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Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants?

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In many sexually dimorphic mammal species, the sexes live outside the mating season in separate social groups ('social segregation'). Social segregation occurs in a wide range of environmental conditions, but its cause is unknown. I suggest that social segregation is caused by a lower level of activity synchrony between individuals in mixed-sex groups than in single-sex groups, owing to sex differences in activity rhythm. As a consequence, mixed-sex groups are more likely to break up than single-sex groups, resulting in a predominance of single-sex groups at equilibrium. To test this hypothesis in red deer (*Cervus elaphus* L.), I developed an index of activity synchronization and showed that deer in mixed-sex groups were significantly less synchronized in their activity than deer in single-sex groups. Thus, low intersexual synchrony in activity can lead to social segregation. However, a lower level of intrasexual (female–female and male–male) activity synchrony within mixed-sex than within single-sex groups implies that additional factors (other than sex differences in foraging rhythm) contribute to the higher degree of instability in mixed-sex groups.

Keywords: activity synchronization; foraging rhythm; group coherence; sexual segregation; social stability; ungulates

1. INTRODUCTION

It is a striking phenomenon that in many sexually dimorphic mammal species, adult animals outside the mating season tend to group together primarily with other adults of their own sex (Newsome 1980; Clutton-Brock *et al*. 1982; Sukamar & Gadgil 1988; Kovacs *et al*. 1990; Bionski 1994). The sexes are then said to be 'socially segregated'. Social segregation is widespread and exists under a wide variety of ecological conditions (e.g. Nievergelt 1981; Clutton-Brock *et al*. 1982; Sukamar & Gadgil 1988; Kovacs *et al*. 1990; Thirgood 1996). However, in most species, it is not understood what the advantages are of socializing only with your own sex: the functional basis of social segregation, its evolution and ecological consequences are largely unknown.

Because social segregation is often accompanied by sex differences in habitat use ('habitat segregation'), several authors have tacitly assumed that it is simply a by-product of habitat segregation (Geist & Petocz 1977; Clutton-Brock *et al*. 1982; Miquelle *et al*. 1992). However, no evidence in support of this notion has been published. Moreover, Conradt (1997) has recently shown that, at least in red deer and in feral Soay sheep, social segregation occurs independently of habitat segregation. She found that degree of social segregation was significantly larger than degree of habitat segregation and that social segregation occurred also within habitat types. Social segregation could therefore not have been a consequence of intersexual segregation between habitat types. Thus, the question remains: if sex differences in habitat use are not responsible, what causes social segregation?

In the present paper, I propose and test a potential mechanism for social segregation in ruminants, using red deer as the study species. Red deer are sexually dimorphic and, outside the mating season, distinctly socially segregated (Darling 1937; Clutton-Brock *et al*. 1982). In red deer, as in many wild ruminant species, animals join and leave groups frequently (e.g. Clutton-Brock *et al*. 1982; Albon *et al*. 1992; Raman 1997). My suggested mechanism for social segregation is based on higher fission rates of mixed-sex groups than of single-sex groups, owing to activity asynchrony between the sexes.

The background and rationale of the mechanism stem from the fact that ruminants within the same social group tend to be synchronized in their behaviour: they sit down to ruminate within minutes of each other and also stand up to forage within minutes of each other (Conradt 1997). Bouts of ruminating and foraging alternate approximately every 1–2 h (Clutton-Brock *et al*. 1982). This activity synchronization within groups is not simply a result of a shared diurnal rhythm, because when watching two independent social groups at the same time of the day, animals in one group are not necessarily synchronized in their behaviour with animals in the other group. However, if animals within a social group are not well synchronized, so that not all animals within a group are active or resting at the same time, the group is likely to break up: foraging animals of the group move away while the remainder of the group still rests and ruminates

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(Conradt 1997). Thus, activity synchronization within a group is crucial for the stability of the group.

I suggest that social segregation occurs because mixed-sex groups are relatively unstable through a low degree of synchrony in activity between males and females. A low degree of intersexual synchrony in activity is plausible, because in sexually dimorphic ruminants, it is likely that males and females differ in the length of foraging–resting bouts. The larger males need more time to forage and fill their rumen (Clutton-Brock *et al*. 1982; Illius & Gordon 1992), and food passage rates through the rumen are longer (van Soest 1982), than in the smaller females. Further, sex differences in diet selectivity could cause sex differences in foraging bout length. If males and females differ in foraging–resting bout length, they should regularly get out of synchrony in activity, even if they are in the same social group. Consequently, mixed-sex groups should be less stable and more likely to break up (into their male and female parts) than single-sex groups. The result, at equilibrium, would be social segregation.

