

SEXUAL SEGREGATION IN RUMINANTS: DEFINITIONS, HYPOTHESES, AND IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

R. TERRY BOWYER*

Institute of Arctic Biology and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775, USA

Present address: Department of Biological Sciences, Idaho State University, Pocatello, ID 83209, USA

The concept of sexual segregation was 1st formally proposed by Charles Darwin. Among mammals, ruminants have been the focus of most research on this phenomenon. Sexual segregation has been defined traditionally as the differential use of space (and often habitat and forage) by sexes outside the mating season, but other hypotheses related to activity patterns of sexes recently have been forwarded. These new hypotheses, however, cannot explain the spatial separation of sexes or their differential use of habitats and forages. Sexual segregation should be considered in a niche framework wherein overlap on 1 niche axis is accompanied by avoidance on another, including space, diet, and habitat. Moreover, sexual segregation is scale sensitive, which limits the usefulness of a comparative approach in investigating differences among species or populations. Failure to discriminate between the potential evolutionary causes of sexual dimorphism in ruminants has led to confusion over whether polygyny or intersexual competition has led to sexual segregation. Neither exploitive nor interference competition, wherein males are competitively excluded by females, is a likely cause of sexual segregation. I suggest that the gastrocentric model, which invokes allometric and life-history differences between sexes, or risk of predation are the only hypotheses necessary to explain sexual segregation. Additional research, however, is necessary to verify some aspects of those hypotheses. The management and conservation of ruminants requires consideration that sexes behave as if they were different species, which holds consequences for estimating populations, manipulating harvest and habitats, and the potential spread of diseases and parasites and might have genetic consequences for some populations. This review attempts to resolve long-standing problems related to studies of sexual segregation, but much research remains to be accomplished, including more manipulative experiments.

Key words: adaptation, behavior, conservation, definition, management, niche, review, ruminants, sexual segregation, theory, ungulates

The concept of sexual segregation is an old one 1st formally articulated by Darwin (1871) in discussing the hypothesis of Boner (1861) for why the sexes of red deer (*Cervus elaphus*) lived apart for much of the year. Indeed, scientific underpinnings for sexual segregation were conceived even earlier by Darwin (1859:93–94) in his discussion of sexual selection, “Thus it is rendered possible for the two sexes to be modified through natural selection in relation to different habitats of life, as is sometimes the case; or for one sex to be modified in relation to the other sex, as commonly occurs.” Although many early ideas concerning sexual segregation have not stood the

test of time (Bleich et al. 1997; Main et al. 1996; Miquelle et al. 1992), the foundation for this discipline clearly rests with Darwin (1859, 1871).

Sexual segregation has been documented for a variety of plants, birds, and fishes (Bleich et al. 1997; Ruckstuhl and Neuhaus 2000), but studies of mammals dominate the literature on this topic. Among mammalian species, ungulates in general and ruminants in particular have been the focus of most research on this subject. For example, over about the last one-quarter century, the number of publications dealing with sexual segregation in ungulates (>98% ruminants) has doubled compared with publications on other mammals (Fig. 1). Among those other mammals, articles on sexual segregation were about equally apportioned among bats, rodents, carnivores, cetaceans, and primates, with a few publications on other orders. Relative to the number of extant species of ungulates, publications on cervids, and to a lesser extent bovids, are most

* Correspondent: bowyterr@isu.edu

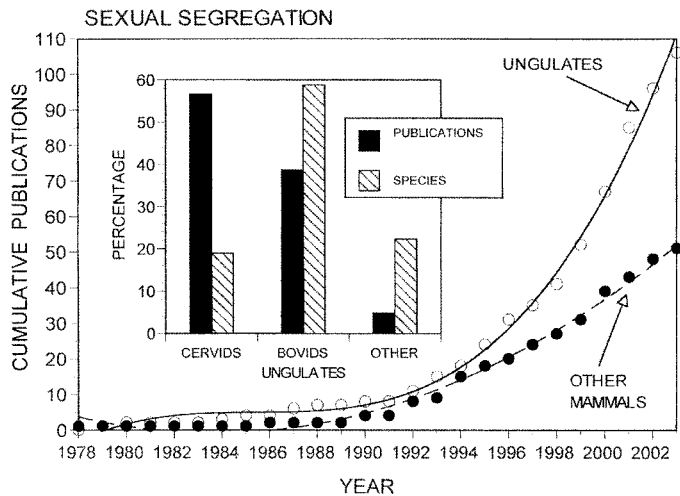


FIG. 1.—Cumulative increases in publications concerning sexual segregation in mammals from 1978 to July 2003 involving literature searches based on the key words “sexual segregation” and “mammal” in ISI Web of Science and Wildlife Worldwide. Publications on ungulates (inset) are compared against the extant number of species for cervids, bovids, and other mammalian families.

common (Fig. 1). The propensity to concentrate research on those families of ruminants likely is a result of their marked sexual dimorphism (Loison et al. 1999; Perez-Barberia et al. 2002; Ralls 1977; Spaeth et al. 2001; Weckerly 1998) and effects of such allometric differences on sexual segregation (Barboza and Bowyer 2000, 2001). Moreover, biology of many cervids is especially well studied compared with other taxa of mammals that exhibit sexual segregation (Kie et al. 2003), which provides unique insights into their life histories (Keech et al. 2000; Kie 1999; Leslie et al. 1999; McCullough 1999).

Although authors have pondered causes of sexual segregation for many years (Bleich et al. 1997; Main et al. 1996; Miquelle et al. 1992), only since about 1990 has a pronounced increase in publications concerning this topic occurred (Fig. 1). Interest among ungulate biologists increased exponentially during that decade (Fig. 1). This domain of study has been especially intriguing to mammalogists because it lies at the interface of theory and application and has far-reaching consequences for how valuable natural resources are conserved and managed. Moreover, large mammalian herbivores have substantial effects on fundamental processes of ecosystems, including nutrient cycling, rates of plant succession, and diversity of other animals (Berger et al. 2001b; Bowyer et al. 1997; Kie et al. 2003; Molvar et al. 1993). Clearly, understanding the distribution of ungulates across the landscape and their subsequent effects on ecosystem structure and function requires knowledge about how sexes partition space, habitat, and forage.

DEFINING SEXUAL SEGREGATION

Barboza and Bowyer (2000) noted that substantial confusion exists over precisely what constitutes sexual segregation and that the lack of an operational definition has hindered progress

in understanding this phenomenon. Traditionally, sexual segregation has been defined as the differential use of space (and often habitat or forage) by sexes outside the mating season (e.g., Barboza and Bowyer 2000; Bleich et al. 1997; Bowyer 1984; Kie and Bowyer 1999; McCullough et al. 1989).

