with a 1.2 x 1.2 m board divided into 100 squares (Griffith and Youtie 1988). We located sampling points with a random numbers table and grid, and stratified samples by vegetation community. The board was held perpendicular to the ground and was observed from a distance of 15 m from 4 cardinal directions at each location. If a square on the board was ≥ 50% covered, that square was recorded as concealed; if < 50% was covered by vegetation, the square was not counted (Bowyer 1986a). Covered squares were averaged over the 4 directions at each sampling point, and concealment cover was determined from the proportion of covered squares. Adequate sample sizes were determined by stabilizing means (Kershaw 1964); 1,440 samples were collected. Brush-fields of chaparral were too thickly vegetated to enter with a sampling board; thus, data were collected on the more open periphery of those stands.

Statistical Analyses

We used data from several published studies of mule deer on East Mesa for purposes of analyzing effects of environmental variables on group size of deer, including Bowyer and Bleich (1980, 1984), Bowyer (1984), Bowyer (1986a), and Bowyer (1991). Where we did so, presentations of summary statistics and descriptions of methods are limited; more complete descriptions of analyses and methods are available in the original publications.

We analyzed most data using MIDAS statistical software at the University of Michigan. Assumptions of statistical inference were evaluated for each variable and the most appropriate test applied. Statistical tests included the Spearman rank correlation (r_s), Kruskal-Wallis test, Friedman test, Mann-Whitney U-test (Siegel 1956), G-test (Sokal and Rohlf 1969), t-test, and 2-sample z-test for proportions (Remington and Schork 1970). Spearman rank correlations make no assumptions concerning the shape of the relation between variables; we provided lines of best fit only to aid in interpretation of those data, or smoothed curves where relationships were especially complex. Degrees of freedom are presented as subscripts to all test statistics. We applied the Bonferroni correction where numerous multiple comparisons were undertaken (Rice 1989), or reduced α to 0.02 where we repeated tests on group and individual characteristics (e.g., social interactions and spacing). We could not conduct multiple regressions on ranked data because the interval between ranks was not equal. Instead, we used partial Spearman rank correlations ($r_{s\ xy \cdot z}$) to examine multivariate relationships (Conover 1971).

RESULTS

Seasonal Variation in Group Size of Deer

Repeated observations of about 250 nonmigratory mule deer on East Mesa yielded a mean (±SD) group size of 3.5 ±2.1 (range = 1-40, n = 2,639 groups). On a seasonal basis, groups were smallest in summer, increased during autumn and winter, and declined in spring (Fig. 1); Mann-Whitney U-tests with Bonferroni corrections indicated differences (P = 0.05) between all seasonal pairings. Distribution of group sizes was skewed toward smaller groups; 78% of all groups contained ≤ 5 deer. Lone deer made up the greatest percentage of deer groups during a year (Fig. 2), but groups of 2-5 contained the greatest percentage of total deer (Fig. 2). Relatively few changes occurred each month in percentage of deer in groups of 2-5 animals. For instance, groups of 2-5 deer exhibited a small CV (14.6%) across 20 months of study, compared with solitary deer (51.6%) or groups of 6-10 deer (66.1%). Disappearance of larger groups (> 10) during June-September was primarily responsible for reductions in mean group size during that period (Fig. 2).

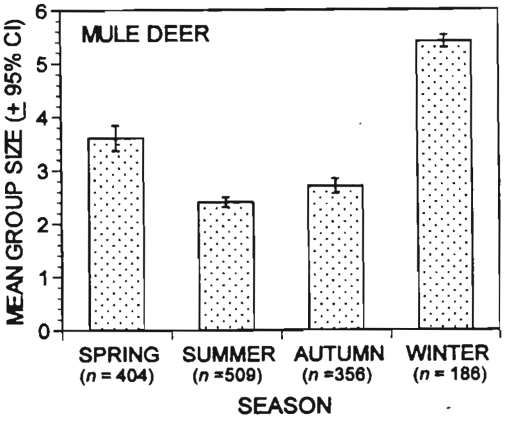

Fig. 1. Seasonal variation in mean (± 95% confidence intervals) group size of mule deer on East Mesa, Cuyamaca Rancho State Park, California, USA, from June 1977 to January 1979. Number of deer groups is provided in parentheses below seasons.

A similar pattern of monthly variation in group size was evident during both years of study (Fig. 2), indicating differences in group size between years were changes in the magnitude of the same general pattern. Indeed, significant correlations occurred between the first and second years of study for both mean monthly group size (r_{s6} = 0.74, $P < 0.05$) and percentage of solitary deer (r_{s6} = 0.952, $P < 0.001$–Fig. 2).

Sex and Age Composition of Deer

On a monthly basis, adult females composed the greatest percentage ($\overline{x}$ ±SD) of deer (64.1±9.5%), followed by adult males (15.0±7.5%), young (12.0± 5.6%), yearling males (6.3±3.7%), and yearling females (2.6±1.8%). No significant monthly variation occurred in percentage of deer in each sex and age class (χ^2_{11} = 2.62, $P > 0.99$). Over the course of a year, mean (±SD) number of young observed per 100 adult females was 18.0± 8.0. Of 1,191 males classified from August-January, 35.1% were male yearlings, 39.8% were 3-4 point males, 16.0% were 5-6 point males, and

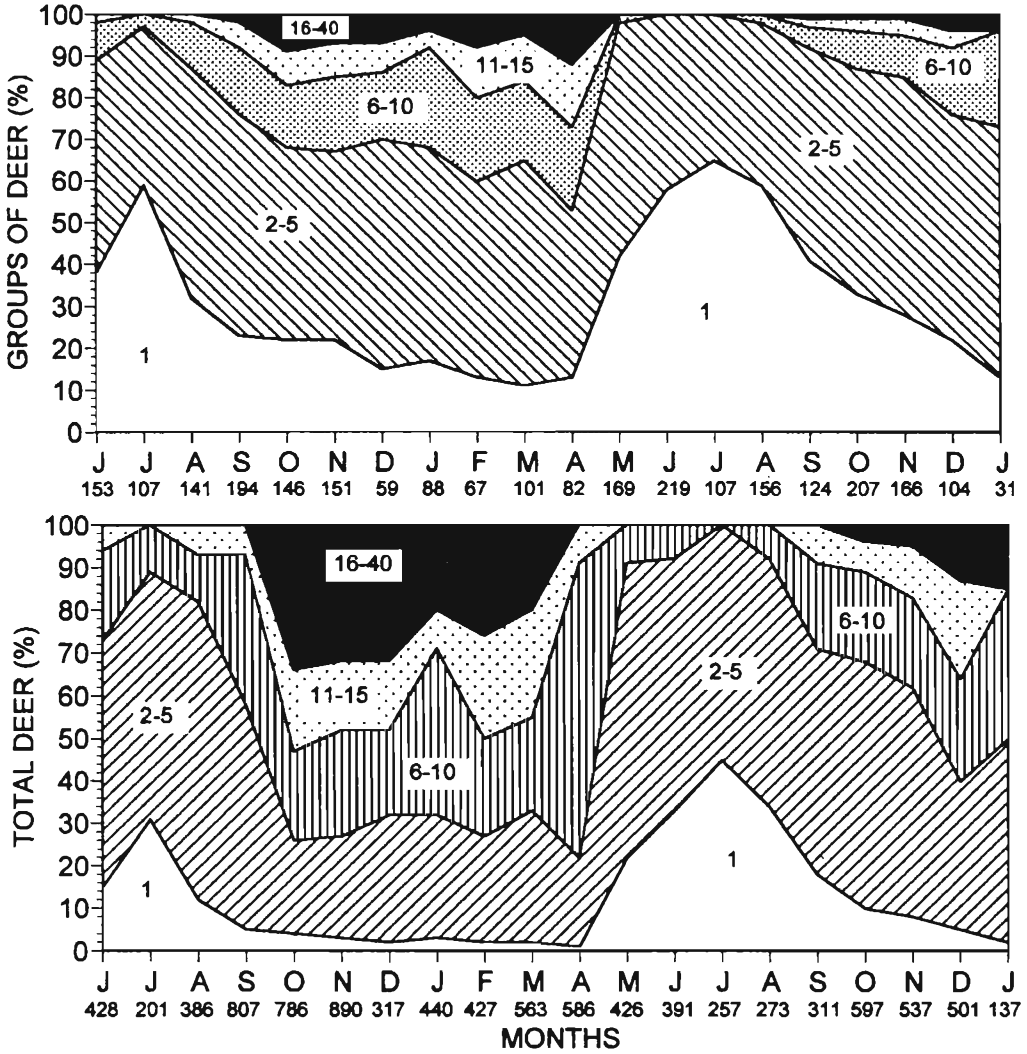

Fig. 2. Monthly changes in size of 2,639 groups of mule deer (above) and 9,260 total deer composing those groups (below) on East Mesa, Cuyamaca Rancho State Park, California, USA, from June 1977 to January 1979. Numbers within the graph indicate categories of group size. Monthly sample sizes, which resulted from repeated observations of about 250 deer, are provided below letters corresponding with months for groups (above) and individuals (below).

