SEXUAL SEGREGATION IN UNGULATES: A NEW APPROACH

by

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Summary

In many mammals, males and females live solitarily or in separate groups outside the breeding season. Sexual segregation is wide-spread in ungulates, but also occurs in whales, seals, monkeys, macropods, elephants, fish and bird species. What causes segregation by sex is still poorly understood, despite intense research done mainly on different ungulate species. In most species studied, males were clearly larger than females. The evolution of sexual dimorphism in body size has largely been attributed to sexual selection and mating strategies. While the consequences of body-size differences on energy requirements and metabolic rates received most attention, studies on consequences of sexual body-size differences on behavior are lacking. This review emphasizes the importance to study a wide range of social mammals with a different or no degree of sexual segregation and sexual dimorphism in body size; something which has not been done and has greatly limited our ability to test alternative hypotheses. More emphasis has to be put on the study of activity budgets, sociality and habitat choice of non-dimorphic species to explain the evolution of permanent territoriality, of long-term bonds of male-female pairs and of the occurrence of mixed-sex groups (adults), as well as its absence in dimorphic species. We review five hypotheses proposed to explain sexual segregation, discuss alternative outcomes and predictions for each hypothesis, suggest alternative explanations for the evolution of sexual segregation and mating systems, and indicate new and important directions for research. We conclude that a phylogenetic comparison of behavior of a wide range of ungulates and other mammals will be needed to solve the enigma of sexual segregation.

Keywords: evolution, sexual segregation, mating systems, sociality.

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Current hypotheses on sexual segregation

The aim of this theoretical paper is to stress the importance of comparative studies on a wide range of ungulate species to tackle the questions of sexual segregation in social ungulates and mammals in general. Hypotheses proposed to explain sexual segregation have only been tested on a limited number of sexually dimorphic species. No data is available on non-dimorphic species, and hence no comparative or other data are presented in this review. Non-dimorphic species may be ideal to explain sexual differences in habitat use, forage selection, predator avoidance or activity budgets, because body-size effects are absent. Furthermore, we propose to put more emphasis on studies of the ontogeny of sociality and foraging behavior.

Both functional and causal explanations have been put forward to explain sexual segregation in ungulates (Main *et al.*, 1996). Hypotheses on sexual segregation, receiving the most emphasis in the literature invoke sexual differences in predator avoidance strategies (ultimate explanation), sexual differences in nutrient requirements, scramble competition, and social preferences (all proximate explanations) (see review by Main *et al.*, 1996). Recently, sexual differences in activity budgets have also been proposed as a proximate cause of sexual segregation (Conradt, 1998; Ruckstuhl, 1998a, 1999). Below follows a short review and discussion of these hypotheses and most recent findings. Because of the lack of comparable studies in non-ungulates this review concentrates on ungulates, and where possible expands arguments to other sexually segregating mammals.

The *predation risk hypothesis* (referred to as reproductive strategy hypothesis by Main *et al.*, 1996) states that larger male ungulates are less vulnerable to predation than females and their offspring. Hence, males seek habitats with high food availability, while females choose habitats that are firstly safe from predators and only secondly include nutrition in their habitat choice (Jakimchuk *et al.*, 1987; Berger, 1991; Young & Isbell, 1991). Increased predator avoidance by females was shown in a variety of species, and males may take more risks while foraging than females (Sukumar & Gadgil, 1988; Prins, 1996). Although ungulates have co-evolved and coexisted with predators for thousands of years (Geist, 1974), many predators have been eliminated from former ranges, and it is not clear to what extent current behavior represents adaptations to the past (Byers, 1997). It is, therefore questionable whether the sexes still segregate due to differential predator

avoidance strategies or due to other unrelated factors. If females avoid predators they may retreat into safe but poor forage quality habitat, *e.g.* steep inaccessible cliffs with little food. This prediction is in clear opposition to the forage selection hypothesis, where females are expected to prefer and use higher quality habitat than males.