Recently, additional mechanistic definitions (e.g., social segregation [living in separate social groups outside the mating season]—Conradt 1998a) involving differences in synchrony and activity patterns of sexes have been used to define and explain sexual segregation (Conradt 1998a; Conradt and Roper 2000; Ruckstuhl 1998; Ruckstuhl and Kokko 2002; Ruckstuhl and Neuhaus 2000). Nevertheless, questions have arisen over whether differences in activities between genders are a cause or consequence of sexual segregation (i.e., are differences in activity a cause of sexual segregation or merely a correlate?—Barboza and Bowyer 2001; Bowyer and Kie 2004) and how broadly applicable this hypothesis is across species or study sites (Bowyer and Kie 2004; Mooring et al. 2003). Moreover, marked changes in degree of segregation have occurred without concomitant alterations in size or sexual composition of groups (Kie and Bowyer 1999). This result means that changes in sexual segregation can alter group composition, but the reverse need not be true (i.e., changes in segregation occurred without changes in the types of social groups—Kie and Bowyer 1999). Indeed, Bowyer and Kie (2004) argued that social segregation needs to be considered under the broader concept of sociality (*sensu* Bowyer et al. 2001a; Hirth 1977; Molvar and Bowyer 1994) to understand this process more fully and to ascertain whether it is related to sexual segregation. A hypothesis concerning activity of free-ranging ruminants, however, will be difficult to test with an experimental approach. One especially problematical aspect with the concept of social segregation is that it does not explain why sexes spatially segregate, sometimes into separate mountain ranges for extended periods (Bleich et al. 1997). I argue that any inclusive hypothesis for sexual segregation should be able to cope with the spatial attributes of this process.

Considerable insight and effort will be needed to sort among the concepts of social segregation, and ecological segregation, which has been partitioned into spatial, habitat, and dietary segregation by Mysterud (2000)—these processes are not independent. I believe the difficulty in finding common ground for a definition is far more troublesome than using different approaches or terminologies to study sexual segregation and stems from the general failure to apply natural selection to better understand this process. I contend that sexual segregation meets the onerous criteria proposed by Williams (1966) for an adaptation. Indeed, sexual dimorphism and sex ratio variation among ungulates span millions of years (Berger et al. 2001a). Moreover, the widespread occurrence of sexual segregation among extant ungulates with diverse phylogenetic backgrounds implies causation by some general process (Bowyer and Kie 2004). Simple mechanistic or reductionist approaches that lack an evolutionary perspective will not suffice.

Bowyer and Kie (2004) extended the framework of Mysterud (2000) to propose a niche-based assessment for understanding segregation of sexes in ruminants (Table 1).

TABLE 1.—A niche model for conceptualizing 3 patterns of sexual segregation in ungulates; + indicates overlap of sexes, – indicates separation of sexes. The model does not intend that overlap or separation be complete on any particular niche axis, but indicates the general direction of outcomes. Other potential combinations of overlap and separation between sexes were judged to be inconsistent with niche theory (e.g., overlap in space, diet, and habitat) or otherwise infeasible (e.g., overlap in space but not habitat); adapted from Bowyer and Kie (2004).

Pattern of segregation	Space	Diet	Habitat
I	+	–	+
II	–	+ ^a	– ^b
III	–	–	+/-

^a Some differences in diet would be expected because of allometric and life-history differences between sexes.

^b Sexes potentially could use the same habitat at different locations.

Because sexes of ruminants behave, in many respects, as if they were different species (Bowyer et al. 2001b; Kie and Bowyer 1999; Stewart et al. 2003b), these large mammals should be considered in a niche framework wherein overlap on 1 niche axis is likely accompanied by avoidance on another (Bowyer and Kie 2004; Kie and Bowyer 1999; Stewart et al. 2002, 2003a; Table 1; Fig. 2). Hence, sexes avoid competition on ≥ 1 niche axis, in a manner analogous to coexisting species (Stewart et al. 2002). For instance, at moderate population density of white-tailed deer (*Odocoileus virginianus*), marked spatial segregation of sexes occurs, with the dietary niche of females included within that of males. At high population density, however, spatial overlap of sexes was greater with concomitant divergence in their diets (Fig. 2). Moreover, competitive exclusion of 1 sex by the other is not necessary to posit this pattern of niche relationships between sexes (Table 1). This niche-based perspective for assessing sexual segregation avoids the conundrum of having sexes segregate on the basis of diet but not on space (or vice versa) and the resulting compartmentalization of ecologically connected processes.

MEASURING AND DETECTING SEXUAL SEGREGATION

Determining whether sexual segregation occurs is not simple. Some niche axes might be easier to measure than others (Table 1), but unless space, habitat, and diet are assessed, an apparent absence of sexual segregation could be no more than the failure to measure the correct axis. Moreover, sexual segregation is extremely sensitive to scale (Bowyer et al. 1996, 2002; Kie and Bowyer 1999) and might elude detection if the wrong temporal or spatial scale is selected (Fig. 3). Bowyer et al. (1996) offer suggestions for determining the correct scale, but the same scale of measurement is unlikely to be appropriate for assessing sexual segregation across taxa. For instance, some species, such as white-tailed deer, might segregate on a scale as fine as a few ha (Kie and Bowyer 1999; McCullough et al. 1989; Stewart et al. 2003b), whereas others, including mountain sheep (*Ovis canadensis*), might sexually segregate into separate mountain ranges that are 15 km apart (Bleich et al. 1997). Consequently, comparisons of degree of sexual segregation from the literature