9.1% were ≥7-point males.

The *z*-test indicated no differences ($P > 0.10$) between first and second years of the study in percentage of deer groups occurring in the 5 social categories. Thus, data for both years were pooled for analyses (Fig. 3). Of 2,639 groups observed, adult females ($\bar{X}$ ±SD) were most frequent (59.6±11.2%), followed by mixed-sex groups (20.4±11.1%), adult male groups (12.8±8.3%), yearling groups (6.4±5.4%), and groups of young (0.8±1.3%). Groups of adult females occurred significantly ($G_1 = 98.6$, $P < 0.001$) more often than all other groups combined. On a seasonal basis, the greatest percentage of mixed-sex groups was observed during autumn; the lowest percentage occurred in spring (Fig. 3).

Groups of adult males were most common during spring, whereas adult female groups occurred most frequently in winter, and yearling groups most frequently in summer (Fig. 3). Seasonal variation in percentage of groups of young was not significant ($P > 0.7$); all other types of groups, except adult females ($P = 0.06$), exhibited significant ($P \leq 0.05$) changes in percentage of groups they composed among seasons.

Monthly lows in percentage of mixed-sex groups (8%) and highs in adult males (28%) and yearling groups (14%) corresponded with the start of the birthing period in June. The greatest percentage of mixed-sex groups occurred during the height of rut in November (35%) and December (42%). A second peak in percentage of groups that were mixed-sexed, however, occurred in April (37%), long after rutting behavior had subsided.

Mean (±SD) group sizes for each type of deer association were: mixed-sex (7.7±6.2), adult female (2.8±1.2), adult male (1.6±1.1), young (1.3±0.5), yearling males (1.2±0.5), and yearling females (1.1±0.3). The Mann-Whitney *U*-test indicated groups of adult females containing young (4.6±3.2) were significantly ($P < 0.01$) larger than adult female groups without them (2.0±1.4). Following Bonferroni corrections, significant ($P = 0.05$) differences also occurred in the size of all group-type pairings, except adult male-young, male yearling-female yearling, and female yearling-young.

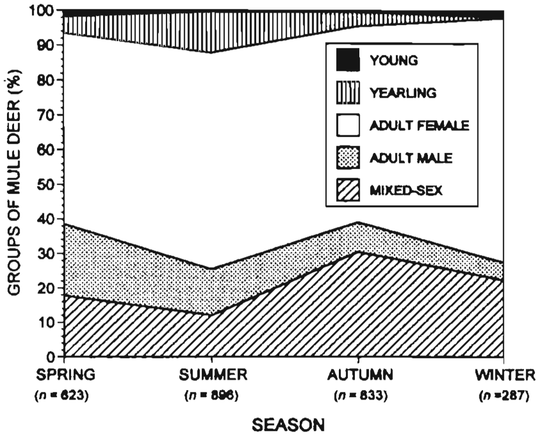

Fig. 3. Seasonal variation in percentage of 2,639 groups of mule deer categorized as young, yearling, adult female, adult male, and mixed-sex on East Mesa, Cuyamaca Rancho State Park, California, USA, from June 1977 to January 1979. Number of deer groups is provided in parentheses below seasons.

Monthly changes in types of groups with which deer associated clearly influenced group size (Fig. 3). Mean monthly group size was correlated positively with the percentage of deer groups that were mixed sex ($r_{s10} = 0.78$, $P < 0.01$), and was inversely related to the percentage of adult male groups ($r_{s10} = -0.80$, $P < 0.01$). The correlation between monthly mean group sizes and percentage of adult female groups was not significant ($r_{s10} = -0.29$, $P > 0.30$).

Patch Size of Vegetation Types and Deer Group Size

Repeated observations of mule deer ($n = 9{,}260$ individuals) indicated that they occurred most often in meadows (94.8%), followed by oak (3.6%), pine (1.4%), and chaparral (0.1%) plant communities. Direct observations indicated meadow (1.1) received the highest preference rating by active deer, followed by oak (0.7), pine (0.4), and chaparral (0.1) communities. Of meadow types, deer exhibited the highest preference for the deer grass (3.6), followed by mustard (3.5), rose (1.2), cheat grass (0.9), wild oat (0.8), chokecherry (0.8), and buckwheat (0.2).

Mean (±SD) size of deer groups varied markedly with respect to the plant community in which they occurred. On a yearly basis, sizes of deer groups were largest in meadows (3.7±2.4), followed by oak (1.8±0.34), pine (1.5±0.98), and chaparral (1.3±0.46) plant communities. The Mann-Whitney *U*-test with Bonferroni corrections indicated group size of deer differed significantly ($P = 0.05$) between all plant communities, except oak-chaparral and pine-chaparral pairings.

Mean (±SD) group sizes for deer occurring in vegetation types within meadows were mustard (6.5±4.11), buckwheat (4.1±4.13), deer grass (4.1±2.2), cheat grass (3.8±2.05), wild oak (3.0±1.39), chokecherry (2.6±1.14), and rose (2.0±0.90). The Mann-Whitney U-test followed by Bonferroni corrections indicated a difference ($P < 0.05$) in group size of deer only between mustard and rose.

A significant correlation occurred between the preference of deer for a vegetation type and their mean group size in that type ($r_{s8} = 0.93$, $P < 0.001$). One way in which vegetation types might produce changes in deer group size is through variation in the size of vegetation patches. Mean (±SD) patch size for deer grass habitat on East Mesa was 1.4±1.7 ha (range = 0.1-6.3 ha, $n = 24$). Although that habitat was highly preferred by deer, correlations between group size and patch size of deer grass were not significant ($P > 0.20$) for spring ($r_{s15} = 0.25$), summer ($r_{s19} = -0.12$), autumn ($r_{s17} = -0.13$), or winter ($r_{s12} = 0.26$). Patch size for rose habitat was 1.0±1.0 ha (range = 0.1-3.8 ha, $n = 11$). Deer only were observed in a sufficient number of rose patches to make legitimate comparisons during summer, and that correlation was not significant ($r_{s4} = 0.13$, $P > 0.20$). Patch size for the wild oat type was 1.3±1.4 ha (range = 0.1-14.7 ha, $n = 28$). Following Bonferroni corrections, no significant correlations ($P > 0.05$) occurred for deer group size and patch size of wild oats for spring ($r_{s3} = -0.20$), autumn ($r_{s11} = 0.36$), or winter ($r_{s7} = -0.22$); however, the correlation for summer was stronger ($r_{s11} = 0.67$). Patch size for cheat grass was 41.6±32.7 ha (range = 4.8-88.2 ha, $n = 7$). Again, correlations between deer group size and patch size were not significant ($P > 0.05$): spring ($r_{s5} = 0.46$); summer ($r_{s5} = 0.14$); winter ($r_{s4} = 0.42$), but a stronger correlation occurred during autumn ($r_{s5} = 0.54$). Other habitat types were used too infrequently by deer or did not occur in discrete enough patches to allow for meaningful analyses.

Patch size of the cheat grass type was not likely directly related to changes in deer group size. The area encompassed by the largest group of deer (40 animals) was only 1.1 ha, whereas the smallest patch of cheat grass habitat was > 4 times larger. Thus, deer exhibited a clumped distribution within patches of cheat grass, which suggests some other factor was most likely responsible for gregariousness among deer. Although several large patches of wild oats existed, most were within a range of sizes that might influence deer groups. Correlation between patch size and the number of deer in each patch ($r_{s11} = 0.78$, $P < 0.01$), however, was higher than the correlation for group size and patch size. Moreover, a significant correlation occurred between mean group size and total number of deer observed in each patch ($r_{s11} = 0.73$, $P < 0.01$). When number of deer was partialed out of the correlation between patch size and group size, the resulting statistic was quite low ($r_{s\,xy\bullet z} = 0.08$). That result indicated effects of resource patch size on group size might be a secondary outcome of the relationship between patch size and its influence on the number of deer.