The *forage selection hypothesis* (referred to as sexual-dimorphism-body-size hypothesis by Main *et al.*, 1996) predicts that the sexes segregate because sexual differences in body size lead to different energy requirements and hence food selection. In many ungulates, males are considerably larger than females. Metabolic rate is allometrically related to body weight, decreasing with increasing body weight, while rumen volume and gut capacity remain a constant fraction of body weight (Kleiber, 1932; Illius & Gordon, 1987, 1992; Van Soest, 1994). Because larger ruminants have a larger rumen and slower passage rate of food than smaller ones (Van Soest, 1994), one may assume that within a species, males are more efficient at extracting energy from fiber than females. If this is the case, females need to compensate for this digestive inferiority by either increasing foraging efficiency or by selecting higher quality forage (high nitrogen levels) than that which is consumed by males (Gross *et al.*, 1996). In addition, energy expenditure and transfer of nutrients through lactation increase selectivity in reproducing females for food sources rich in nitrogen, sodium, or calcium (Clutton-Brock *et al.*, 1982b; Iason *et al.*, 1986). Sexually dimorphic males and females may, therefore, select different plant species or habitats with differing plant and nutrient availability and hence segregate in space (Beier, 1987; Main & Coblentz, 1996). Males and females often use different habitat types, but also overlap in habitat use (du Toit, 1995; Thirgood, 1996; Villaret *et al.*, 1997). Some studies showed that females used higher quality forage habitat than males (Beier, 1987; Putman *et al.*, 1993) while other studies showed the contrary, (Shank, 1982; Koga & Ono, 1994; Bleich *et al.*, 1997), or found no difference between the sexes in either habitat choice or ingested plant quality (LaGory, 1986; Ruckstuhl, 1998b). The forage selection hypothesis is controversial, also because it was often interpreted that males should opt for abundant low-quality forage even when high-quality forage is available (Gross, 1998; Main, 1998). Evidently, this would only occur if good quality food were very sparse and not worthwhile for males to select (Clutton-Brock *et al.*, 1987; see scramble competition hypothesis).

The *scramble-competition hypothesis* (Main *et al.*, 1996) is based on argu-
ments presented in the forage selection hypothesis and proposes that inter-
sexual competition over resources leads to sexual segregation. Female red
deer (*Cervus elaphus*) may exclude stags from preferred swards through
scramble competition. Large males are less competitive feeders because of
allometric relationships of bite-size to body-size; males have a relatively
small incisor arcade width in relation to their body size compared to females
and higher absolute metabolic requirements (Illius & Gordon, 1987). Smaller
females can therefore tolerate lower plant biomass than larger males and ex-
ploit it more efficiently (Clutton-Brock *et al.*, 1987; Illius & Gordon, 1987).
This hypothesis, however, will only apply where forage is scarce or plant
height is greatly reduced.

The *social preference hypothesis* proposes that sexual segregation is caused
by social affinities among males. From a young age, male ungulates prefer
to interact and play with each other. If this persists into adulthood, early
preference of same-sex peers could cause the formation of male and female
groups (Bon, 1991; Villaret & Bon, 1995; Bon & Campan, 1996). In male-
only groups males learn fighting skills, interact with potential rivals and
establish a dominance hierarchy; important determinants during the breeding
season, when males compete for access to females in estrous. Male-male
preference would, therefore, be a function of differing selective pressures on
male fighting abilities and reproductive success, while sexual segregation
may be a mere consequence of male-male preference without any direct
function. Although social preferences were observed in young mouflon
males (*Ovis gmelini*) (Bon & Campan, 1996; Cransac *et al.*, 1998), such
affinities may not necessarily lead to sexual segregation unless intersexual
aggressive interactions forced one sex to leave the group; for which so
far there is little evidence (Romeo *et al.*, 1997). Social preferences, as
proposed by Bon & Campan (1996) will increase group cohesion within
male or female groups, but similarities in nutritional requirements and
activity budgets are more likely to hold groups together. In groups of similar
nutritional and activity demands, behavioral synchrony is facilitated and
probably less costly, than synchrony with animals of differing body-size
(Ruckstuhl, 1999).

This line of arguments recently lead to the formulation of the *activity budget
hypothesis* (referred to as the body-size-predation hypothesis by Ruckstuhl,

1998a), which proposes that sexual differences in activity budgets and move-ment rates are key factors of sexual segregation in social ungulates (Ruck-stuhl, 1998a). Basic assumptions of this hypothesis are that sexual differ-ences in adult body size lead to sexual differences in energetic requirements and digestive efficiencies (Robbins, 1993) and therefore to differences in for-aging behavior. The activity budget hypothesis differs from the forage selec-tion hypothesis in that it proposes differences in activity budgets, rather than differences in habitat or food selection, to be responsible for sexual segre-gation. Males and females should show different activity budgets even when feeding on the same forage plants and in the same habitat. Differences in activity budgets may consequently lead to sexual segregation but not neces-sarily to habitat segregation. If activity budgets differ substantially according to sex, males and females will become separated over time, even if initially in the same group (Ruckstuhl, 1998a, b, 1999). Synchronization of activi-ties in mixed-sex groups may be energetically too costly to be maintained. Animals with similar body sizes and energetic needs should form groups of their own, to minimize cost of synchrony. In addition to incompatibilities of activity budgets and potential costs of synchrony, predator avoidance by fe-males with offspring could further increase segregation. Females could show higher movement rates than males to make themselves less predictable for predators (Ruckstuhl, 1998a).