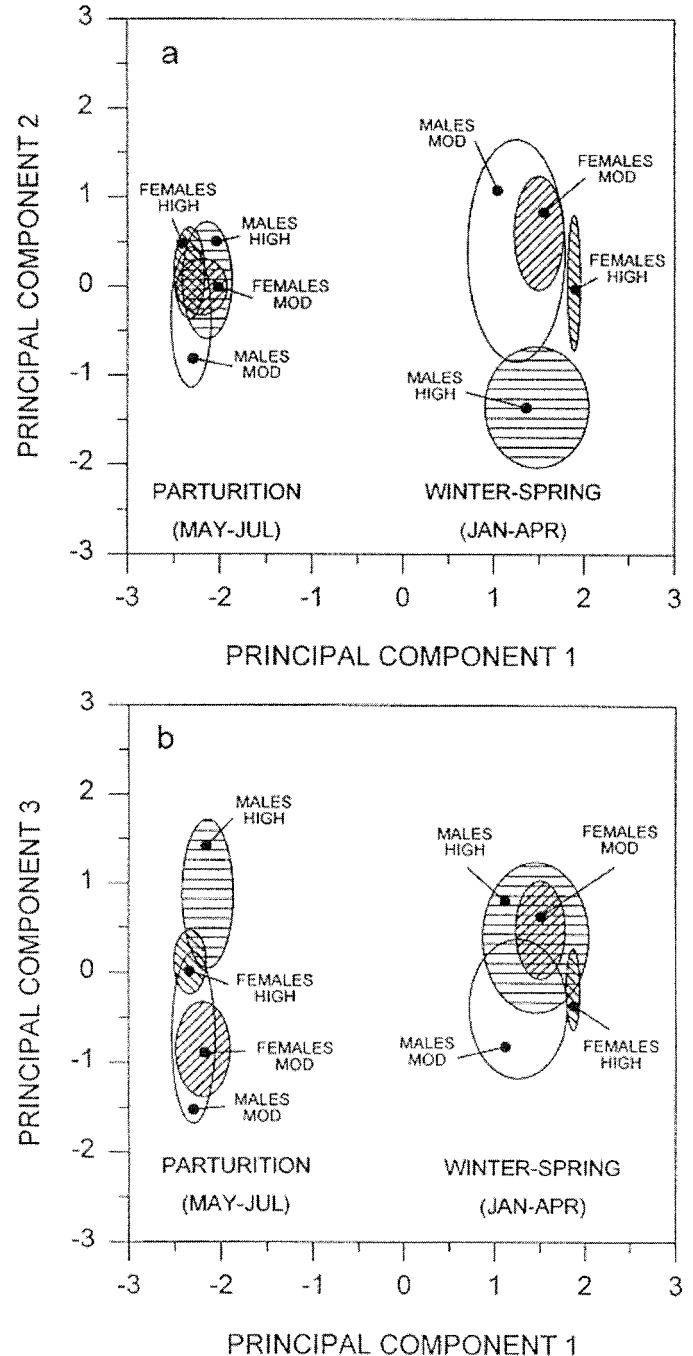


FIG. 2.—a) Principal components 1 and 2 and b) 1 and 3 for diets of white-tailed deer (*Odocoileus virginianus*) at moderate and high densities during winter–spring and parturition in south Texas, 1977 (from Kie and Bowyer 1999). Ellipses are 95% confidence intervals, with principal component 1 separating seasons. Note that at moderate density during winter–spring (panel a), with more spatial segregation of sexes, substantial overlap in diets of males and females occurred. At high density with greater spatial overlap, however, sexes diverged in their dietary niche (panel a). This same pattern occurs during parturition (panel b), illustrating that overlap on one niche axis is accompanied by avoidance on another.

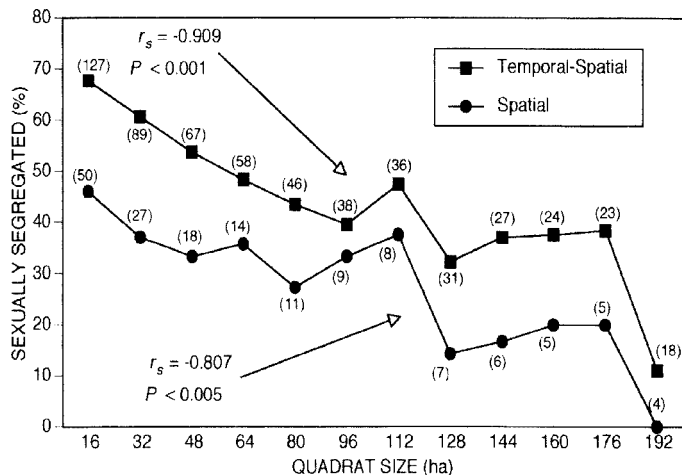


FIG. 3.—Effects of temporal and spatial scales on measures of sexual segregation in black-tailed deer (*Odocoileus hemionus*) on the basis of percentage of quadrats containing $\geq 90\%$ of a single sex in northern California, July 1992. The spatiotemporal scale was analyzed by week (and consequently contains more quadrats), whereas the spatial scale combines weeks. Number of quadrats sampled is in parenthesis (from Bowyer et al. 1996). Note that a shorter sampling interval or smaller quadrat size increases the degree of sexual segregation.

are unlikely to be meaningful because of difficulties in reconciling the various scales at which such niche partitioning was measured (Myserud 2000). Yes-or-no answers concerning whether a particular species sexually segregates, or determining the temporal and spatial scales at which segregation occurs, also could be problematic. In some instances, an observed absence of sexual segregation could be methodological rather than biological.

Some demographic differences that occur between sexes of ungulates could be misinterpreted as sexual segregation or might not provide sufficient evidence to demonstrate that phenomenon. For example, polygynous ungulates often exhibit sex ratios that are biased strongly toward females, ostensibly a result of differential mortality of males resulting mostly from strenuous rutting activities (Berger and Gompper 1999; Bowyer 1981, 1991; Kie and White 1985) or harvest (McCullough 1984). Accordingly, noting that males compose a lower proportion or occur at a lower density than females on particular sites is not adequate evidence for sexual segregation. Differences in the relative proportions of sexes on differing areas or habitats or testing for a difference in the proportion of 1 sex occupying a particular area relative to the population as a whole is required (Bowyer and Kie 2004; Kie and Bowyer 1999; Stewart et al. 2003b; Fig. 4). Conradt (1998b) developed a method for measuring sexual segregation that corrects for sex ratio. That metric, however, can exclude lone individuals. Many species of ungulates have social systems that include solitary individuals (Bowyer et al. 2001a; Kie and Bowyer 1999; Molvar and Bowyer 1994), and excluding those lone animals from calculations of sexual segregation seems unnecessarily conservative. Likewise, observing dissimilarity in

the spatial distribution (or other differences in niche axes) between sexes of ungulates during the period of sexual segregation alone does not suffice because that pattern might not differ from periods of aggregation. If a near-identical pattern occurs during sexual aggregation (e.g., rut), then observed differences in spatial distribution (or other niche parameters) could be no more than an artifact of sampling at too fine a scale—a sufficiently small scale will result in segregation of sexes in most circumstances (Bowyer et al. 1996, 2002; Fig. 2). Annual changes in degree of segregation are necessary to document that process.

Simply noting that adult males and females use habitat differently during parts of the year might not be sufficient to understand reasons for sexual segregation in ruminants. Natural selection favoring segregation of sexes presumably operates via habitat selection by individuals, a process that might not be reflected in habitat use. For example, if availability of habitats differed between areas used by males and females during segregation, identical patterns of habitat selection would result in differing patterns of habitat use by sexes. Measurements of habitat selection by males and females (e.g., Bleich et al. 1997, Kie and Bowyer 1999), rather than use, are required to understand sexual segregation. Caution should be used, however, in obtaining such measurements because habitat selection by ruminants also is scale dependent (Boyce et al. 2003; Kie et al. 2002).

Population density of ungulates relative to environmental carrying capacity (K) also holds potential to affect measures of sexual segregation. Increasing population density resulted in changes in habitat selection, diet, and use of space by sexes of white-tailed deer (Kie and Bowyer 1999; Fig. 2). A simple model for sexual segregation likewise demonstrated alterations in degree of segregation with changing population density (Bowyer et al. 2002). Moreover, sufficiently small scales of measurement at low population density might indicate segregation where patterns of habitat selection by sexes were identical (Bowyer et al. 2002). Those outcomes make absolute comparisons of segregation among species, or even among populations of the same species, difficult at best, and thereby limit the usefulness of a comparative approach to resolve questions concerning sexual segregation.