Concealment Cover

Concealment cover also holds the potential to affect group size of deer. Meadows provided the least concealment cover; oak, pine, and chaparral offered increasing cover for deer (Fig. 4). Deer group size was inversely related to the concealment cover of the vegetation type in which deer occurred (Fig. 4). Concealment cover of vegetation in more open cheat-grass and wild-oat types, where deer were observed

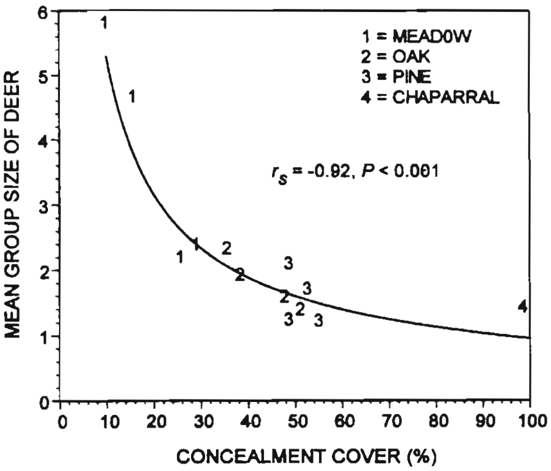

Fig. 4. Relation between mean group size of mule deer and concealment cover provided by vegetation communities during each season on East Mesa, Cuyamaca Rancho State Park, California, USA, from June 1977 to January 1979. Chaparral (4) was 100% cover during all seasons.

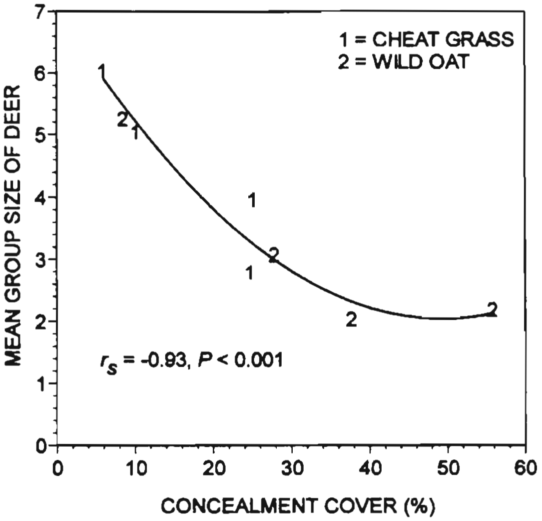

Fig. 5. Relation between mean group size of mule deer and concealment cover provided by cheat grass and wild oat types during each season, East Mesa, Cuyamaca Rancho State Park, California, USA, from June 1977 to January 1979.

readily, also was correlated inversely with group sizes of deer for each season (Fig. 5).

Mean (±SD) distance deer occurred from concealment cover was 34.6±28.8 m. As deer moved farther from concealment cover, group size increased significantly (Fig. 6). For solitary deer, adult males (29.8 m) and yearling males (29.8 m) occurred farthest from concealment cover, followed by yearling females (25.1 m), adult females (25.0 m), and young (9.2 m). If the influence of group size is neutralized by holding it constant at 2 individuals, groups of adult females without young (36.0±33.4 m;) occurred significantly ($P < 0.001$) farther from cover than those with young (24.3±19.8 m).

Overall group sizes were larger for adult females than for adult males, and the mean (±SD) distance from concealment cover for female groups (31.3±26.9 m) was not significantly different ($t_{1889} = 0.96$, $P > 0.30$) than for groups of adult males (32.3±30.0 m). Similarly, when the mean distance from cover was compared for group sizes of adult females without young (31.6±28.8 m) and groups of adult females with young (30.8±22.5 m), the difference was not significant ($t_{1553} = 0.55$, $P > 0.50$).

Acorn Production and Group Size of Deer

Most (> 80%) acorns of *Quercus kelloggii*, fell during the first 10 days of October 1978. Although acorn traps also were set for *Q. agrifolia*, no acorns fell within 5 protected plots or 20 unprotected ones. Mean density of acorns that accumulated in protected traps beneath *Q. kelloggii* was high (30/m^2) during October. Over 85% of acorns from *Q. kelloggii* were removed by wildlife (mostly deer) from unprotected plots by 20 October.

A comparison of mean (±SD) group sizes of deer in the oak community revealed that groups were smallest in September (1.5±0.86) prior to acorn drop, increased in October during acorn drop (1.8±0.81), but continued to increase in November (2.0±0.56) after most acorns had been re-

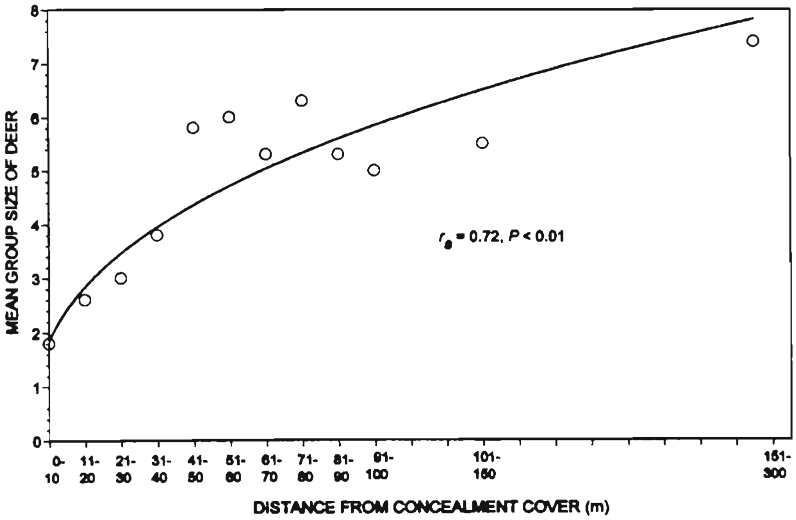

Fig. 6. Relation between mean group size of mule deer and their distance from concealment cover on East Mesa, Cuyamaca Rancho State Park, California, USA, from June 1977 to January 1979. Distances are arranged into 10-m increments; categories between 0 and 100 m are weighted to their midpoints, with larger categories of distance weighted to their means.

moved. Significant changes in mean group size occurred neither from September to October (t_{37} = 0.12, $P > 0.50$) nor from October to November (t_{18} = 0.85, $P > 0.50$) in the oak community.

Preferred Forbs

Repeated scans totaling 4,960 feeding individuals indicated deer fed on vegetation with herbaceous stems more often than they ingested species with woody stems. Less than 5% of all deer were observed browsing over the course of the study. *Sisymbrium altissimum* was concentrated in 2 meadow habitats: cheat grass (1.9%) and mustard (11.8%). Of 168 *S. altissimum* examined, 55% showed signs of deer feeding; 38% of each plant had been removed. Of plants exhibiting deer use around 973 fecal groups of deer, *S. altissimum* occurred most frequently (30.2%).

The relation between deer density and percent cover of *S. altissimum* for vegetation types was significant (r_{s8} = 0.88, $P < 0.002$). Moreover, deer density was correlated with the percentage cover of *S. altissimum* in 8 meadow systems on East Mesa during all seasons for which appropriate data were collected (r_{s6} = 0.51, $P < 0.05$). Similar correlations with deer group size as the dependent variable, however, were not significant for all vegetative types combined (r_{s8} = 0.21, $P > 0.50$) or for the cheat-grass type alone (r_{s5} = -0.26, $P > 0.50$).

Topography

Topography of East Mesa was relatively flat and rolling. Mean (±SD) steepness of slope on which deer were observed was 4.0±1.8°. Brokenness of terrain was measured by depth of gullies and washes running parallel to slope exposures; areas where deer occurred averaged 2.5±1.3 m in depth. Neither steepness nor brokenness of terrain correlated significantly ($P > 0.20$) with the mean group size of deer. Nonetheless, significant inverse correlations occurred between maximum group size of deer and both steepness and brokenness of terrain (Fig.7).