Predictions and discrimination between the different hypotheses

Which hypothesis most likely explains sexual segregation? A single factor, more than one factor or a combination of all different factors may be responsible for the evolution of sexual segregation in ungulates and other mammals. The question of why sexual segregation evolved can best be solved by making predictions on possible outcomes of mutually exclusive hypotheses. Assuming that the different hypotheses proposed to explain sexual segregation are exclusive, predictions can be made on whether or not social ungulates should segregate by sex depending on differences in body size. This is best achieved by first studying non-dimorphic species, because body size differences affect most of the factors under consideration. If differences in body size are controlled for, by studying the behavior of non-dimorphic species, the effects of other variables on sexual segregation

can be evaluated. Once these factors are identified, predictions on the extent of sexual segregation and sexual differences in behavior according to sexual size dimorphism can be made.

(a) Predation risk

Current mechanisms thought to be responsible for sexual segregation in ungulates are summarized in Fig. 1. If the reproductive strategy hypothesis is true, males and females should segregate into separate groups independent of the degree of sexual dimorphism in body size between them, because their offspring are the ones primarily at risk (Main *et al.*, 1996) (Fig. 1, points 2, 4 and 6). As females care for the young, females will seek habitat that is safe in terms of predation for their offspring (Jackimchuk *et al.*, 1987). Females without young should not be segregated from males unless differences in body size of adults *per se* makes the smaller females more vulnerable to predation than the larger males (points 6 and 7, Fig. 1). Females with young would therefore be found in habitat, which is safer from predation, whereas females without young are expected to use the same habitat than adult males (Young & Isbell, 1991).

In non-dimorphic species, non-reproducing females should not be more vulnerable to predation than males (points 1 and 3). If these females still segregate from males, predation cannot be the cause. Studies have focused on dimorphic species alone (points 5 and 6, Fig. 1). Comparable data of non-dimorphic species is needed to solve this problem. If non-reproducing females of non-dimorphic species stay in adult male groups, whereas reproducing females do not, predation or differing energy and nutrient requirements due to reproduction could be responsible for this outcome (points 4 or 11 in Fig. 1). If reproducing females segregate from males and non-reproducing females, but feed on the same plants or have similar energy and nutrient intake, then predation could be the driving factor responsible for segregation. Females would therefore be found in safer habitat (hide in bushes, stay close to cliffs *etc.*), but eat on the same plants, have similar intake (similar bite rates, activity budgets and food selection). If they are looking out for predators, female vigilance (the rate with which they lift their head to scan the environment) should be higher than for either males or non-reproducing females. Sukumar & Gadgil (1988) showed that Asian elephant (*Elephas maximus*) males are taking more risks while foraging

Fig. 1.   A predictive model of sexual segregation in ungulates. Numbers in bold indicate alternative pathways of the model which lead to conclusions on whether or not ungulates should segregate. Sexual difference in predation risk is used as an ultimate explanation for sexual segregation, while all other factors are proximate explanations.

than females. Accordingly, sexual segregation could have evolved because males take more risks while foraging than females. Males would hence be found in more dangerous habitat than females and their offspring. Whether males take more risks or females avoid predation because of offspring does not matter, because the outcome is in both cases sexual segregation by habitat.

One may be tempted to test the predator avoidance hypothesis by either removing predators from a population of ungulates or by comparing different populations of the same species with and without predation, or lower levels of predation. One would then expect females of populations with low predator pressure to show less use of escape terrain and an increased use of good quality food habitat compared to females of populations with high predator pressure. However ungulates have co-evolved with their predators for thousands of years and even in the absence of natural predators, anti-predator behavior may still be present (Byers, 1997). We may therefore still observe high vigilance or use of "predator-safe" habitats in the absence of direct predation; a phenomenon Byers (1997) called the 'ghost of predators past'. If this is the case, females may still retreat into inaccessible terrain to give birth to their young, unless there is strong selection against this behavior, *e.g.* if it is costly. We suggest that effects of predator avoidance on sexual segregation be best evaluated by comparing anti-predator behavior of males, non-reproducing and reproducing females of non-dimorphic species. Adult body size and anti-predator behavior should be similar in non-reproducing adults.