Few studies of sexual segregation in ungulates have considered potential biases associated with measurement scale, sex ratios, habitat and diet selection, population density, potential interactions among those variables, and how they change during the annual cycle (Bowyer et al. 2002). Until biologists adopt standard methods for measuring and assessing sexual segregation, I foresee only a limited opportunity for furthering our understanding of this intriguing topic, especially for free-ranging ruminants.

PROBLEMS WITH EXPLANATIONS FOR SEXUAL SEGREGATION

Numerous hypotheses have been forwarded to explain sexual segregation in ungulates, many of which have been rejected. Miquelle et al. (1992), Main et al. (1996), and Bleich

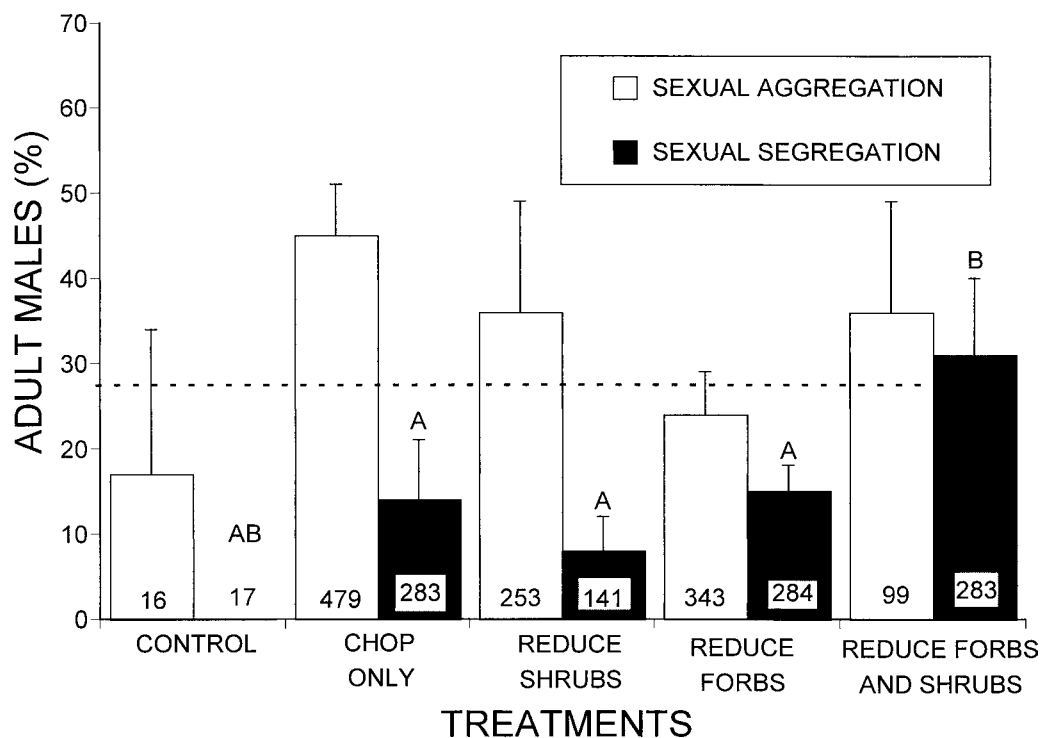


FIG. 4.—Percentage (\pm SE) of male white-tailed deer (*Odocoileus virginianus*) using vegetation treatments during sexual aggregation and sexual segregation in south Texas, 1995–1996. The dashed line represents the overall percentage of adult males observed on the study area. Different letters above bars indicate significant ($P < 0.03$) differences from the overall percentage; sample sizes are indicated within each bar (adapted from Stewart et al. 2003b).

et al. (1997) provided detailed lists of hypotheses forwarded to explain sexual segregation, the rationale underpinning those hypotheses, and evidence for rejecting some of them. My purpose here is not a re-examination of all possible ideas. Instead, this review takes advantage of previous work and begins with the framework provided by those publications. My purpose is to clarify and discuss viable hypotheses for sexual segregation. I believe, however, more care is needed not to continually resurrect old, rejected ideas or hypotheses that are site specific and hold little promise for explaining this widespread phenomenon across areas and species. I also concur with Bleich et al. (1997) that it is not worthwhile simply to describe sexual segregation for a particular species or study area for which it has not been documented previously. Such descriptive studies do little to further our understanding of why sexes segregate. More focus on testing viable hypotheses concerning sexual segregation is needed. Moreover, such findings should be placed in an evolutionary context.

I believe hypotheses should be restricted to those likely to explain sexual segregation in polygynous ruminants; monomorphic ruminants do not sexually segregate (Barboza and Bowyer 2000, 2001). The unique diet, digestive system, mating behavior, sexual dimorphism, and overall size of many ruminants are distinct from other animals. Even hypotheses for other large mammals with differing evolutionary histories are not appropriate for ruminants. For example, infanticide in grizzly bears (*Ursus arctos*), which is thought to affect sexual segregation in those large carnivores (Wielgus and Bunnell

1994), offers an improbable explanation for large, herbivorous mammals that seldom engage in that behavior. The breadth and scope of hypotheses addressed by biologists must consider the life-history characteristics of the animals under study.

Too often the literature on sexual segregation fails to distinguish proximal from ultimate causes, which has led to confusion and wasted effort. For instance, the need for free water by lactating females has been hypothesized as a cause of sexual segregation in some species (Bowyer 1984; Main and Coblenz 1996). This requirement likely is species and site specific, with desert-adapted ruminants probably coping better with such needs than others (Bleich et al. 1997). The requirement for free water is better understood in a broader framework encompassing reproductive requirements of females (sensu Bowyer et al. 1999), which might vary across species and environments. The need to test for water-related or other proximal effects (such as snow depth, temperature, or feeding style) in every situation is nil and could obscure evolutionary causes of sexual segregation. Such proximal factors might exacerbate or limit sexual segregation under specific circumstances but are not the root cause of that phenomenon. Distinguishing proximal correlates of sexual segregation from hypotheses capable of explaining the near-ubiquitous occurrence of this behavior among polygynous ruminants should be the standard for future research. Proximal attributes of niche separation of sexes might be of local interest but should not be presented in too narrow a framework or proffered as the sole explanation for sexual segregation, especially where ultimate causes were not considered.

TABLE 2.—Requirements for demonstrating and understanding sexual segregation in ruminants.

1. There must be seasonal variation in the degree of sexual segregation—the sexes must segregate and aggregate in an annual pattern.
2. The ratio of the sexes must differ between areas or from the sex ratio of the population during sexual segregation.
3. Differences in selection (use relative to availability) of habitat by sexes, not habitat use, are required to understand the role of habitat when sexes are segregated (i.e., when availability of habitat differs by sex).
4. Scale must be considered in measuring sexual segregation. The failure to detect sexual segregation may be the result of sampling at the wrong scale.
5. Space, habitat, and diet must be evaluated in determining whether sexual segregation occurs (Table 1).