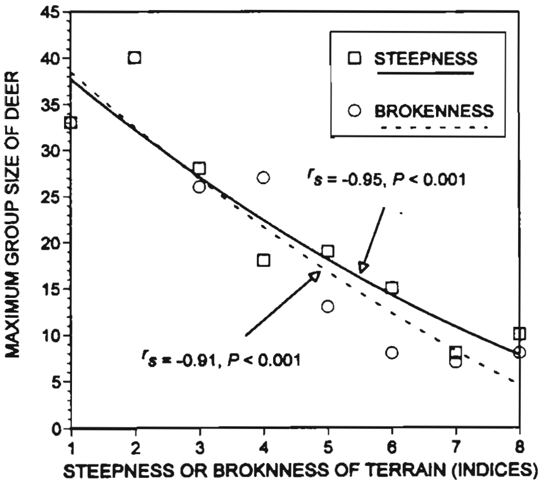

Fig. 7. Relation between maximum size of mule deer groups and steepness and brokenness of terrain on East Mesa, Cuyamaca Rancho State Park, California, USA, from June 1977 to January 1979. Categories of slope steepness range from 0 to 14% in increments of 1.75%; brokenness ranges from 0 to 10 m in depth in increments of 1.25 m.

Free Water

Availability of free water substantially influenced distribution of mule deer in summer. Mean (±SD) distance deer occurred from free water in the extremely dry period of June-September was 380±256 m (n = 3,053 deer); 77% of deer occurred within 500 m of free water. Further, a significant inverse correlation existed between the percentage of deer observed and their respective distances from free water (r_{s8} = -0.967, $P < 0.001$). No significant relationship occurred, however, between deer group size and distance from free water ($P >$ 0.10).

Climate

Mean monthly group size of deer was correlated directly with mean monthly precipitation (r_{s18} = 0.70, $P < 0.001$) and inversely with mean monthly temperature (r_{s18} = -0.72, $P < 0.001$). That relationship was investigated further by examining effects of climatic variables on group size during times when deer were under observation. Mean (±SD) relative humidity on East Mesa during periods of deer observations was 51.0±12.4% and mean temperature was 29.0±6.8° C. Deer group size was not correlated with relative humidity (r_{s8} = -0.55, $P > 0.10$); however, an inverse correlation occurred for temperature and group size (r_{s8} = -0.88, $P < 0.001$).

Group size of deer and wind speed also were correlated (r_{s8} = 0.87, $P < 0.001$). Mean (±SD) wind speed during periods of deer observation was 2.9±4.3 km/h. The relationship between wind speed and group size was not the result of an interaction between temperature and wind; that composite variable (temperature x wind speed) was not correlated significantly with deer group size (r_{s8} = - 0.41, $P > 0.20$).

Interactions Between Predators and Deer

Responses of deer to coyotes or a human observer were evaluated by assessing the degree of alarm shown by group members ($\geq$ 50% of the group) encountering those disturbances (Table 1). A significant relation occurred for distance between deer and coyotes and categories of increasing alarm (r_{s23} = 0.731, $P < 0.001$). Similar data were collected on the responses of deer to approach by a human on foot (Table 1); again, distance between an observer and deer was responsible for determining the degree of alarm among deer (r_{s131} = 0.769, $P < 0.001$). The Kruskal-Wallis test indicated that deer showed a significantly ($P <$ 0.01) greater alarm at farther distances when approached by predators than when approached by a human.

Deer Feeding and Alert-alarm Behavior

Scans of deer ($\overline{X}$ ±SD) indicated adult females fed most frequently (52.4 ±7.5%, n = 5,937) followed by young (47.5±6.6%, n = 1,110), adult males (36.2 ±13.1%, n

Table 1. Alert-alarm behaviors and gaits used by mule deer in response to approaches by coyotes and a human observer, East Mesa, Cuyamaca Rancho State Park, California, USA, from June 1977 to January 1979. Responses of deer ordered from least (alert) to greatest (gallop) alarm.

	Distance of disturbance from deer (m)							
	Coyote				Human			
Response of deer[1]	*n*	$\bar{X}$	SD	Range	*n*	$\bar{X}$	SD	Range
Alert	8	154	106	40-300	45	130	79	40-350
Stiff-legged walk	3	83	61	30-150	40	64	16	30-150
Trot	5	61	51	20-150	40	56	22	30-150
Stot	6	34	7	25-40	26	41	14	25-70
Gallop	3	28	13	15-40	4	14	6	10-20

[1] Responses of deer were scored only once for each encounter and included the closest approach and most severe response.

=1,288), yearling females (35.1±8.6%, *n* = 246), and yearling males (29.6±12.4%, *n* = 553). The *z* -test followed by Bonferroni corrections indicated all sex and age classes differed (P = 0.05) in the percentage of observations in which they fed, except pairings involving adult males-female yearlings, and male yearlings-female yearlings. Lower rates of feeding by males probably were related to rutting behavior in autumn; only 17.1% of observations totaling 511 adult males and 15.2% of 194 male yearlings were observed feeding, while 56.6% of 2,411 adult females fed during that season. In addition, a direct correlation existed between group size and percentage of deer observed feeding (Fig. 8).

Variation occurred in percentage of time spent in alert-alarm postures by different sex and age classes of deer. With group size held constant at one individual, adult males ($\bar{X}$ ±SD) were alerted or alarmed in 28.6±45.3% of the observations, followed by adult females (35.0±47.7%), yearling females (37.0±49.2%), yearling males (38.7±48.9%), and young (61.5±50.6%). The *z*-test followed by Bonferroni corrections indicated a significant difference in percentage of deer alerted or alarmed only between adult males and young. Additionally, for groups of 2, adult females with young (37.8±42.0%) were alerted or alarmed (P < 0.01) more often than adult females without young (24.0±35.6%). In general, the smaller and presumably more vulnerable the group, the larger percentage

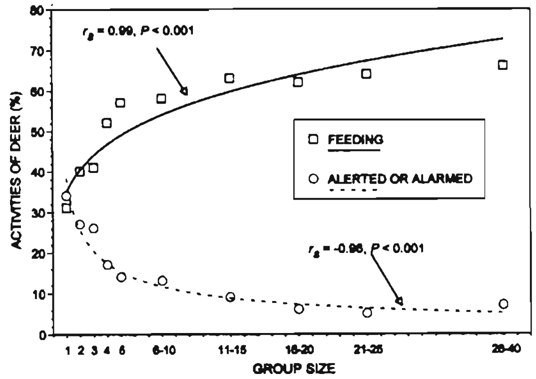

Fig. 8. Relations between feeding and alert-alarm behavior with increasing group size of mule deer, East Mesa, Cuyamaca Rancho State Park, California, USA, from June 1977 to January 1979. Group sizes are in increments of 1 deer; groups > 5 are weighted to midpoints of their categories. Feeding and alert-alarm behaviors do not sum to 100% because deer engaged in other activities.

of time deer spent in surveillance for predators. This observation is supported by an inverse correlation between mean percentage of deer alerted or alarmed and deer group size (Fig. 8).

Differences in percentage of observations in which lone deer were feeding or in alert-alarm postures changed with the plant community they occupied (Fig. 9). As deer moved from open meadows into densely vegetated plant communities with more concealment cover, the percentage of time spent feeding declined, whereas amount of alert-alarm behavior increased (Fig. 9).

Percentage of deer feeding or in alert-alarm postures also was evaluated with respect to distance from concealment cover for 799 solitary deer observed in meadows. Maximum feeding and minimum alert-alarm behavior occurred 25 m from concealment cover, whereas minimum feeding and maximum alert-alarm postures were observed at 80 m from cover (Fig. 10); variability in feeding and alert-alarm behavior beyond 80 m likely is an artifact of small sample size.

Social Behavior

Most behavior by adult males was sexual in nature, whereas yearling males emphasized aggressive interactions (Table 2). Behavior of adult females was composed largely of aggressive interactions but included some care-giving activities. Yearling females exhibited a high proportion of aggressive acts but also engaged in care-seeking interactions with adult females. Young were involved in care-seeking interactions with adult females but also behaved aggressively among themselves. Overall rates of behavior (acts per active hour [A/AH] x 10^3) were highest for male yearlings (13.5), followed by adult males (8.9), female yearlings (5.5), young (2.1), and adult females (0.3).