This mechanism is particularly plausible for ruminants, because of their frequent activity changes between foraging and ruminating and the consequently great scope for activity asynchrony between the sexes. However, the principle of the mechanism could be applied to any sexually dimorphic mammal species that segregates socially and in which body size differences lead to sex differences in activity rhythm.

To test the hypothesis that asynchrony in activity between the sexes causes social segregation in red deer, I first developed an index of activity synchronization in social groups. I then examined whether (i) deer in mixed-sex groups are less synchronized in activity than deer in single-sex groups, and (ii) males and females within mixed-sex groups are less synchronized with animals of the opposite sex than with animals of their own sex.

2. METHODS

(a) *Data*

Unpublished data on social group composition and activity in red deer on Rum were provided by T. H. Clutton-Brock and F. E. Guinness.

The data had been collected during regular censuses on foot of the study site on Rum. In 1974–1993, five censuses per month were conducted in at least nine months per year. For each observed deer group, the sex, age and activity of all its adult members were noted. Detailed descriptions of the study site, red deer population and censusing methods are given in Clutton-Brock *et al*. (1982). Only adult females ($\geqslant$2 years) and adult males ($\geqslant$5 years) were considered.

(b) *Index of activity synchronization*

Animals in many ruminant species forage predominantly at dawn and dusk and rest mainly at midday (Georgii 1980; Georgii & Schroeder 1983). However, not all animals do the same at exactly the same time. Therefore, at any time of the day, some of the animals in a population are active (i.e. standing or moving), whereas others are resting (i.e. sitting). If animals within each group are doing the same, so that some groups contain only active animals, and other groups only resting animals, animals are completely synchronized in activity within groups. On the other hand, if animals taken from the same group are not more likely to be engaged in the same activity (i.e. either active or resting) than animals taken from different groups at the same time of day, there is no synchronization of activity within groups. In a previous paper (Conradt 1998), I developed a 'coefficient of segregation' to measure the degree of social segregation in a population of animals. Because degree of synchronization can be measured in a very similar way to degree of segregation, the same method can be used to derive a 'synchronization coefficient' (*SynC*; see Appendix A and Conradt (1997) for mathematical details), defined as follows:

$$SynC = 1 - \sum_{h=08.00}^{20.00} \left(\frac{N_h}{N} \frac{(N_h - 1)}{A_h R_h} \sum_{i=1}^{k_h} \frac{a_{h,i}\, r_{h,i}}{(n_{h,i} - 1)} \right),$$

where h is hour of the day, N is total number of animals observed, N_h is total number of animals observed in h-th hour of the day, A_h is total number of active animals observed in the h-th hour of the day, R_h is total number of resting animals observed in the h-th hour of the day, $n_{h,i}$ is number of animals observed in h-th hour of the day in i-th group, $a_{h,i}$ is number of active animals observed in h-th hour of the day in i-th group, $r_{h,i}$ is number of resting animals observed in h-th hour of the day in i-th group, and k_h is number of groups observed in h-th hour of the day.

The synchronization coefficient can range from 0 ('no synchronization in activity within groups') to 1 ('complete synchrony of activity within groups'). Note that *SynC* is not suited for measuring activity synchronization if animals within groups are less likely to be engaged in the same activity than animals taken from different groups. *SynC* takes into account the diurnal activity rhythm (i.e. the fact that the proportion of animals in the population which are active changes with time of day). It also allows comparison of the degree of synchrony between group types of different sizes (mixed-sex groups tend to be larger than single-sex groups (Clutton-Brock *et al*. 1982)) without confounding effects of group size (see Appendix A; compare also to Conradt (1997, 1998)).

In each month of each year, I calculated the degree of synchronization for groups seen in that month, using only adult animals for the analysis. Minimum sample sizes were 60 animals per month. When I measured the degree of synchronization within female (male) groups or within female (male) parts of mixed-sex groups, I considered only the respective groups or parts of groups for the calculation of *SynC*. To measure the degree of synchronization between males and females in mixed-sex groups, *SynC* had to be modified further ($SynC_{(\mathrm{male-female})}$; see Conradt (1997) for mathematical details):

$$SynC_{(\mathrm{male-female})} = 1 - \sum_{h=08.00}^{20.00} \left(\frac{N_h}{N} \frac{N_h^2}{A_h R_h} \sum_{i=1}^{k_h} \frac{x_{a,h,i}\, y_{r,h,i} + x_{r,h,i}\, y_{a,h,i}}{2\, x_{h,i}\, y_{h,i}} \right),$$