PREVIOUS HYPOTHESES FOR SEXUAL SEGREGATION

Nearly a decade ago, Main et al. (1996) organized hypotheses for sexual segregation among ungulates into 3 categories: reproductive strategy, sexual dimorphism–body size, and social factors. Until recently, these hypotheses helped guide research on this important topic. These ideas have not completely outlived their usefulness and require explanation and discussion for historical and conceptual reasons.

The reproductive strategy hypothesis posits that ecological factors are largely responsible for sexual segregation. Because reproductive success of males likely is influenced by size, strength, and endurance, selective pressures favor behaviors that maximize rate of growth and formation of energy reserves. Reproductive success of females is determined primarily by survival of offspring but also by engaging in activities that provide resources necessary to meet the requirements of lactation and promote survival of females. Consequently, predation, or risk thereof, often is a key component of this hypothesis. DePerno et al. (2003), however, treated predation and the reproductive strategy hypothesis as separate entities.

The sexual dimorphism–body size hypothesis implicates physiological factors related to nutrition as being largely responsible for sexual segregation. Sexual segregation is a reflection of each sex sequestering resources that satisfy their different physiological requirements. Larger males, with greater absolute metabolic requirements, feed on abundant, high-fiber forages that are degraded most efficiently by long retention in a proportionally capacious rumen. Smaller-bodied females selectively feed on low-fiber, high-quality forages to satisfy nutritional demands of gestation and lactation. This hypothesis has been invoked to infer competitive displacement of males by females from areas with less-abundant but high-quality forage (Clutton-Brock et al. 1987, Main and Coblentz 1996).

The social factors hypothesis presumes that various aspects of sociality are primarily responsible for sexual segregation. Those aspects include the need for males to form associations to develop fighting skills, establish prerut dominance hierarchies, and learn locations of potential mates. For females, learned skills would include where to find food, water, and suitable birthing areas. This hypothesis also encompasses aggressive behavior of females displacing males and mutual avoidance of one sex by the other (*sensu* Weckerly 2001; Weckerly et al. 2001).

TABLE 3.—Characteristics needed for hypotheses forwarded to explain sexual segregation among ruminants.

1. Hypotheses should not be so proximal or site specific that they cannot explain the near-ubiquitous occurrence of sexual segregation in polygynous ruminants.
2. Hypotheses must cope with the temporal and spatial nature of this phenomenon across species of ruminants.
3. Hypotheses must be independent, if not mutually exclusive.
4. Hypotheses must distinguish cause from effect.
5. Hypotheses must be testable.

The 1st problem with hypotheses advanced by Main et al. (1996), as well as many others forwarded to explain sexual segregation, is that they are not mutually exclusive (Bleich et al. 1997). This makes an unequivocal test of a particular hypothesis difficult and clouds interpretation of results. Perhaps the best that can be accomplished under this framework is to ascertain the relative contribution of each hypothesis in explaining the degree of sexual segregation.

A 2nd problem, inherent in some aspects of the reproductive strategy hypothesis of Main et al. (1996), is that this hypothesis might be too general to test. Most characteristics of ungulates can be attributed to some reproductive strategy, all too often in an *a posteriori* manner, including outcomes that were not primary objectives of the original study design. Consequently, this hypothesis can be invoked to explain most ungulate adaptations related to their behavior, ecology, and physiology. Whether such interpretations are associated with causes of sexual segregation or simply related to other aspects of ungulate biology are uncertain and difficult to test. Aspects of this hypothesis relative to predation, however, are testable.

The 3rd and most problematic aspect of hypotheses postulated by Main et al. (1996) is that they are not independent. For instance, differences between sexes invoked in explaining the sexual dimorphism–body size hypothesis also relate to susceptibility of sexes to predation (Pierce et al. 2000a, 2000b), which is encompassed under the reproductive strategy hypothesis. Social factors, especially aggressive interactions, ostensibly are related to body size dimorphism, and various reproductive strategies almost certainly involve social behavior. Even mutual avoidance of sexes could have its underpinnings in body size differences related to differing ecological and physical requirements of sexes (Weckerly et al. 2001). The need to organize hypotheses for sexual segregation into a testable framework in keeping with modern evolutionary theory is urgent.

Recommendations for characteristics of hypotheses for obtaining critical tests concerning sexual segregation are set forth in Table 3. Many existing hypotheses fall short of these criteria and thus fail to provide a viable approach for understanding sexual segregation. Adhering to this framework will allow more focused designs for future research on sexual segregation and help distinguish between studies that simply describe this process and those that are designed to determine causation. What existing hypotheses, then, have the necessary evolutionary underpinnings and conform to criteria in Table 3?

RESOURCES AND PREDATION

I maintain that there may be no more than 2 hypotheses necessary to explain sexual segregation in ruminants: acquisition of resources, as modified by allometric and life-history differences between sexes, and predation. These paradigms are not simple extensions of the reproductive strategy and body size–sexual dimorphism hypotheses (Main et al. 1996), in part, because of the lack of independence among previously forwarded hypotheses. Moreover, these 2 hypotheses have strong evolutionary foundations leading to predictions concerning niche partitioning by sexes of ungulates.

Understanding evolution of sexual size dimorphism in ungulates is a necessary 1st step in developing and testing hypotheses concerning sexual segregation in these mammals. For instance, current thought holds that sexual dimorphism in ungulates evolved via highly polygynous mating systems, which resulted in directional selection for large males (Loison et al. 1999; Ralls 1977; Weckerly 1998). Ralls (1977) warned that bird models, which emphasized intersexual competition as the cause of dimorphism (*sensu* Selander 1966; Temeles et al. 2000), might not be applicable to mammals because of their diverse evolutionary histories. Indeed, the body size–sexual dimorphism hypothesis (Main et al. 1996) makes no prediction concerning the direction of differences in size between sexes.

The assumption that exploitive competition between sexes was the cause of sexual dimorphism in ungulates presumably led several authors (Clutton-Brock et al. 1987; Main and Coblentz 1996) to propose that sexual segregation resulted from competitive exclusion of males by females. This hypothesis has been rejected repeatedly by both experimental and observational studies (Bleich et al. 1997; du Toit 1995; Kie and Bowyer 1999; Miquelle et al. 1992; Spaeth et al. 2004), including 2 similar publications by members of the research group who originally proposed the idea (Conradt et al. 1999, 2001). Research by Kie and Bowyer (1999) was especially damaging to this hypothesis because that study documented a reduction in sexual segregation with increasing population density. Nonetheless, intersexual competition continues to be forwarded as a viable hypothesis for sexual segregation (Focardi et al. 2003), usually without a critical test of this hypothesis.