Total rate of aggressive interactions by mule deer increased with group size (Fig. 11). Rates of aggressive encounters for

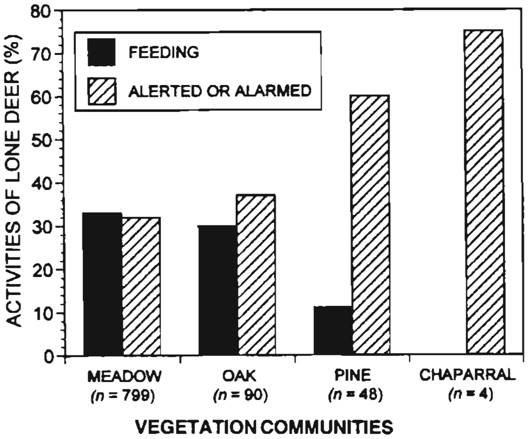

Fig. 9. Feeding and alert-alarm behavior exhibited by solitary mule deer in various vegetation communities, East Mesa, Cuyamaca Rancho State Park, California, USA, from June 1977 to January 1979. Number of deer is provided in parentheses below vegetation communities. Feeding and alert-alarm behaviors do not sum to 100% because deer engaged in other activities.

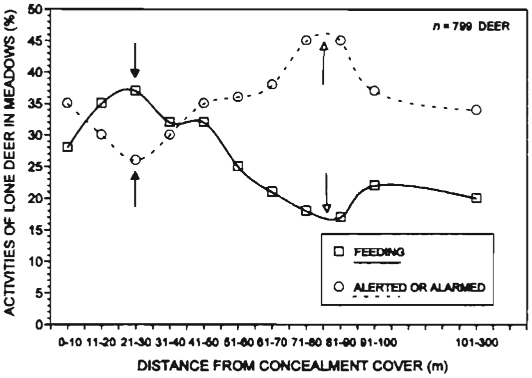

Fig. 10. Feeding and alert-alarm behavior exhibited by solitary mule deer in the open meadow community, Cuyamaca Rancho State Park, California, USA, from June 1977 to January 1979. Closed arrows indicate points of maximum feeding and minimum alert-alarm behavior; open arrows show points of minimum feeding and maximum alert-alarm postures. Distances are arranged into 10-m increments with categories between 0 and 100 m weighted to their midpoints; larger categories of distance are weighted to their means.

Table 2. Categories of behaviors performed by sex and age classes of mule deer, East Mesa, Cuyamaca Rancho State Park, California, USA, from June 1977 to January 1979.

		Categories of social behavior (%)			
Sex and age class	n	Aggressive	Sexual	Care seeking and giving	Other
Adult male	1938	30.0	68.0	0.1	1.9
Yearling male	540	70.7	26.5	0.6	2.2
Adult female	958	82.2	0.0[1]	8.1	9.7
Yearling female	27	66.7	0.0[1]	22.1	11.1
Young	245	48.1	0.4	32.7	18.8

[1] Females were not observed directing sexual behavior toward males; sexual behavior of males (Bowyer 1986b) toward females was tallied as male acts only.

individual group members, however, were inversely related to group size (Fig. 11). Total rate of sexual behavior also increased with group size (r_{s7} = 0.87, $P < 0.001$); however, the correlation between group size and per capita rate of sexual behavior did not differ (r_{s7} = 0.40, $P > 0.20$). Total rate of care-giving and care-seeking behaviors was not correlated with group size (r_{s7} = -0.07, $P > 0.50$), but individual rates of this behavior were related to size of groups (r_{s7} = -0.85, $P < 0.001$).

As group size of deer increased, so did the area encompassed by the group (Fig. 12); that relationship also held for mean spacing between group members (Fig. 12). Spacing between individuals, however, reached an asymptote for larger groups (Fig. 12).

DISCUSSION

Studies of group formation have provided important insights into the evolution of sociality in cervids (Peek et al. 1974, Hirth 1977, LaGory 1986) and bovids (Jarman 1974, Gosling 1986). Nonetheless, previous research on large herbivores has not discriminated the relative contributions of predation and resources to gregarious behavior. We investigated the roles of predation and resources, including effects of resource patch size, on sociality in mule deer to arrive at a new understanding of how gregariousness in these large herbivores likely evolved.

Environmental Funneling

Groups of mule deer were highly labile. Changes in group size and membership occurred during peaks of activity at sunrise and sunset, and groups declined in size as deer moved to oak stands where they bedded at midday (Bowyer 1986a). Relatively unstable groups also have been noted for female pronghorn (*Antilocapra americana;* Kitchen 1974) and red deer (*Cervus elaphus;* Clutton-Brock et al. 1982). Indeed, apparently random associations of female bison (*Bison bison*) led Lott and Minta (1983) to speculate that groups formed primarily in response to 3 general categories of environmental funneling: topographic; phenological (limited sources of water and forage); and rut-related (mates).

Groups of mule deer were stable in neither time nor space, but several lines of evidence suggest that environmental funneling was not the primary cause of gregariousness for these herbivores. Mean group size of deer was not correlated significantly with either steepness or brokenness of terrain; topography cannot be invoked as a mechanism to explain variation

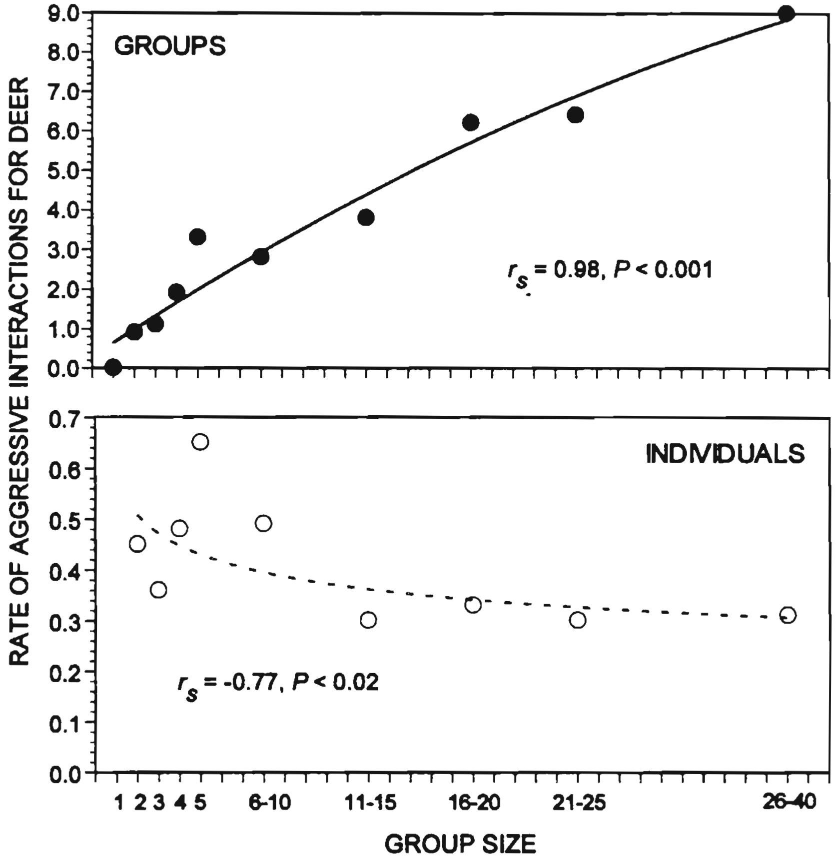

Fig. 11. Rates of aggressive interactions (behavioral acts per active hour [A/AH] x 10^3) for mule deer groups (above) and individual deer in those groups (below), East Mesa, Cuyamaca Rancho State Park, California, USA, from June 1977 to January 1979. Group sizes are in increments of 1 deer, with groups > 5 weighted to midpoints of their categories.

in group size. Those topographic features, however, were related to the maximum size of groups (Fig 7), indicating they may help set the upper limits to gregariousness.

Mule deer were concentrated around limited sources of free water in summer (Bowyer 1984, 1986a); however, the correlation between group size of deer and distance from this highly clumped resource was not significant. In addition to the previous examples, the funneling hypothesis does not account adequately for the significant correlation between deer group size and amount of concealment cover (Figs. 4 and 5) or for the relationship between group size and the distance deer occurred from concealment cover (Fig. 6).