where $x_{a,h,i}$ is number of active males observed in h-th hour of the day in i-th group, $x_{r,h,i}$ is number of resting males observed in h-th hour of the day in i-th group, $x_{h,i}$ is number of males observed in h-th hour of the day in i-th group ($x_{h,i} = x_{a,h,i} + x_{r,h,i}$), $y_{a,h,i}$ is number of active females observed in h-th hour of the day in i-th group, $y_{r,h,i}$ is number of resting females observed in h-th hour of the day in i-th group, and $y_{h,i}$ is number of females observed in h-th hour of the day in i-th group ($y_{h,i} = y_{a,h,i} + y_{r,h,i}$).

(c) *Statistics*

The data distributions justified parametric testing. To avoid seasonal biases and ensuing confounding effects, I treated data

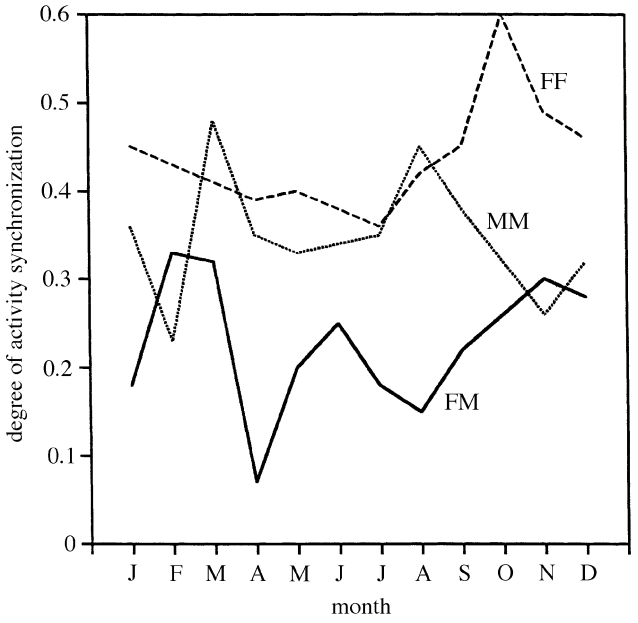

Figure 1. Mean degree of activity synchronization over the course of the year in female-only (FF), in male-only (MM) and in mixed-sex (FM) groups. There were no obvious seasonal trends, therefore comparisons were made for all data combined.

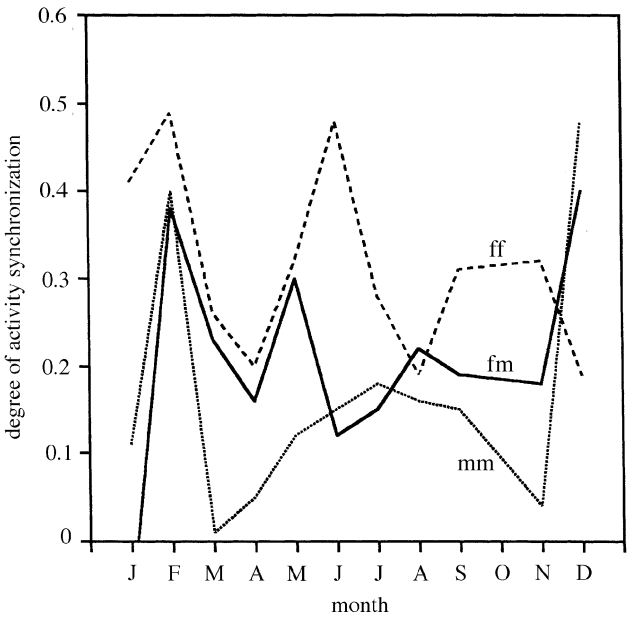

Figure 2. Mean degree of activity synchronization over the course of the year between females (ff), between males (mm) and between females and males (fm) within mixed-sex groups. There were no obvious seasonal trends, therefore comparisons were made for all data combined.

from the same month of the same year as dependent and used related-samples *t*-tests for comparisons.

3. RESULTS

(a) *Were deer in mixed-sex groups less synchronized in activity than deer in single-sex groups?*

The degree of activity synchronization (figure 1) was significantly lower in mixed-sex groups than in male-only groups (difference: $\Delta = -0.13$, *t*-test: $t = -4.5$, $p < 0.001$, $n = 135$) or in female-only groups ($\Delta = -0.20$, $t = -11.2$, $p < 0.001$, $n = 153$). Furthermore, degree of activity synchronization was significantly lower in male-only groups than in female-only groups ($\Delta = -0.07$, $t = -2.9$, $p < 0.01$, $n = 137$).