Interference competition, which has been documented among species of ruminants (Stewart et al. 2002), will not explain sexual segregation because this competitive mechanism allows sexes to use the same space at different times (Spaeth et al. 2004). Admittedly, sexual segregation is sensitive to the temporal scale at which it is measured (Bowyer et al. 1996, 2002; Fig. 3). Nonetheless, interference competition cannot account for spatial separation of sexes over the long time intervals and large spatial scales for which it has been reported in some ruminants (Bleich et al. 1997; Miquelle et al. 1992). I believe this same line of reasoning makes social aggression between sexes an unlikely cause of sexual segregation. Certainly, there is no aspect of either hypothesis that would result in long-term differences in use of space or diets between sexes.

I concede that clear conceptual models detailing how polygyny and intersexual competition might differ in their

predictions concerning sexual segregation in ungulates would be useful; unfortunately, such models are beyond the scope of this paper. I conclude, however, that intersexual competition resulting in competitive exclusion of males by females is an unlikely explanation for sexual segregation and is not a fruitful area for future research.

The basic tenet that polygyny resulted in increased sexual dimorphism among ruminants, which in turn effected sexual segregation, is the foundation of current hypotheses for why sexes tend to live separately for much of the year. Clearly, sexual dimorphism in body size results in allometric differences between sexes that profoundly influence their ecology and life-history traits (Barboza and Bowyer 2000, 2001; Jenks et al. 1994). Nonetheless, body-size differences between sexes and resulting allometric differences cannot single-handedly explain sexual segregation.

Allometric differences associated with increasing body size occur among ruminants because energy requirements per unit body mass scales to a power of less than unity, whereas rumen volume scales directly with body mass (Demment and Van Soest 1985). Consequently, larger species of ruminants (and presumably larger sexes of the same species) have proportionately larger rumens than smaller ruminants. Care should be taken in these extrapolations because allometric differences among species might not hold within species (Barboza and Bowyer 2001). Nevertheless, marked morphological and physiological dissimilarities between sexes likely facilitate differential use of forage, because animals with larger rumens can digest forages of poorer quality more completely than those with smaller rumens, even though large animals require absolutely more forage (Demment and Van Soest 1985). Whether similar models can be developed for nonruminant ungulates that exhibit hindgut fermentation of forages remains to be seen. Nonetheless, such models are not sufficient by themselves to explain sexual segregation; they address why sexes should remain apart but are not sufficient to account for sexes aggregating during part of the year, which often includes rut, but also periods other than the mating season (Bleich et al. 1997; Bowyer 1984; Pierce et al. 2004). The gastrocentric hypothesis of Barboza and Bowyer (2000, 2001) incorporates allometric differences between sexes and accommodates annual changes in the social behavior of ruminants on the basis of their life-history characteristics (*i.e.*, explains periods of aggregation and segregation).

The gastrocentric model (Barboza and Bowyer 2000, 2001) elucidates causes of sexual segregation in ruminants on the basis of allometry, minimal food quality, digestive retention, and differing reproductive requirements of sexes (Fig. 5). The model predicts that larger male cervids consume abundant forages high in fiber because ruminal capacity prolongs retention and permits greater use of fiber for energy than in nonpregnant females. Low density of animals, high abundance of forage, and specific adaptations of ruminal microflora result in males using fibrous forages until the quantity of food declines. Smaller-bodied females are better adapted to post-ruminal digestion of forage, as related to increased intake, to accommodate energy and protein necessary for reproduction.

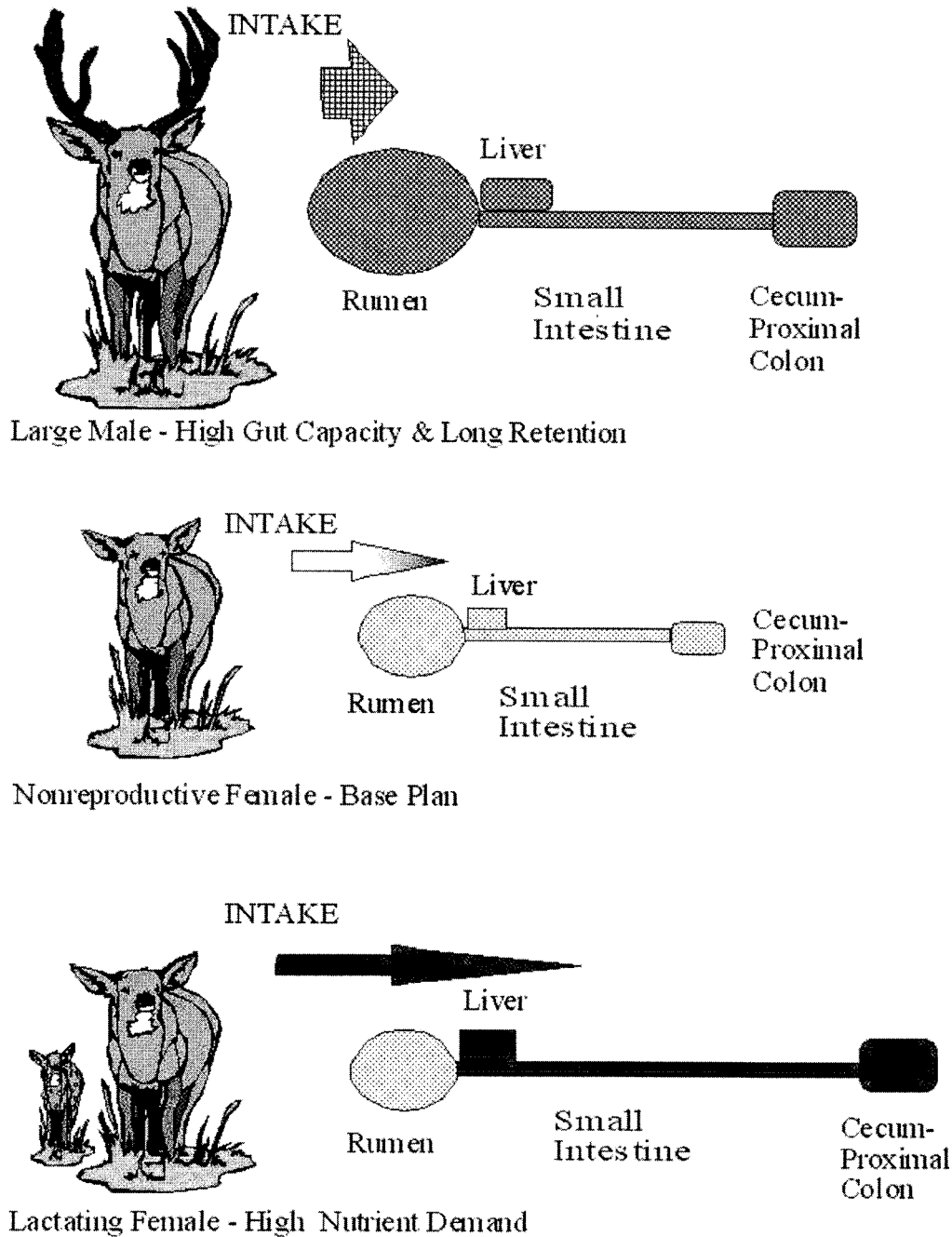


FIG. 5.—The gastrocentric model for intake and digestive function in nonreproducing female ruminants compared with large males and lactating females. Width of arrows reflects amount of food intake; length of arrows indicates rate of digesta passage; shading indicates density of nutrients in food. Diagrams of digestive tracts are stippled to reflect potential changes in fibrousness of food for males and increases in post-ruminal size and function of lactating females (adapted from Barboza and Bowyer 2000).