If predation is not the main factor driving segregation, we may expect to see sexual differences due to social preferences or forage selection. Consequently, no difference in distance to cliffs, or use of cover should be found between reproducing females and other adults.

(b) Social preferences

The social factors hypothesis predicts that males and females prefer each other's company from a young age on (Bon, 1991). If non-dimorphic species segregate into male and female groups, but do not differ in activity budgets, habitat and food preference, anti-predator behavior, vigilance or movement rate, social factors may be responsible for segregation. Social preferences as the sole cause of sexual segregation may be expected between males and

non-reproducing females of non-dimorphic species, although it was origi-
nally proposed for dimorphic species (point 15, Fig. 1). The social preference
hypothesis is difficult to assess, but could be tested experimentally on non-
dimorphic social species. If captive males who where raised in female-only
groups still prefer to associate with other males, outside the breeding season,
then social preferences may indeed be important in individual group choice.
However, even if social preferences are strong, there is no reason why males
and females should segregate into different groups, unless they display other
differences in behavior, or actively avoid each other's company.

(c) Forage selection

The forage selection hypothesis proposes that males and females of sexually
dimorphic ungulates segregate into different groups because of differing
nutritional requirements (Main *et al.*, 1996). These differing requirements
will lead to differences in nutrient acquisition, plant selection and therefore
habitat use. If this hypothesis is true we will first of all find a clear segregation
by space, and not much overlap of habitat use, or a clear difference in
plant selection within the same habitat. Again, this has only been tested
for one species at a time; no inter-specific comparisons have been made
so far (point 12, Fig. 1). No study has looked at sexual differences in diet
selection or habitat overlap in non-dimorphic species (point 11). If habitat
or diet selection differed among the sexes in non-dimorphic species, then
body size alone cannot explain segregation. Males and non-reproducing
females would be expected to feed on the same plant species and use the
same habitat. Reproducing female have higher energy requirements due to
gestation and lactation (Robbins, 1993) and therefore should opt for high
quality food (high in protein content or energy) and differ in habitat use
from males and non-reproducing females (point 11, Fig. 1). If differences
in body-size affected forage selection, we would expect to find increasing
sexual differences in forage selection with an increase in sexual body-size
dimorphism when comparing different ungulate species.

(d) Scramble competition

In situations where forage is sparse or of low standing crop, larger males
may be outcompeted by smaller females when feeding on preferred sites

(Clutton-Brock *et al.*, 1987). Accordingly, we would expect to find mixed-sex groups where forage is abundant and sexually segregated groups where forage is sparse (point 14). The scramble competition hypothesis could best be tested by an experiment in captivity. Sexually dimorphic males and females could be presented with forage of different standing crop and abundance. Measurements of forage selection, bite sizes, and giving-up times of males and females could then be used as indirect measure of competition for mutually preferred food, similar to an experiment done on Soay sheep by Pérez-Barbería & Gordon (1999). However, the scramble competition hypothesis may only apply to a limited number of ungulate populations, living on islands or in other places where food is extremely limited.

(e) Activity budgets

Most studies have focused on predator avoidance strategies (points 5 and 6), and on sexual differences in diet choice or competitive abilities (points 9, 10, 12 and 14). Data on sexual segregation due to differences in activity budgets and movement rates (point 13) are lacking (Ruckstuhl, 1998a). If the activity budget hypothesis applies, males and females should segregate into different groups because of an incompatibility in activity budgets (Ruckstuhl, 1999). The larger the sexual differences in body size, the more activity budgets should differ between males and females. As body size differences between males and females increase, a clear tendency to form sex segregated groups should be observed (Ruckstuhl, 1999). Sexual segregation therefore should be least pronounced in species with little sexual dimorphism in body size (Fig. 1, points 1 and 3). Consequently, males, reproducing or non-reproducing females of non-dimorphic species are expected to show similar activity budgets and hence to form mixed-sex groups unless reproducing females need to compensate for their higher energy demands of gestation and lactation by spending more time foraging. In that case, we would expect reproducing females to share the same habitat, show similar vigilance rates and feed on the same plants as other adults, but spend more time feeding than either non-reproducing females or adult males. With increasing sexual body size dimorphism, non-reproducing females would be expected to feed on the same plants and use the same habitat as males, but they would segregate from male groups because of differences in activity budgets. Activity budgets should differ increasingly because time allocated to foraging per unit body