Finally, group size of mule deer increased significantly during rut, and group size was correlated directly with the percentage of mixed-sex groups. Although availability of mates might funnel deer into an area, this hypothesis cannot explain the large group sizes and high proportion of mixed-sex groups in April after rutting behavior had ceased (Bowyer 1984, 1986b).

Despite the fluid nature of mule deer groups, they fit definitions of aggregations poorly, and are best described as social groups; they move and feed as cohesive units, and groups provide advantages relative to avoiding predators and increasing feeding. Thus, we assume gregariousness in this species evolved because of concrete advantages that accrued to individuals that formed groups (Moynihan 1962).

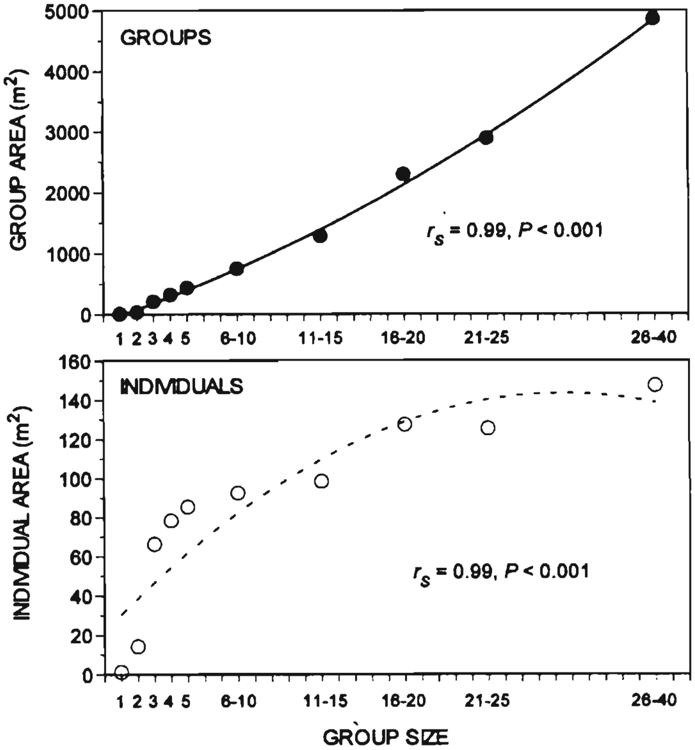

Fig. 12. Estimates of area encompassed by groups of mule deer (above) and spacing among individuals (below), East Mesa, Cuyamaca Rancho State Park, California, USA, from June 1977 to January 1979. Spacing for individuals was calculated by dividing group area by number of deer in that group. Group sizes are in increments of 1 deer; groups > 5 are weighted to midpoints of their categories.

Environmental Homogeneity

Distribution and quality of resources may play a role in formation of groups. Jarman (1974) postulated that the dispersion of food items influenced the degree of gregariousness among large herbivores. Ungulates that live alone or in small groups typically inhabit woodlands and are highly selective feeders upon widely dispersed leaves and stems of browse species. Conversely, animals that occur on open plains live in large groups that were postulated to exhibit low forage selectivity and feed on more evenly distributed grasses and forbs. Thus, Jarman (1974) proposed that in coarse-grained environments like woodlands, feeding activities of 1 animal limited forage availability to conspecifics by removing the entire food item (e.g., leaf or stem). Competitors must avoid the area where others already have foraged and, consequently, animals are widely dispersed and tend not to form groups. In fine-grained environments such as open grasslands, herbivores remove food items a little at a time so that the amount of forage is reduced, but the distribution remains relatively constant. Hence, animals can feed closer together and form groups (Jarman 1974). This hypothesis explains why large herbivores can form groups, but not why they should do so.

Groups of mule deer were largest in meadows, where distributions of palatable forbs and grasses were relatively homogeneous (Bowyer 1986a). Conversely, deer groups were smaller in woodlands, where the stems and leaves of browse species were considerably more dispersed. This pattern of forage distribution and group size followed predictions by Jarman (1974) concerning influence of resource distributions on aggregations of herbivores. Nevertheless, Hirth (1977) reported variation in group sizes of white-tailed deer (*Odocoileus virginianus*) with respect to vegetation types, but attributed changes in size of groups to amounts of concealment cover offered by the vegetation. Thus, occurrence of larger groups of deer in grasslands and smaller ones in forested areas does not necessarily support the hypothesis forwarded by Jarman (1974).

Marked changes in the availability of highly preferred acorns in the oak community (Bowyer and Bleich 1980) failed to produce concomitant changes in size of deer groups. Moreover, deer density was related to the cover of *Sisymbrium altissimum*, but correlations between deer group size and abundance of this succulent forage were not significant. The hypothesis of Jarman (1974) predicts that groups of mule deer in oaks should increase as forage on both woody and herbaceous species became more abundant in spring. Group size of deer in the oak plant community, however, declined from winter to spring. Moreover, large groups (16-40 deer) increased markedly in October (Fig. 2) while meadows were still dry and vegetation of low quality (Bowyer 1991). That result also does not follow the pattern predicted from the distribution and quality of resources proposed by Jarman (1974). The ideas forwarded by Jarman (1974) still may explain differences in foraging and gergariousness among species of large herbivores, but cannot account for changes in sociality within a species such as mule deer.

Hirth (1977) reported that groups of white-tailed deer were largest in winter when resource quality was low. Indeed, studies of bird flocks have indicated groups tended to be largest in times of resource scarcity, and declined markedly when food was superabundant (Davies 1976). Nonetheless, groups of mule deer were large during April when food was readily available. Thus, neither distribution of food items within plant communities nor seasonal changes in forage quality appear to be the primary cause of gregariousness in mule deer. These variables, however, probably affect the number of herbivores available to form groups and, thereby, set constraints on group living.

Clumped Resources

There is little doubt that the abundance, quality, and distribution of resources play a crucial role in the behavior of large herbivores (Belovsky 1978, 1981, 1984; Belovsky et al. 1999). One problem in relating group formation in deer to clumped resources, however, is the matter of scale. A preferred forage or vegetation type might be highly clumped within a micro-scale of a square meter. That scale would present an extremely fine-grained distribution to a mammal with the size and mobility of a deer. Moreover, only 1 deer at a time could occupy that patch. This is an extreme example, but points out that grouping in deer could not be favored by patches of vegetation that small. Additionally, this hypothetical outcome indicates that size of a resource patch must bear some relationship to the size, mobility, and social spacing of deer. Accordingly, the minimum size of a clumped resource must be sufficiently large to accommodate social groupings of deer if it is to influence group size. Conversely, the resource patch could not exceed the area encompassed by a group of deer by too much if the patch was responsible for producing gregariousness among those herbivores. For instance, if deer were distributed evenly over a large, relatively uniform vegetation type, that outcome would indicate deer were responding to the patch size of the resource. Conversely, if deer congregated into groups within that resource patch, the implication would be that some other variable was affecting gregariousness. Therefore, if resource patches are responsible for gregariousness, a strong correlation should exist between group sizes of deer and patch sizes of resources, and groups of deer should not exhibit too clumped a distribution within a resource patch.

Mule deer exhibited a strong preference for deer grass, yet correlations between deer group size and the size of deer-grass patches were poor. Indeed, no significant correlations occurred between group size and the patch size of vegetative types on East Mesa. Distributions of deer were highly clumped relative to the large size of cheat-grass patches. For the wild oat type, the correlation with patch size was higher for the number of deer in a patch than for deer group size; when number of deer was partialed out of the correlation between group size and patch size, the resulting value was very low. That result indicated that where clumped resources influenced deer group size, they did so by constraining the number of animals available to form groups.

Enhanced Foraging Efficiency

McNab (1963) noted that for animals to be social, sufficient resources must exist to allow group living. Further, Schoener (1968) suggested there might be a threshold density for a particular resource at which group formation occurred. There is little doubt that animals congregate about clumped and limited resources (Alexander 1974, Clark and Mangel 1986). These explanations for sociality, however, fail to account for the retention of group members when traveling between resource patches.

One factor that may favor maintenance of groups when moving between resource patches is the increased likelihood of locating the next clump. Numerous authors have postulated that a group of animals is more likely to locate clumped resources than are lone individuals (Crook 1965, Horn 1968, Morse 1970, Krebs et al. 1972, Orians 1972, Verbeek 1972, Thompson et al. 1974, Emlen 1975).