High demands for absorption of nutrients during lactation cause investment in intestinal and hepatic tissue in females, increasing costs of maintenance, thereby reinforcing differential use of habitats and forages when sexes are segregated. One major advantage of this new approach is that it explains sexual segregation without requiring competitive exclusion of males by females. This hypothesis also clarifies why males do not occupy higher quality ranges preferred by females; digestive morphology and physiology of males is poorly equipped to

digest forages of too high a quality (Barboza and Bowyer 2000). Furthermore, this hypothesis relies on differences in forage rather than requiring heterogeneous habitats; sexual segregation has been described where sexes do not select habitat differentially (Bowyer 1984, 1986; Conrath 1999). Nevertheless, heterogeneous habitats and their distribution on the landscape might help explain the scale at which some species segregate sexually (Bleich et al. 1997; Bowyer et al. 2002; Miquelle et al. 1992) or why the same species

might segregate at differing scales in separate study sites. Moreover, a heterogeneous landscape, composed of either different habitats or amounts and quality of forage, offers multiple niches to support requirements of sexually dimorphic ruminants.

Likewise, predation need not be invoked to explain segregation of sexes under the gastrocentric model (Barboza and Bowyer 2000). Some aspects of this hypothesis still require testing (Barboza and Bowyer 2001). I believe such tests will refine this model, however, rather than lead to its rejection. This hypothesis also meets requirements set forth in Table 3 for a viable approach to understanding sexual segregation.

Predation also holds potential to cause sexual segregation in ungulates. Bleich et al. (1997) clearly demonstrated that female mountain sheep inhabit ranges with fewer predators than areas occupied by males (Fig. 6), even though females ranges are of lower quality than those inhabited by males. Indeed, predation is sufficient to explain segregation of sexes but might not be necessary (*sensu* the gastrocentric hypothesis). For instance, sexual segregation occurs in red deer under circumstances in which predators are absent (Clutton-Brock et al. 1987). Care should be taken, however, in inferring that predation plays no role in sexual segregation even where predators are missing. Again, an evolutionary perspective is necessary to understand this process. Some responses of ungulates to predators might wane quickly in the absence of large carnivores, but others could persist for millennia (Barten et al. 2001; Berger 1999). Moreover, there might be a need to differentiate between the immediate responses of ungulates to predators and behaviors that involve the risk of encountering a predator in a particular habitat or other set of circumstances to understand why sexes segregate (Bleich 1999; Bowyer 1987).

Good examples exist in which female ruminants trade off a higher quality diet for greater security from predators during sexual segregation (Barten et al. 2001; Berger 1991; Bleich et al. 1997; Corti and Shackelton 2002; Kie and Bowyer 1999; Rachlow and Bowyer 1998). Consequently, when females occur on poorer ranges than males while sexes are separated, predation can be invoked as the primary cause of sexual segregation (obviously, females still must meet their nutritional requirements for reproduction for such populations to persist). Predation likely interacts with forage abundance (the hypotheses are not mutually exclusive) when male moose (*Alces alces*) inhabit areas with greater forage abundance but not quality, whereas females segregate to areas with less forage but more concealment cover, ostensibly a result of females and young being more susceptible to predators (Bowyer et al. 2001b). Instances in which females occupy better ranges than males (Bowyer 1984; Clutton-Brock et al. 1987; Main and Coblenz 1996) are likely a result of differences in nutritional needs of sexes (*sensu* Barboza and Bowyer 2000, 2001). Nevertheless, such females might simultaneously select sites with high-quality forage while minimizing risk of predation in areas with more concealment cover. Understanding whether females are trading off forage against predation risk or minimizing the predation risk to forage ratio (Bowyer et al. 1998, 1999) will be necessary to sort among these potential

causes of sexual segregation. The important point is that the 2 primary hypotheses for sexual segregation could interact to produce a variety of outcomes with respect to quality of diets obtained by sexes in different environments, which cannot be interpreted readily without an awareness of how predation risk and nutritional needs of sexes lead to their niche separation.

MANAGEMENT AND CONSERVATION OF SEXES

My colleagues and I have suggested that niche requirements of sexes of polygynous ruminants were sufficiently different that they should be managed as if there were separate species (Bowyer et al. 2001b; Kie and Bowyer 1999; Stewart et al. 2003b). Biologists have known for decades that the harvest of females does more to affect productivity (i.e., recruitment of young) of ungulate populations than does killing males (e.g., Kie et al. 2003; McCullough 1979). This outcome results from sexes living apart for much of the year and, consequently, males not competing as intensively with young for forage as do adult females. Accordingly, habitat manipulations that affect forage (or other niche requirements) for one sex have the ability to influence productivity of that sex disproportionately to the other. Likewise, altering habitat occupied by one sex during segregation might benefit one sex over the other (Bowyer et al. 2001b; Stewart et al. 2003b; Fig. 3). Little attention has been given to how habitat manipulation might differentially affect sexes of ruminants. Indeed, range managers have largely ignored differential effects of habitat manipulations on sexes of large mammals, and only the most recent texts on wildlife management even mention this topic (Bolen and Robinson 2003; Krausman 2002).

Sexual segregation of ruminants can affect predator-prey dynamics (Bowyer et al., *in press*). For example, a male ruminant killed by a predator will have a proportionally lower affect on recruitment of young into the prey population than would the death of a female (McCullough 1979). Because males of dimorphic ruminants are considerably larger than females (Weckerly 1998), however, the greater amount of food they supply is likely to affect reproduction of predators more than would smaller-bodied females or young. Both outcomes have potential to affect predator-prey dynamics in ways that are not considered in existing models (Bowyer et al., *in press*). How sexes of ruminants are distributed spatially and effects of this pattern on predator-prey dynamics is a topic in dire need of additional research.