weight is estimated to decrease with increasing body size (Hudson & White, 1985). Segregation may not only occur between the sexes, but also between age or reproductive status classes (Ruckstuhl, 1998a, b; Ruckstuhl & Festa-Bianchet, 1998). Young males with an intermediate body size between the adult sexes should form groups of their own, as was found in ibex or mouflon (Bon *et al.*, 1993; Villaret & Bon, 1995; Ruckstuhl, 1999). Segregation due to reproductive status should occur when non-reproducing and reproducing females differ in their energy demands and predator avoidance strategies. Indeed, non-reproducing wood bison (*Bison bison athabascae*) cows tend to associate among themselves or with males instead of staying in nursery groups (Komers *et al.*, 1993). Among non-dimorphic species, body size per se should not affect activity budgets, habitat choice, or predator avoidance and we would consequently expect the formation of long-term male-female bonds or mixed-sex groups, because females and males could easily coexist.

As mentioned in the activity budget hypothesis (Ruckstuhl, 1998a) females with young may exhibit increased movement rates compared to males or non-reproducing females because of different predator avoidance strategies. Increased movement rates by females and their offspring may further increase segregation initially caused by sexual differences in activity budgets (Ruckstuhl, 1998a).

Exceptions to the rule

Although, sexually dimorphic males and females usually segregate, sexual segregation may be absent in species with large differences in body size. Limited food availability could lead to the formation of mixed groups on clumped food patches; such as in some populations of Asiatic ibex, *Capra ibex sibirica* (Fox *et al.*, 1992) or mouflon of Kerguelen Islands (Moncorps *et al.*, 1997). Sexual segregation could also be absent in small populations, where the number of males and females is too low to form segregated groups: males and females may group together because of benefits of detection and dilution effects (Dehn, 1990). The latter was found in fallow deer (*Dama dama*), where males joined female groups in years when male population density was very low (Thirgood, 1996). Hence, factors such as clumped food distribution, differential predator pressure, or territoriality in males may override effects of body-size differences. Sexual segregation may for

example exist with little difference in body size, such as where males are territorial or leking while females live in groups year round (Jarman, 1983).

A combination of different factors instead of a single one may be responsible for sexual segregation. Males and females of dimorphic species may be segregated because of differences in predator avoidance, forage selection, social preferences or activity budgets. Each factor and a combination of all will have to be carefully assessed and taken into account.

Body size, mating systems and sexual segregation in mammals

Sexual selection was proposed to lead to the evolution of large body size in males, because relative body size effectively determines a male's fighting ability, and, therefore, his success when competing with other males over the access to females in estrous (Darwin, 1871). While increased body size enhances a male's fighting ability (Geist, 1974), body size also affects his energy demands and his activity budget (Ruckstuhl, 1998a). A male may allow himself to forego feeding to follow females and defend a territory during a short breeding season (Miquelle, 1990), but the difference in body size with the females may ultimately determine the extent and duration to which he can actively synchronize his behavior with them (Conradt, 1998; Ruckstuhl, 1998a). Following the activity budget hypothesis, it is conceivable, that a male can only be territorial and have a permanent female or females in his territory, if both sexes are of similar body size and therefore have similar activity budgets. Activity synchrony helps to keep members of the group or pair in close proximity, since it prevents individuals being left behind when the others become active (Dunbar & Dunbar, 1980).

In small, monogamous, non-dimorphic, territorial antelopes, such as Kirk's dik-dik (*Madoqua kirkii*) or klipspringer (*Oreotragus oreotragus*), males and females are highly synchronized in their activity (Dunbar & Dunbar, 1980; Estes, 1991), and may because of their synchrony, be able to co-exist and form permanent male-female bonds with male protection of females (Brotherton *et al.*, 1997). Other non-dimorphic ungulates, such as oryx (*Oryx gazella*) or pronghorn (*Antilocapra americana*) lek or defend a territory during breeding, but join with females in mixed-sex groups after breeding (Estes, 1991; Byers, 1997). Medium-sized non-dimorphic ungulates such as equids or camelids live in harems (with long-term harem holders), bachelor male, female or mixed herds (Nowak, 1991). It is not known, whether

non-dimorphic males and females are in mixed-sex groups because they synchronize their behavior with each other. Because camelids and equids are sexually non-dimorphic, medium-sized species, and sometimes form mixed-sex herds (Groves, 1974; Nowak, 1991), they are ideal to compare to sexually dimorphic, social bovids or cervids of similar size.

