



Sexual segregation among feral goats: testing between alternative hypotheses

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Sexual segregation occurs widely in ungulates, and four principal hypotheses (predation, forage quality, social preferences and activity patterning) have been suggested as possible explanations. However, no single explanation has so far received widespread support. We used data on the grouping behaviour of feral goats, *Capra hircus*, on the Isle of Rum, Scotland, U.K. to test between competing hypotheses. We first used Conradt's (1999, *Animal Behaviour*, **57**, 1151–1157) test to show that sexual segregation is not a consequence of sex differences in habitat preference. Since the predation risk hypothesis can be ruled out by both the absence of important predators on Rum and the tendency for those individuals most sensitive to predation (mother–offspring pairs) to be the furthest away from their neighbours, any explanation for sexual segregation must either lie in differences in activity patterning or be the consequence of a social preference for associating with same-sex individuals. We analysed data on the patterns of fission, behavioural synchrony and neighbourhood in relation to party size and composition to show that the activity budget hypothesis is the more likely. However, the data also suggest that the social preferences hypothesis none the less has a residual influence on segregation tendencies of the Rum goats. We conclude that one likely reason for the conflicting results in the literature may be that all four hypotheses in fact apply simultaneously, but that their relative weightings may depend on habitat- and species-specific characteristics.

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Sexual segregation (whereby males and females live in separate groups) is commonly observed in ungulates (Main & Coblenz 1990; Main et al. 1996). However, the reason why sexual segregation occurs remains the subject of much debate (Ruckstuhl & Neuhaus 2000, 2002). To date, four principal hypotheses have been proposed: predation risk, forage selection, social preference and activity budget differences (Main et al. 1996; Ruckstuhl & Neuhaus 2000).

Although there have been a number of attempts to test between these hypotheses, both on particular populations of ungulates and using comparative data (e.g. Ruckstuhl & Neuhaus 2002; Bonenfant et al. 2004; Bowyer & Kie 2004; Ciuti et al. 2004), these have focused almost exclusively on the fact of segregation (whether or not the two sexes range separately) and seem to have completely ignored the behavioural processes that lead up to segregation

(namely, fission and fusion of foraging groups, and the levels of behavioural synchrony that precede these events). Where the underlying mechanisms have been addressed, this has invariably been done with indices that are at best crude (e.g. ratio of body masses as an index of differences in foraging behaviour: Ruckstuhl & Neuhaus 2002). This is particularly surprising, because it is at the level of mechanisms that most hypotheses actually differ.

In this paper, we applied two novel approaches to the problem. First, we tested directly between the four hypotheses using a 'critical tests' approach (van Schaik & Dunbar 1990) that allowed us both to test simultaneously between alternative hypotheses and to assess their likely interaction. Second, we focused on the behavioural dynamics of the fission process that underlie segregation: since these tell us about the mechanisms that produce fission (and hence segregation), these are likely to provide us with a purchase on hypothesis testing that is heuristically more powerful than any alternative approaches. For these purposes, we focused on the stability and internal spatial structure of foraging groups, and the behavioural synchrony of their members, in relation to their size and composition, and the characteristics of the vegetation communities on which they occur.

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We explored the dynamics of foraging groups in a population of feral goats, *Capra hircus*, inhabiting the Isle of Rum in northwest Scotland, U.K. This population offers a number of advantages for such a study. First, in contrast to many ungulate populations (including feral goats at more southerly locations in the British Isles: R. Dunbar, unpublished data), the Rum goat groups undergo high rates of fission and fusion: this allowed us to sample many fission events and the behavioural circumstances leading up to them. Second, while there was considerable variation in group size, the modal size was small (three animals), allowing us to monitor the behaviour of all group members relatively easily.