Male mountain sheep can make extensive movements (15 km) from areas occupied during segregation to female ranges for rut (Bleich et al. 1997). Sexes of mountain sheep clearly make use of different habitats during such movements, an outcome that requires consideration in models for their conservation. Nonetheless, too little attention has been given to corridors necessary for movements to and from areas of segregation and aggregation in the conservation of these unique mountain ungulates (Bleich et al. 1997). Moreover, the manner in which sexes segregate and then aggregate for mating could affect gene flow and thereby the genetic diversity of populations (Rubin and Bleich, *in press*). Indeed, any process

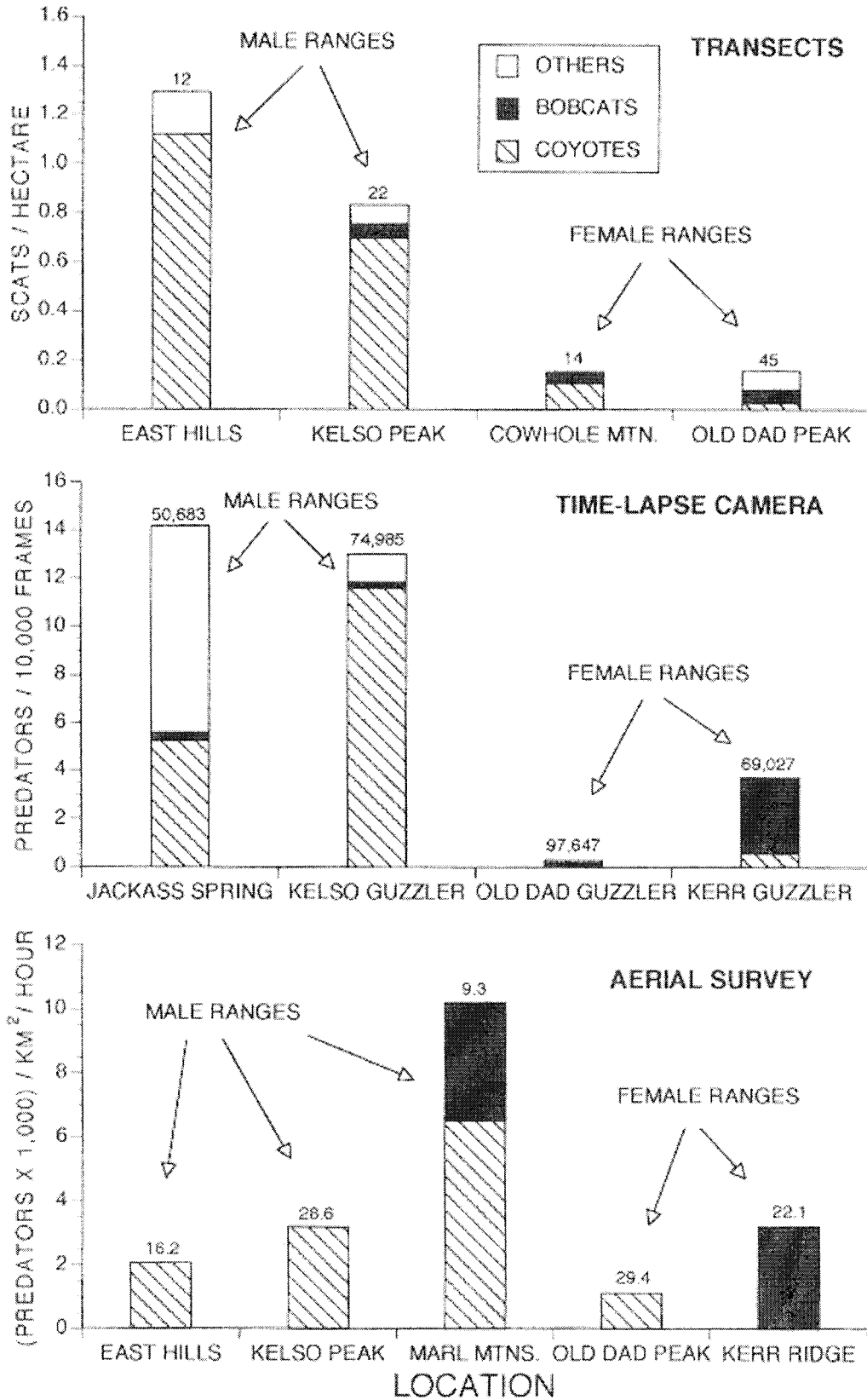


FIG. 6.—Relative abundance of predators on ranges occupied primarily by mature male or females mountain sheep (*Ovis canadensis*), San Bernardino County, California, 1987–1990. Sample sizes appear above bars and represent number of transects, frames of time-lapse camera film evaluated, and h of helicopter flight time (from Bleich et al. 1997).

that results in a noncontiguous distribution of animals on the landscape holds potential to affect gene flow and diversity (Chesser 1991a, 1991b). The study of sexual segregation, however, has yet to advance from the disciplines of ecology and behavior into the realms of conservation biology and genetics—a challenge for the future.

Likewise, changes in the social organization and distribution of sexes of ruminants across the landscape might affect the spread of some parasites and diseases (Schauber and Woolf 2003). For example, where male bighorn sheep use less precipitous terrain than females (Bleich et al. 1997), males could come into contact with livestock, which carry infectious agents (Krausman and Bowyer 2003), or be more susceptible than females to other sources of mortality such as collisions with vehicles (Rubin and Bleich, in press). Clearly, sexes need to be considered separately when considering rates and causes of mortality.

Sexual segregation also has the potential to bias population estimates for large herbivores. If sexes are not sampled during periods of aggregation, then a complete knowledge of their spatial distribution is needed to design sampling protocols so that both sexes are included in estimates of population size. All too often, population estimates and measurements of habitat use and selection are presented for the population as a whole, with no regard to the differing niche requirements and resulting spatial distributions of sexes. Such an approach is shortsighted and likely will lead to management errors related to harvest of animals and manipulation of habitat. There is a clear need to incorporate existing knowledge of sexual segregation among ruminants into conservation and management planning.

FUTURE NEEDS FOR RESEARCH

Several areas for fruitful research are likely to further our understanding of sexual segregation. The gastrocentric hypothesis requires testing (*sensu* Knott et al., in press), especially differences in ability of sexes to digest and assimilate diets of different quality (Barboza and Bowyer 2001). Moreover, this allometric model, which incorporates life-history strategies of sexes, will not explain why nonreproductive females spatially segregate from males in a similar manner as females that bear costs of gestation and lactation. Perhaps aspects of predation risk or other social factors will be necessary to resolve this question (Bon and Campan 1996; Bonenfant et al. 2004). I believe, however, that such questions need to be cast within the general framework of existing hypotheses for sexual segregation and avoid pitfalls of being too proximal. Hypotheses also should explain the widespread nature of sexual segregation, not confuse cause and effect, and be testable (Tables 2 and 3).

The concept of sexual segregation must be integrated more fully into the disciplines of range and wildlife management and become a standard consideration, not just in designing research, but also in planning for habitat manipulations and harvests of animals. Likewise, there is a need for the fields of conservation biology and genetics to begin embracing hypotheses related to sexual segregation and incorporating those ideas into their disciplines.

Finally, more manipulative experiments are required to test hypotheses concerning sexual segregation. Some authors already have begun to pursue such research (Bowyer et al. 2001b; Kie and Bowyer 1999; Spaeth et al. 2004; Stewart et al. 2003b), but more work will be needed, especially to resolve questions involving free-ranging species. Although I believe this review resolves many long-standing problems in studies of sexual segregation, it is by no means the final answer. I hope this review provides a framework for future research.

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