Ward and Zahavi (1973) suggested that the adaptive significance of groups might relate to the transmission of information concerning locations of resources. Why individuals associated with these "information centers" should altruistically lead others to a food source is uncertain. Perhaps unrelated group members acquire information on the location of resources intended for kin or mates. Group members also might follow well-fed or experienced individuals to resources. If food was sufficient, costs to an individual of eluding group members might outweigh detriments of the group depleting a resource. Whatever the cause, animals are attracted to areas where conspecifics are feeding (Murton 1971; Kruuk 1972; Fryxell 1991, 1995). Repeated use of areas by groups of ungulates might occur because foraging and deposition of urine and feces by those large herbivores increase rates of nutrient cycling at such sites (Fryxell 1995), thereby enhancing forage quality and attracting conspecifics (sensu McNaughton 1985, Molvar et al. 1993, Bowyer et al. 1997).

Rates of feeding in mule deer increased with group size (Fig. 8). Differences in group size between years (Fig 2) were most likely the result of drought conditions in the first study year and unusually high precipitation in the second. Indeed, such differences may help explain the inverse relation between temperature and group size of deer. Observed changes in group size likely represent the extreme responses of mule deer on East Mesa to those climatic and subsequent vegetative fluctuations. Nevertheless, if the adaptive significance of groups was related directly to their ability to locate food, then groups should be largest when resources were most dispersed and difficult to locate. Mule deer declined in group size as they occupied plant communities with poorer resources. Moreover, during both study years, groups were smallest in summer (Fig. 1) when resource quality reached yearly lows (Bowyer 1991).

Cody (1971, 1974) suggested that group members might expend less energy than solitary individuals in searching for resources by avoiding areas where the group had foraged previously and concentrating feeding activities on unexploited zones. He further proposed that a group would give each food source a longer rest between feedings than would lone animals that did not coordinate their activities; consequently, individuals living in groups would obtain a higher yield with each visit to a food source than would their solitary counterparts. This hypothesis requires that groups forage within discrete areas, or if overlap occurs, that groups maintain visual contact so that others can avoid areas where 1 group has foraged. The unstable nature and large number of mule deer groups in a relatively small area strongly argues against the notion that groups were avoiding areas that had been previously utilized and, thereby, improving their feeding efficiency. Clutton-Brock et al. (1982) came to a similar conclusion regarding groups of foraging red deer.

Mule deer spent a greater proportion of their time feeding in vegetation communities with more forage (e.g., meadows) compared with oak, pine, and chaparral (Fig. 9) that possessed less food (Bowyer 1986a); increases in feeding activity of deer also corresponded with increases in size of groups across those plant communities. Feeding efficiency, however, cannot account for the increase in alert-alarm behaviors that accompanied decreases in feeding as deer ventured into more densely vegetated plant communities (Fig. 9). Although feeding behavior increased significantly with increasing group size, benefits from enhanced foraging efficiency alone cannot explain the inverse pattern between alert-alarm behavior and group size (Fig. 8). Molvar and Bowyer (1994) demonstrated that gregariousness in moose (*Alces alces*) was a detriment to foraging efficiency. Consequently, evolution of group living does not require enhanced foraging efficiency, and some behaviors that facilitate group living in herbivores may be secondary adaptations to cope with sociality rather than its cause (Molvar and Bowyer 1994).

Significant correlations occurred for deer density and quality of habitat (as indexed by preferences of deer), and deer exhibited a marked predilection for particular types of vegetation (Bowyer 1986a). The relationship between size of a resource patch and number of animals that occur in the patch will not be surprising to most biologists. Indeed, that relationship also may explain the significant correlation between group size and preference. Thus, where a relationship exists between patch size and group size, it is most likely brought about through the influence of the patch upon the number of animals available to form groups. The number of deer inhabiting an area clearly would set the upper limits to group size. Sufficient resources to allow deer to occupy an area are a prerequisite of gregarious behavior. Nonetheless, we conclude that resources are not the primary cause of gregariousness in mule deer; rather, resources allow sociality to occur.

Predation and Sociality

Patterns of antipredator behavior among vertebrates can be immediate and direct (e.g., flight or fight), or indirect, such as use of particular habitats, vigilance postures, or group formation (Kruuk 1964, Bleich 1999). Moreover, sex and age classes of animals that are more susceptible to predation behave differently than other less-vulnerable individuals. For instance, adult female mule deer with young spent more time in alert and alarm postures, less time feeding, and were closer to concealment cover than other deer. Similar data are available for moose (Molvar and Bowyer 1994). Likewise, mountain sheep (*Ovis canadensis*) sexually segregate for much of the year, with females and young inhabiting separate mountain ranges from males, ostensibly a result of their greater vulnerability to predation (Bleich et al. 1997). Thus, presence of predators, likelihood of encountering and eluding predators in a particular habitat, and vulnerability of sex and age classes of ungulates play important roles in understanding predation risk and, in consequence, shaping sociality in those large herbivores.

Mule deer engaged in a suite of presumably adaptive behaviors that helped reduce risk of predation, including use of particular gaits to elude or outdistance predators (Table 1), direct attacks on predators (Bowyer 1987), adjustment of patterns of vigilance with respect to habitat and group size (Figs. 8 and 9), and altering group size in relation to habitat (Figs. 4 and 5). Studying sociality of large herbivores in the wild where natural predators are present is crucial to interpreting behavior of these mammals; some behavioral responses of prey can wane quickly in the absence of predation (Berger 1999). That mule deer responded with more alarm to the approach of coyotes than to a human observer (Table 1) is additional evidence that predation played a major role in the behavior of these large herbivores.

Vine (1971, 1973) developed a theoretical model that predicted a predator will have more difficulty locating a group of prey visually than the same number of randomly dispersed individuals. Treisman (1975a, b) embellished this model by making the scanning pattern of the predator and the dimension of the prey by which the predator locates them more realistic. The predicted outcome, however, remained the same; regardless of number of prey in a habitat, probability of randomly scattered individuals being discovered by a predator always was greater than for prey occurring in a group. Conversely, Alexander (1974) suggested that groups might be more conspicuous than individuals and, thus, easier for predators to detect. Although the influence of group size on the detection of deer by predators is uncertain, a wealth of direct and indirect evidence exists to support the notion that group formation in mule deer was related to predation (Bowyer 1987; Figs. 4, 5, 8, and 9).

The value of a clumped spatial distribution to prey may have a number of facets. The classic model of a "selfish herd" developed by Hamilton (1971) indicates that by becoming part of a group, individuals reduce their "domain of danger" and, consequently, lower their probability of being selected as prey. That outcome appears to hold regardless of the hunting style employed by a predator (Taylor 1976). Additionally, some group members may avoid being preyed upon by positioning themselves so that others are between them and the predator. Dominant male ungulates may force their way into the center of a fleeing herd (McCullough 1969, Kitchen 1974) or females may conceal young by leading them to the side of the group opposite the predator (Estes 1976). If groups form solely in response to predators, then less-than-optimal positions in a group must provide more protection from predation than is available to lone animals, or the group would disintegrate (Pulliam 1973). Nonetheless, there may be instances where grouping of prey may increase rather than lessen the intensity of predation (Tinbergen et al.

1967, Kelsall 1968, Croze 1970). Predators occasionally may exploit groups of prey more efficiently than individuals. Information on frequency of such attacks, whether the predator commonly preys on the species in question, or whether the group of prey attacked is of a normal size generally is lacking (Williams 1966), which makes the importance of such rare events in the evolution of sociality difficult to judge.

Another proposed advantage to gregariousness is that the collective awareness of the group may allow it to detect predators at a greater distance than would be possible for solitary animals (Pulliam 1973). Such behavior may neutralize any advantage the predator gains from surprising prey and also results in more time spent feeding and less in predator surveillance for group members. A wealth of evidence from this study (Figs. 8, 9, and 10) and others exists to support this contention (Gadgil 1972, Berger 1978, Kenward 1978, Siegfried 1979, Tilson 1980, Lipetz and Beckoff 1982, Berger et al. 1983, Aldos 1985, Dehn 1990, Berger 1991, Illius and Fitzgibbon 1994, Coulson 1999, McCullough and McCullough 2000).

