

Cambridge University Press

978-0-521-18421-2 - Sexual Segregation in Vertebrates: Ecology of the Two Sexes

Edited by K. E. Ruckstuhl and P. Neuhaus

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## Part I Overview

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KATHREEN E. RUCKSTUHL AND TIM H. CLUTTON-BROCK

## 1

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## Sexual segregation and the ecology of the two sexes

According to Greek mythology, Amazons were female warriors who lived on an island. They occasionally met with men of another people to mate, keeping female offspring and sending male offspring back to their fathers. In many animals too, males and females live apart for most of the year, only gathering for mating. These include many fish species (Sims *et al.*, 2001a), birds (Myers, 1981), lizards and snakes (Parmelee & Guyer, 1995; Shine *et al.*, 2003a), and most mammals with a pronounced sexual dimorphism in body size (Ruckstuhl & Neuhaus, 2000). This book aims at synthesizing our current understanding of the evolution of sexual segregation in different vertebrates, focusing on taxa in which there is sufficient evidence to investigate causes of sexual segregation.

Sexual segregation has caused confusion in the literature, as it can occur at different levels (see Chapter 2 for details). Why, for example, do house mice, *Mus musculus*, embryos segregate by sex in their mother's womb (Terranova & Laviola, 1995)? Why do African ground squirrels, *Xerus inauris*, live in separate male and female groups within the same area (Waterman, 1997)? Why do female dogfish, *Scyliorhinus canicula*, use different feeding and resting areas than males (Chapter 8)? Or why do humans prefer to socialize with same-sex peers (Chapter 12; Maccoby, 1998)? Some species show social segregation of the sexes: males and females are found in different groups outside the mating season, but use the same areas and habitat types (see Chapters 9 and 10). In other cases, males and females may use different habitats, either within the same or in different areas. This type of segregation is referred to as habitat segregation.

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Published by Cambridge University Press. © Cambridge University Press 2005.

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What causes segregation of the sexes, and what are its adaptive advantages? Sexual segregation has been an important research focus in ungulate ecology, but until recently only a few studies had been done on other vertebrate species. There may be more than one reason why the sexes segregate, and the factors responsible for segregation may vary within and across the different vertebrate taxa. It has been suggested that social segregation is caused by habitat segregation but this need not necessarily be so (see Chapters 2, 8, 10 and 11). Let us start by looking at what could cause habitat segregation and social segregation separately, and then we will discuss how they could affect or be independent of each other.

The causes of habitat segregation may vary. In some cases, for example, sex differences in body size may be responsible for habitat segregation. Dimorphism in body size could result in divergent nutritional and energetic requirements, reproductive strategies, activity budgets and social affinities (Main & Coblentz, 1990; Bon, 1991; Ruckstuhl & Neuhaus, 2002). Comparative analyses on ungulates confirm that size-monomorphic social species generally live in mixed-sex groups or pairs displaying similar social and habitat preferences and behaviours, while sexually dimorphic species segregate outside the breeding season (Myserud, 2000; Ruckstuhl & Neuhaus, 2002). Sexual dimorphism in body length or body size could also allow males and females to access different food items. Male giraffe, *Giraffa camelopardalis*, or elephants, *Loxodonta africana*, are able to feed higher up in the canopy than the smaller females (Ginnett & Demment, 1999; see also Chapter 2). Other examples including diving birds (i.e. some penguins, see Chapter 18), Antarctic fur seals, *Arctocephalus gazella* (Chapter 4), or larger whales (Chapter 16). Males in these species might be able to dive deeper and exploit other food sources than their smaller female counterparts, who are limited to foraging closer to the surface. In such cases sexual segregation in diet would not be adaptive, but a by-product of sexual differences in body size.

Body size dimorphism seems a likely candidate to explain sex differences in ecology. There are, however, notable exceptions, which include some species of bats (see Chapter 15), in which sexes segregate despite a lack of size dimorphism, chimpanzees, *Pan troglodytes* (Chapter 17), many social carnivores, and killer whales, *Orcinus orca* (Chapter 16), where size-dimorphic males and females are found in mixed-sex groups. Resource limitations (Oli, 1996), the distribution and receptivity of females (chimpanzees and whales), physiological limitations (bats),

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predator avoidance and other factors may well explain these departures from the rule.