We argue, that in general, non-dimorphic males and females share a territory or form a group because they can afford to do so, while sexually dimorphic males and female cannot afford the constant costs of activity synchrony or territorial defense. Indeed, adults of sexually dimorphic ungulates live sexually segregated except for short periods of breeding. During breeding, males spend enormous efforts and time fighting for females and following females in estrous (Hogg, 1984). During breeding, males form leks (Clutton-Brock *et al.*, 1988), have temporary territories (Estes, 1991), harems (Clutton-Brock *et al.*, 1982a), or tend single females at a time (Hogg, 1984; Weckerly, 1998), but do not defend females against rivals outside the breeding season (Jarman, 1983). African buffalo (*Syncerus caffer*) and eland (*Taurotragus oryx*) show high sexual dimorphism; while buffalo males never stay in female groups over a long period of time (Prins, 1996), eland males may be long-term harem holders (Nowak, 1991). Whether sexual segregation in eland could be driven by territorial males, excluding all other rival males, is not clear and needs to be investigated. To make any conclusions it would be important to know how and for how long a large male, relative to smaller females, could maintain body size/condition as a long-term harem holder in this species. Further it is questionable if segregation is forced by territorial males, because young eland males have a strong tendency to form peer groups (Nowak, 1991) instead of joining with other ousted adult males.

Sexual dimorphism in body size is very widespread in mammals (Nowak, 1991). Females are larger than males in fin (*Balaenoptera physalus*), blue (*Balaenoptera musculus*), sei (*Balaenoptera borealis*) and minke (*Balaenoptera acutorostrata*) whales where sexual and age segregation has been observed (Gaskin, 1982). In other mammalian species, where sexual and age segregation occurs, males are always larger and heavier than females. For example right whales (*Balaena glacialis*), segregate into bachelor male and nursery groups outside the breeding season, as do beluga (*Delphinapterus leucas*), and humpback whales (*Megaptera novaeangeliae*) (Gaskin, 1982; Nowak, 1991; Christal *et al.*, 1998). Narwhal (*Monodon monocrus*) males are almost double the mass of females and they either live in families

with one male or are segregated into male and female groups (Nowak, 1991). It is not clear how long a narwhal male can last in a harem group. Sexual segregation also occurs in sexually dimorphic chimpanzees (*Pan troglodytes*), spider monkeys (*Ateles geoffroyi*), coatis (*Nasua narica*), and some macropods (Nowak, 1991). What causes this segregation by sex or age is not clear, but similar mechanisms can be assumed, such as sexual incompatibilities of activity budgets and movement rates or competition over resources.

Conclusion and new directions for research

As shown, most of the five current hypotheses may explain sexual segregation in ungulates to some extent. To date, the predation risk hypothesis and the activity budget hypotheses are the most promising explanations for sexual segregation in dimorphic ungulates and may explain sexual segregation in other mammals as well. Obviously, different factors may affect sexual segregation. More effort should be put into investigating the neglected social factors and the new activity budget hypotheses. Both hypotheses are proximal explanations for sexual segregation, not necessarily implying ultimate causation (Bon, 1991). The study of the ontogeny of behavior in young, growing animals, their activity budgets, group choice and social preferences from birth to adulthood may help to detect mechanisms underlying sexual segregation (Bon & Campan, 1996; Ruckstuhl, 1998b, 1999). In a recent paper, Conradt (1999) stated that social segregation is independent of habitat segregation and that social factors may be more important in determining sexual segregation, than environmental factors. Conradt (1999), therefore, concluded that it is no longer necessary to look for a universal ecological mechanism to explain the phenomenon of spatial and habitat segregation in ungulates. Although we do agree on the importance of studying social factors, we believe that only a phylogenetic comparison of behavior, testing all hypotheses, can support or refute the idea that a single factor affects sexual segregation.

The five hypotheses should be further explored by comparing a wide range of ungulate species with varying degrees of sexual dimorphism and sexual segregation. This new approach may allow researchers to detect the most important factors affecting sexual segregation and hence solve the enigma of sexual segregation in ungulates and other sexually or age-segregating mammals.

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