(b) *Were deer within mixed-sex groups less synchronized in activity with deer of the opposite sex than with their own sex?*

Within mixed-sex groups (figure 2), females were significantly less synchronized in activity with males than with other females ($\Delta = -0.09$, *t*-test: $t = 3.3$, $p < 0.001$, $n = 89$). However, males were significantly more synchronized in activity with females than with other males ($\Delta = +0.07$, $t = 2.2$, $p < 0.05$, $n = 89$).

The low male–female activity synchronization within mixed-sex groups was not the only reason for the relatively low overall activity synchronization in mixed-sex groups (compare figures 1 and 2): female–female synchronization was significantly lower within mixed sex groups than within female-only groups ($\Delta = -0.13$, $t = 6.0$, $p < 0.001$, $n = 143$), and male–male synchronization was significantly lower within mixed-sex groups than within male-only groups ($\Delta = -0.22$, $t = -6.0$, $p < 0.001$, $n = 89$).

4. DISCUSSION

In the present paper, I have proposed and tested the hypothesis that sex differences in activity synchronization can lead to social segregation. I found that activity synchronization was significantly lower within mixed-sex groups of red deer than within single-sex groups. Activity asynchrony of individuals within a group often leads to the splitting-up of the group (Conradt 1997), whereby the foraging subgroup separates from the resting subgroup until it is found as close to new groups as it is to the subgroup which it left. Thus, a re-fusion of the original subgroups is not more likely than a fusion of each subgroup with a new group, and the subgroups can be considered as new, independent groups. Through this process, the lower activity synchrony in mixed-sex groups renders them more likely to break up than single-sex groups. Within mixed-sex groups, activity synchronization was lower between females and males (intersexual) than between females and females (intrasexual). However, intersexual female–male activity synchronization was higher than intrasexual male–male synchronization. This suggests that when mixed-sex groups split, they most commonly break up into their female part and into solitary males. The consequently higher fission rates of mixed-sex groups than of single-sex groups can lead to social segregation in red deer.

If social segregation were caused solely by sex differences in activity synchronization, social segregation would be a relatively passive process, as it is unlikely that deer actively seek asynchrony in activity with animals of the opposite sex. Intersexual activity asynchrony due to sex differences in body size is thus a purely mechanistic explanation of social segregation. It does not preclude a functional explanation, but no functional advantages would be necessary to explain the evolution of social segregation.

However, an unexpected result of the present study was that the degree of intrasexual (female–female and male–male) activity synchronization was lower within mixed-sex groups than within single-sex groups. Therefore, passive sex differences in foraging–resting rhythm cannot have been the only reason for lower activity synchronization of individuals within mixed-sex groups. This result implies that in mixed-sex groups, the coordination of activity synchronization between same-sex group members was disturbed by the presence of the opposite sex. It is thus likely that social factors contributed to the relatively low activity synchronization within mixed-sex groups, and thus, to social segregation. This renders a functional explanation of social segregation necessary, in addition to the mechanistic explanation of social segregation offered by intersexual activity asynchrony. Potential functional explanations of social segregation are: (i) male avoidance of intermale aggression caused by the presence of females (Prins 1987); (ii) female avoidance of male harassment (Wielgus & Bunnell 1994); (iii) optimization of social learning in single-sex groups (Appleby 1982, 1983); and (iv) males leaving groups in which they are conspicuous to predators (Geist & Bromley 1978). The apparent disturbance of intrasexual activity synchronization within mixed-sex groups suggests that social conflicts are involved and therefore favours notion (i) or (ii).

Activity synchronization also differed between different types of single-sex groups. Male-only groups were less synchronized (and therefore presumably less stable) than female-only groups. This is surprising, as inter-individual variance in foraging–resting rhythm does not seem to be larger between males than between females (Clutton-Brock *et al*. 1982), and one would therefore expect a similar degree of activity synchronization in male-only as in female-only groups. An explanation for the observed difference could be that activity synchronization involves costs, and that females make more of an effort (i.e. they pay higher costs) to maintain activity synchrony with one another (and thus, to maintain group stability) than do males. This interpretation would fit in with other reported sex differences in grouping behaviour in red deer: males tend to join groups that are open to all males and relatively unstable in individual composition, whereas female groups seem to be relatively restricted in composition, but also more stable (Clutton-Brock *et al*. 1982; Appleby 1982, 1983). Thus, activity synchronization in ruminants does not seem to be a simple or passive process, but might involve costs, and could be influenced by social conflicts.