Aggregations of fleeing prey may confuse and make it difficult for predators to select an individual animal to attack (Walther 1969, Jungius 1971, Lazarus 1972, Jarman 1974, Kitchen 1974). Moreover, avian (Page and Whitacre 1975, Kenward 1978) and mammalian (Schaller 1968, 1972; Kruuk 1972, 1975; Miller 1975) predators are more efficient at capturing prey separated from the group. Vocal and visual alarm signals, which often accompany predator-prey interactions, may promote group formation of prey and further contribute to confusion of predators (Maynard Smith 1965, Charnov and Krebs 1975, Hirth and McCullough 1977).

Finally, groups may employ an active defense to deter predators, whereas similar behavior by lone individuals may be ineffective or risky. Mobbing of predators is widespread among birds (Harvey and Greenwood 1978 for review), and group defenses against predators are known to exist for both primates (Bertram 1978 for review) and ungulates (Tener 1965, Kruuk 1972). Among ungulates, reactions to predators range from fleeing to overt attacks (Bleich 1999).

Importance of predators in shaping sociality for deer can be surmised by observations of coyotes hunting and attacking deer and remains of deer occurring in feces of those predators (Bowyer et al. 1983, Bowyer 1987, Pierce et al. 2000). Further, coyotes interacted aggressively less often with larger groups of mule deer than with smaller ones (Bowyer 1987). We suggest that variation in group size of deer with respect to amount of concealment cover provided by vegetation (Figs. 4 and 5) and with the distance deer occurred from concealment cover (Fig. 6) were adaptations to avoid predation. Significant correlations between those variables and group size offer strong support for the concept of the selfish herd (Hamilton 1971). Moreover, individuals in larger groups spent more time feeding and less time in alert-alarm postures than their solitary counterparts (Fig. 8); this outcome clearly is a major advantage of sociality. Additionally, solitary adult males spent less time in alert-alarm postures and occurred farther from concealment cover than did adult females, yearlings, or young. The tendency for older, larger deer to exhibit less alarm behavior and to venture farther from concealment cover probably relates to their being less vulnerable to predators. Groups of adult females and adult males did not differ significantly in distances they occurred from concealment cover; however, groups of adult females were significantly larger than groups of adult males. Perhaps deer that were more susceptible to predators required larger groups to utilize areas an equivalent distance from cover than those used by groups composed of less susceptible sex and age classes. Indeed, young mule deer are more vulnerable and often are selected as prey by large carnivores (Bowyer 1987, Pierce et al. 2000).

In dense vegetation, deer occurred in small groups or singly. Perhaps deer in such habitats do not require conspecifics to elude predators because they can flee into dense vegetation or employ cryptic behavior. Additionally, we suggest that smaller groups may be better able to detect ambush predators that lurk in dense habitats than would a large number of animals, because of the noise and confusion that accompanies a large group moving through dense brush. Other deer may interfere with the ability of an individual to detect a stalking predator; hence, members of large groups in closed habitats might be more susceptible to predation. Lower rates of feeding, and more time spent in surveillance for predators by solitary deer in dense vegetation, as opposed to more open areas (Fig. 9), supports this notion. Solitary deer exhibited minimal rates of alert-alarm behavior and maximal rates of feeding at a distance of 25 m from concealment cover (Fig. 10). Ambush predators would have been ineffective in stalking deer in open meadows, but considerable cover existed for this purpose in denser vegetation types (Bowyer 1986a). Deer in dense vegetation would not require conspecifics to elude predators. We interpret higher rates of alert-alarm behavior and lower rates of feeding in denser vegetation types and open areas close (< 25 m) to concealment cover as a result of surveillance for ambush predators. Moreover, as deer moved farther from concealment cover, there was a tendency for alert-alarm postures to increase and feeding to decline. This outcome may have occurred in response to presence of coursing predators and increased susceptibility of lone deer as they ventured further from concealment cover. Perhaps an optimum distance from concealment cover for minimum predator surveillance and maximum feeding occurred at 25 m because it was far enough from cover to neutralize the advantage of a sudden attack by an ambush predator but was close enough to cover to elude the persistent chase of a coursing hunter.

Even the direct relationship between deer group size and wind speed may involve predation. Wind noise, swirling air currents, and movements of vegetation all increased with wind speed and likely interfered with ability of a deer to locate predators. Deer in open meadows may have formed groups to overcome those difficulties by having many eyes, ears, and noses with which to detect predators. Likewise, deer also could better detect alarm signals in other group members in more open landscapes.

The weight of evidence indicates an important role for predation in group living of mule deer. Nonetheless, many life-history characteristics of ungulates represent a tradeoff between resources and predation (Festa-Bianchet 1988, Berger 1991, Bleich et al. 1997, Nicholson et al. 1997, Rachlow and Bowyer 1998, Bowyer et al. 1999, Kie 1999, Barten et al. 2001). Consequently, fully understanding the role of predation in the evolution of sociality of ungulates also requires consideration of essential resources. Deer altering group size and composition to use areas far from concealment cover is best explained by the importance of acquiring food at those sites.

Limits to Sociality

Resources unquestionably help set the upper limits to group size by regulating the number of deer available to form groups. Likewise, significant inverse correlations occurred between maximum group size and both steepness and brokenness of terrain (Fig. 7). Rugged or steep slopes may hamper formation of large groups by limiting the ability of group members to maintain contact with each other, detect predators, bunch tightly together when confronted by predators, or effectively elude pursuit.

Aggressive interactions did not limit group size of mule deer. Individuals behaved aggressively less often in larger groups (Fig. 11), ostensibly because they spaced themselves farther apart in large aggregations (Fig. 12). This wide spacing of individuals may help prevent deer on the periphery of a group from interfering with the surveillance of predators by those nearer the center of the group. Lipetz and Beckoff (1982) reported that pronghorn lifted their heads at random with respect to other group members. Thus, maximum vigilance would occur only where individuals did not obscure the ability of one another to detect predators. In addition, individuals in larger groups may have exhibited wider spacing because they were less vulnerable to predators than deer in smaller groups; ungulates often bunch together when confronted by a predator (Tener 1965, McCullough 1969, Kitchen 1974).

Relationships in Figure 8 indicate an upper limit where the addition of group members does not appreciably increase vigilance and, thereby, the likelihood of locating a predator. Similar patterns of feeding and surveillance for predators with increasing group size have been reported for other ungulates (Berger 1978, Siegfried 1979, Lipetz and Beckoff 1982, Underwood 1982, Bøving and Post 1997, Frid 1997). Such declining benefits with increasing group size may help limit gregariousness, especially where costs of group living are appreciable.

Another potential detriment to living in groups is increased competition for food. Rates of feeding, however, were higher for individuals in larger groups (Fig. 8). Moreover, interference competition, as reflected in rate of aggressive behavior, apparently was not intensified by group living (Fig. 11). Nonetheless, we have no data on diets obtained by individuals in groups, and exploitive competition cannot be ruled out. Likewise, we have no information on how rapidly resources might be depleted in a patch by foraging deer, which is likely to affect the amount of time spent in the patch and perhaps the likelihood of deer returning to forage later (Stephens and Krebs 1986). Other potential detriments to sociality exist, including parasitism and disease, and misdirected parental investment (Alexander 1974). Finally, heterogeneity of habitats affects the distribution of mule deer at scales well beyond the size of their home range (Kie et al. 2002); whether those landscape variables influence group living is unknown. We cannot directly test those aforementioned hypotheses. We note, however, that none are sufficient to explain patterns of alert-alarm behavior we observed with respect to distance from concealment cover, and with group size (Figs. 8 and 10). Likewise, those hypotheses cannot account directly for variation in group size of mule deer with concealment cover (Figs. 4, 5, and 6) and, consequently, will not stand alone as an explanation for sociality.

Searching for a single determinant of gregariousness may be futile. Deer are adapted to an environment that contains both predators and many necessary resources—tradeoffs between those variables are expected (Lima and Dill 1990). Studies that offer a single explanation for sociality are too simple; it is more useful to ask how predation and resources interact to influence social groups. Food, water, and topography greatly affected distributions of mule deer on the landscape, but correlated poorly with group size. Thus, those resources likely set the upper limits to group size by constraining the number of deer available to form groups. Resource limitation of populations is well documented for ungulates (Klein 1968; McCullough 1979, 1999; Keech et al. 2000). The evidence strongly indicates that groups of mule deer formed as an adaptation against predation while trying to acquire necessary resources.

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