What causes social segregation? Although habitat segregation will invariably lead to social segregation, social segregation can occur in the absence of habitat segregation (see Chapters 2, 10, 11). Differences in social affinity (Chapter 11), sexual avoidance (Geist & Bromley, 1978), sexual differences and asynchrony in activity budgets (Chapter 10) have all been suggested to lead to social segregation in the absence of habitat segregation. Ruckstuhl (1998) and Conradt (1998a) have independently suggested that sexual differences in activity budgets could lead to social segregation. If male and female activities differ considerably the cost of synchronizing activities could be too high, leading to the fission of mixed-sex into uni-sex groups. According to this hypothesis social segregation could even occur on different levels and lead to groups assorted by sex, age and reproductive status. Bon (1991), on the other hand, suggested that innate social preferences for the same sex lead to social segregation in adulthood. Geist and Bromley (1978) further suggested that male deer, for example, would segregate from females when they had antlers and only return into female groups once they had shed their antlers. They argued that males with antlers are conspicuous to predators, while males without antlers are using female mimicry to avoid predation. Lastly, males and females might avoid each other due to increased aggression in mixed-sex groups. Increased intra-sexual aggression was shown in the Roosevelt elk, *Cervus elaphus roosevelti*, where females were more aggressive towards each other in the presence than in the absence of males in their group (Weckerly *et al.*, 2001).

What then, if at all, is the relationship between social and habitat segregation? There are three equally likely scenarios one could propose. Firstly, habitat segregation leads to social segregation (Main *et al.*, 1996). Secondly, it is possible that habitat and social segregation are two independent phenomena (Conradt, 1999). Thirdly, social segregation leads to habitat segregation, as suggested in the model by Ruckstuhl and Kokko (2002). We will not investigate these different scenarios here, as they will be dealt with in more detail in Parts II to VI of the book.

The factors that cause or constrain sexual segregation appear to vary and are difficult to differentiate. Sexual segregation could be caused by a multitude of factors. Or is it not? Is there a single or a defined set of factors that could explain sexual segregation in all vertebrates? Although it may seem unlikely, there are at least some

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factors that can explain social and habitat segregation across taxa. These potential candidates are sexual differences in energy requirements and sensitivity to temperatures (Chapters 2, 3, 4, 15), sexual differences in reproductive strategies and predator vulnerability (Chapters 7, 8, 9, 13 and 18) and sexual differences in social affinities and activity budgets (Chapters 10 and 11), all of which are discussed in depth in this book.

What are the ecological consequences of sexual segregation? The study of sexual segregation has important implications for studies on population viability, gene flow, management of economically relevant species and the conservation of rare species (Clemmons & Buchholz, 1997; Komdeur & Deerenberg, 1997). The abundance and spatial distribution of food may affect the spacing or habitat use of males and females differently. Hence, the further male and female ranges are apart the less likely an encounter for breeding will occur. It is therefore conceivable that gene flow in small or reintroduced populations is limited if only subgroups of males and females of adjacent home ranges meet during breeding cycles (Komdeur & Deerenberg, 1997). While differences in body size may allow males and females to exploit resources differently (as mentioned earlier), this might also expose one sex to a higher predation risk than the other. Asian elephant bulls, *Elephas maximus*, for example, raid crops in India and are sometimes killed because of their transgressions, while females avoid human settlements (Sukumar & Gadgil, 1988). Female wandering albatross, *Diomedea exulans* (see Chapter 5), or females of some fish species (Wirtz & Morato, 2001) are at higher risk than males, because their foraging range overlaps with fishery activities, where they often get trapped and killed. Such cases of sex-biased mortality could lead to local extinctions of a species, particularly if female numbers are low or populations are small (see Chapters 5 or 18). It is therefore imperative to better understand the requirements of each sex of a species in order to protect the species effectively. Chapters 18 and 19 will focus on these conservation aspects. To summarize, it is possible that sexual segregation has many different ecological consequences that need to be taken into account by conservation groups and management, such as affecting sex specific carrying capacity, sex ratio in space and time, population distribution, variability in emigration and immigration and gene flow.