The coherence of social groups necessarily depends on inter-individual activity synchronization. Results of the present study imply that individuals have to pay costs to maintain activity synchrony in order to maintain group coherence. Such costs are unlikely to be evenly distributed within groups: for example, dominant animals might 'set' the activity rhythm and subordinate animals might be obliged to follow. However, little seems to be known about the instigation and costs of activity synchronization and its consequences for group coherence and social organization in mammals. The present study suggests that important patterns of social organization, such as social segregation of the sexes, can be influenced by activity synchronization and, therefore, by its costs. In addition, the degree of activity synchronization in social groups could be a useful indication of social group stability and intensity of social conflicts. The suggested 'synchronization coefficient' *SynC* could thus supply a relatively simple measure of social stability in groups of different types.

After preparing the present paper, I became aware of a manuscript by Ruckstuhl (1998), presenting similar results and conclusions in relation to bighorn sheep.

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APPENDIX A. EXPECTED VALUES *E*(*SynC*) OF THE SYNCHRONIZATION COEFFICIENT *SynC*

To develop a reliable and comparative measure of activity synchronization within groups, it has to be taken into account that group sizes ($n_{h,i}$) and the proportion of animals in the population that are active at any time of the day (A_h/N_h) can vary, and that these influence the number of groups in which animals are synchronized. I give an example to illustrate the problem. Suppose one compares activity synchronization between three populations (1, 2 and 3). Let group sizes be constant and equal to two (i.e. $n_{h,i} \equiv \bar{n} = 2$) in populations 1 and 2, and equal to three in population 3. Further, let the proportion of animals that are active at any time be 50% (i.e. $A_h/N_h \equiv A/N = 0.5$) in populations 1 and 3, and 10% in population 2. Suppose that there is no synchronization of activity within groups in any of the populations, and active and resting animals are therefore distributed in a random (hypergeometrical, i.e. approximately binomial) fashion between groups. Then the proportion of groups in which all members are doing the same (either being active or resting) is 50% in population 1, 82% in population 2 and 25% in population 3 (i.e. $(A/N)^{\bar{n}} + (1-A/N)^{\bar{n}}$). Therefore, although the degree of activity synchronization is the same in all three populations (namely: 0), the populations differ in the proportion of groups in which all members are doing the same. *SynC* avoids this stochastic problem. In the following, I give the expected values of *SynC* at different degrees of activity synchronization and show that *SynC* is stochastically independent of group sizes and of the proportion of animals that are active at any time of the day.

1. In the case of no synchronization, active and resting animals are distributed randomly (i.e. hypergeometrically) into groups. Therefore,

$$E\left(\sum_{i=1}^{k_h} \frac{a_{h,i}\ r_{h,i}}{(n_{h,i}-1)}\right) = \frac{A_h\ R_h}{N_h\ (N_h-1))} N_h.$$

It follows that

$$E(SynC) = 1 - \sum_{h=08.00}^{20.00} \left(\frac{N_h}{N} \frac{(N_h-1)}{A_h\ R_h} E\left(\sum_{i=1}^{k_h} \frac{a_{h,i}\ r_{h,i}}{(n_{h,i}-1)}\right)\right)$$

$$= 1 - \sum_{h=08.00}^{20.00} \left(\frac{N_h}{N}\right) = 0.$$

2. In the case of complete activity synchronization within groups, all members of each group are doing the same

(either they are all active or they all rest). Thus, either $a_{h,i} = 0$ or $r_{h,i} = 0$, and $a_{h,i}r_{h,i} = 0$ for all h,i. It follows that

$$SynC = 1 - \sum_{h=08.00}^{20.00} \left(\frac{\mathcal{N}_h}{\mathcal{N}} \frac{(\mathcal{N}_h - 1)}{A_h\ R_h} \sum_{i=1}^{k_h} \frac{0}{(n_{h,i} - 1)} \right) = 1.$$

3. If the degree of activity synchronization is intermediate between no synchronization and complete synchronization, it can be shown that the value of *SynC* increases with the proportion of active animals that synchronize within groups and with the proportion of resting animals that synchronize within groups. It can be also shown that *SynC* is stochastically independent of group sizes and of the proportion of animals in the population that are active (see Conradt (1997) for proofs).

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