In feral goats, females live in spatially exclusive matrilineal communities (heft groups) with which males associate to variable degrees (Boyd 1981; Gordon et al. 1987; Shi et al. 2005). Members of a heft group associate in foraging groups that have limited temporal and spatial duration (Boyd 1981; Gordon et al. 1987; Dunbar et al. 1990; Shi 2002). Sexual segregation has been reported in temperate populations of feral goats (Riney & Caughley 1959; Boyd 1981; Shi et al. 2005), although this does not always seem to be the case in tropical environments (Yocom 1967). We focused on the prerut summer months when segregation is most likely to occur (Shi et al. 2005). On Rum, the goats spend the night in caves and other shelters at beach level, and then forage slowly up the cliff face above the beaches during the day (Shi et al. 2003). Shi et al. (2005) showed that segregation commonly arises because individuals drift apart while foraging. As a result, segregation was more common during spring and summer months (except during the rut) when the longer day-lengths allowed the animals to forage further afield and, hence, drift further apart. However, Shi et al. (2005) did not test alternative hypotheses for segregation.

HYPOTHESES AND PREDICTIONS

The essence of the critical test method is to derive series of predictions at the behavioural level for each of a set of

alternative hypotheses (van Schaik & Dunbar 1990; see also Dunbar et al. 2002). Comparing the pattern of predictions across a series of behavioural indices with those actually observed then allows us to determine which hypothesis provides the best fit to the data. To do this, we first summarize briefly both the main points of the four hypotheses that have been offered for sexual segregation in ungulates and then give the predictions we derived from them (summarized below in Table 1).

The predation risk hypothesis (previously the 'reproductive-strategies' model: Main et al. 1996) is based on two main premises. The first is that predation risk is a function of body size, with smaller individuals being more susceptible to predation (Gaillard et al. 1998). Segregation is then a consequence of the second premise: different criteria affect male and female lifetime reproductive success (Main et al. 1996). Sexual selection will favour males that are willing to tolerate high predation risk to gain access to high-quality vegetation that will allow them to maximize growth and condition in the interests of successful rutting (Shank 1982; Main & Coblentz 1990; Miquelle et al. 1992), whereas females will prefer to compromise foraging conditions in the interests of minimizing predation risk for their offspring (Bunnell & Gillingham 1985; Main et al. 1996). Females without dependent young, however, should not segregate from males unless adult size dimorphism per se leads to differences in vulnerability (Ruckstuhl & Neuhaus 2000).

Although extensively supported (Main et al. 1996), the predation risk model has a major shortcoming that arises from a more or less exclusive focus on species under considerable predation pressure living in heterogeneous habitats, where areas differ in both predation risk and vegetation quality or abundance (Main et al. 1996; Ruckstuhl & Neuhaus 2000, 2002). It overlooks alternative ways of minimizing predation risk, other than choice for inaccessible habitats or those with increased cover (Ruckstuhl & Neuhaus 2000). These can include larger group sizes for dilution effects or active defence (e.g. Dunbar 1988; Dehn 1990) or increased movement rates for spatial

Table 1. Summaries of predictions for behavioural indices for the main hypotheses, together with the observed results (with critical tests identified in capitals)

Behavioural index	Predicted relation for individual hypotheses				Observed outcome
	Predation	Forage	Social	Activity	
1. Habitat influences group fission rate	Yes	Yes	NO	Yes	Yes
2. Group size influences group fission rate	Yes	Yes	NO	Yes	Yes
3. Group composition influences group fission rate	NO	Yes	Yes	Yes	Yes
4. Habitat influences synchrony	No	No	No	YES	Yes
5. Group size influences synchrony	No	No	No	YES	Yes
6. Group composition influences synchrony	No	No	No	YES	Yes
7. Group stability influences synchrony	No	No	No	YES	Yes
8. Synchrony increases after fission	No	No	No	YES	Yes
9. Neighbours assort by sex	No	Yes	Yes	Yes	Yes
10. Females avoid males	No	No	YES	No	Yes
11. Females with kids avoid each other	No	No	YES	No	Yes
12. Group size influences neighbour distance	Yes	NO	Yes	Yes	Yes
13. Group composition influences neighbour distance	No	No	Yes	Yes	Yes
Number of correct predictions:	3	4	6	11	
Number of correct critical tests (number available):	0(1)	0(1)	2(4)	5(5)	

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