What does this book cover? This book reviews and discusses the different ecological factors affecting sexual segregation in fish (Chapters 7 and 8), reptiles (Chapter 13), birds (Chapters 5, 6 and 18), bats (Chapter 15), ungulates (Chapters 2, 3, 9, 10, 11 and 19), seals

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(Chapter 4), whales (Chapter 16), marsupials (Chapter 14), monkeys, apes (Chapter 17) and humans (Chapter 12), and discusses important conservation aspects. The book is divided into eight parts. Part I is meant as an introduction to the topic, while Part II deals with definitions and measures of segregation. Part III describes in detail sexual differences in foraging ecology, while Part IV describes cases where predator avoidance and reproductive strategies may cause ecological segregation. Part V discusses sex related activities and social preferences and how these could cause social segregation. Part VI gives an overview of sexual differences in ecology within different taxa of vertebrates, while Part VII deals with implications for conservation and management. Part VIII includes a short conclusion and directions for future research. With this book, we portray and discuss sexual segregation in its many different forms and possible causes. By doing so, we will not only clarify ideas and concepts, but also initiate and focus on promising future research on this topic.

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## Part II Concepts and methodology

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LARISSA CONRADT

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## Definitions, hypotheses, models and measures in the study of animal segregation

### OUTLINE

In this chapter, the term 'segregation' is clarified, the different types of segregation are defined, and the importance of using terms accurately and consistently is illustrated. The rationale of the key hypotheses relating to causes of different types of segregation is briefly explained and a measure of the degree of segregation (the 'segregation coefficient') is presented that is suitable (i) to test hypotheses relating to segregation; and (ii) to make comparisons between populations, species and types of segregation. The chapter concludes with a model to predict the degree of social segregation in a population and ends with three brief empirical examples.

### DEFINITIONS OF DIFFERENT TYPES OF SEGREGATION AND DISTINCTION BETWEEN THEM

In many group-living animals, individuals of different classes such as, for example, males and females, subadults and adults, or large and small individuals tend to form separate social groups (e.g. Croft *et al.*, 2003). This is termed 'social segregation' (Villaret & Bon, 1995, 1998; Bon & Campan, 1996). Further, classes of animals often differ in their habitat use, which is called 'habitat segregation', and/or they differ in their area use, which is termed 'spatial segregation' (e.g. Clutton-Brock *et al.*, 1982), whereby 'spatial segregation' should be treated as an auxiliary concept (see later). Additionally, the terms 'diet segregation' (the classes differ in diet choice) and 'temporal segregation'

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(the classes use the same area but at different times of the year) are used by many authors (e.g. see Chapter 14). In the past, many authors have failed to distinguish social segregation clearly from habitat segregation (see Main *et al.*, 1996). In particular, the wide and indiscriminate use of the unfortunate term ‘sexual segregation’ (referring to either social or habitat segregation between males and females) has significantly confounded theoretical arguments (Villaret & Bon, 1995; Bon & Campan, 1996; Conradt, 1997, 2000). The term ‘ecological segregation’ has also been used when referring to ‘habitat segregation’ (e.g. Bon & Campan, 1996). However, for reasons of consistent terminology (see Ruckstuhl & Neuhaus, 2000) the term should be avoided in future.

Habitat segregation describes differences between animal classes in their spatial distribution and, thus, in their use of the physical environment (e.g. Clutton-Brock *et al.*, 1982). Its calculation is based on the categorization of habitat types, whereby habitat categorization carries the danger of not being adequate from the point of view of the animals. Therefore, habitat segregation should be studied complementarily with spatial segregation (Conradt *et al.*, 2001), whereby spatial segregation is based on grid references (e.g. Clutton-Brock *et al.*, 1982). However, it has to be remembered that the concept of ‘spatial segregation’ is an auxiliary concept, since, lastly, social segregation leads also to small-scale spatial segregation.

Social segregation needs to be clearly distinguished from habitat segregation (Villaret & Bon, 1995; Conradt, 1998a) for the following reasons. Firstly, social segregation could occur independently of habitat segregation. For example, animals of different classes could use the same habitats but at different times, and, thus, be segregated socially, but not with respect to habitat use (Fig. 2.1(c); Conradt, 1999). Alternatively, animals of different classes could prefer different habitats, but when found within the same area they might randomly socialize with individuals of other sex or age classes (e.g. bats: Russo, 2002). They would then display habitat segregation but no social segregation beyond the social segregation caused as a by-product of habitat segregation (Fig. 2.1(b)). Secondly, social and habitat segregation are likely to have different causes and consequences (e.g. Ruckstuhl & Neuhaus, 2000). For example, social avoidance of aggressive, large individuals by small individuals might explain social segregation between size classes but not necessarily habitat segregation, since animals can often exploit the same habitat types at different times or in different areas (Fig. 2.1(c)). Differences in activity rhythms between animal classes might also explain social segregation (Conradt, 1998b; Ruckstuhl, 1998,

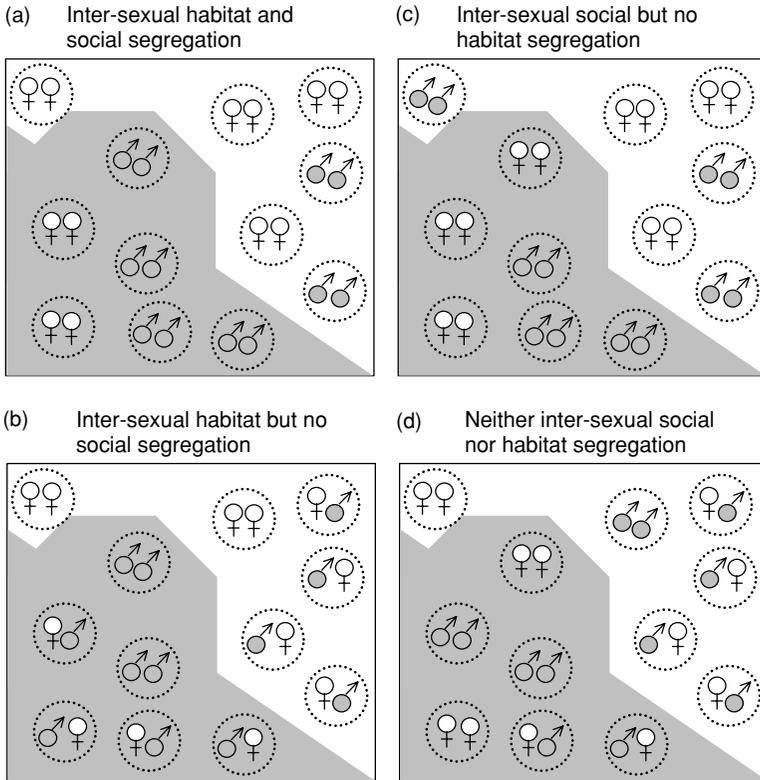


Figure 2.1 Relationships between social and habitat segregation. The diagrams depict the distribution of twelve social groups (circles) of two animals each between two habitats (grey and white). The degree of inter-sexual habitat segregation is the same in (a) and (b): females prefer the white and males the grey habitat (i.e. eight females and four males are in the white habitat and four females and eight males in the grey habitat). In (a) the sexes segregate into separate social groups *within* each habitat additionally to the segregation *between* habitats (all groups are uni-sex); while in (b) the sexes form groups at random *within* each habitat (two-thirds of groups are mixed-sex). In (c) and (d) the animals do not segregate between habitats (i.e. six males and six females in each habitat). However, in (c) the sexes segregate socially (all groups are uni-sex); while in (d) the sexes form groups at random within each habitat (half of the groups are mixed-sex).