Sexual segregation in ungulates: from individual mechanisms to collective patterns

Overview

Sexual segregation is an integral aspect of the socio-spatial organization of ungulate populations. Very often, the social, spatial and ecological components have been confounded (Bon, 1992) and we have argued that it is necessary to define and distinguish between each of them (Bon & Campan, 1996; see also Chapter 2 by Larissa Conradt). In the present chapter, we point out that sexual segregation is a complex phenomenon that can be produced by distinct mechanisms. One of the main issues is to know whether segregation by habitats necessarily derives from sexual difference in habitat choice, or can derive from alternative causes, i.e. spatial and social mechanisms (see also Chapter 2). Habitat segregation implies heterogeneous habitat (Miquelle et al., 1992), which we assume not to be obligatory for social and spatial segregation to occur. We distinguish hypothetical mechanisms relevant only in a heterogeneous environment from those relevant in both heterogeneous and homogeneous environments. We focus on behavioural mechanisms that may generate social and spatial segregation/aggregation, and the problem of the scale at which segregation may occur. Finally, we suggest that segregation cannot only be considered as a result of individuals behaving independently of each another, but also as a result of interactions between individuals on a larger (population) scale.

Habitat versus social segregation

Miquelle et al. (1992) noted that differences in habitat selection often lead to sexual segregation and resource partitioning between the sexes.
For many researchers, sexual segregation is the differential use of space by the sexes (Kie & Bowyer, 1999; Weckerly et al., 2001). This statement is motivated by the conviction that the sexes are segregated because of differences in habitat choice (see Habitat segregation, Chapter 2). However, social and habitat segregation are not necessarily linked: segregation can occur by using the same resources but at different times (Francisci et al., 1985; Jakimchuk et al., 1987) or by using different resources within the same areas (Staines et al., 1982; Bowyer, 1984) (see Chapter 2 and 3). In addition, it is difficult to decide whether segregation derives from habitat choices or is a consequence of differences in social or spatial behaviour in the wild (Shank, 1982; LaGory et al., 1991). The idea that sexual segregation is strictly determined by differences in habitat choice can be challenged by a point of semantic and by empirical evidence.

Understanding sexual segregation implies defining its meaning (Bon & Campan, 1996; Main et al., 1996). Segregation comes from the Latin segregare ‘separate from the flock, isolate, divide’ or the Greek σε ‘apart from’ and γρεξ ‘herd, flock’ which means separating, isolating an individual or a group from conspecifics (Chambers Encyclopedic English Dictionary, 1994; Grand Usuel Larousse, 1997). Thus, etymologically speaking, segregation refers to a socially motivated action, although this social component has been considered secondary by most authors. The phrase ‘males and females live apart’ can mean living in distinct groups, living in distinct areas, or living in distinct habitat types (Bon, 1998; Bon et al., 2001). While sexual segregation is most often considered as ecologically determined (Polis, 1984), we argue that it is relevant to recognize the social, spatial and habitat components/dimensions that sexual segregation may involve as well (Main & Coblentz, 1990; Bon, 1991; Weckerly, 1993; Miquelle et al., 1992; Bon & Campan, 1996; Conradt, 1999).

Sexual segregation is an outcome at a population level, resulting from several possible mechanisms (Fig. 11.1). It is therefore necessary to define the components of sexual segregation as objectively as possible, and without inferring from the supposed individual mechanisms (see Chapter 2). In this chapter we will mainly be concerned with social segregation and the mechanisms supposed to be involved in it.

We propose to define social segregation as the trend for individual animals to aggregate with animals or subjects belonging to the same social category, e.g. sex and age (Bon & Campan, 1996; see also Conradt, 1998b). Before developing hypotheses involving mechanisms that may generate social and spatial segregation, we state some basic conditions to consider gregariousness.
Figure 11.1 Theoretical population of dimorphic and social ungulates in which sexual segregation involves high levels of habitat, spatial and social segregation. (1) Habitat segregation: habitat A is only used by males, while habitat B is only used by females. (2) Spatial segregation: the females are located near the centre and the males at the periphery of the area occupied by the whole population; furthermore, habitat C is used by females or males according to the location of the corresponding patches. (3) Social segregation: single-sex groups are more frequent than expected by chance and this remains true within a portion of space supporting a single habitat and used by both sexes (habitat D patch).

It is important to recognize that animals could aggregate simply as a result of individuals of solitary species being attracted by the same environmental stimulus (feeding patches, refuge or migration corridors, for instance) without any social attraction. However, when the attractive environmental stimulus disappears, the groups will dissolve. Accordingly, all hypotheses discussed in this chapter implicitly assume that the species concerned are social, i.e. individual animals aggregate in more or less stable groups.

Some assumptions must be met for animals to aggregate in groups (see also Krause & Ruxton, 2002). Aggregation occurs by interattraction between mobile individuals, via visual contact for most of the wild ungulate species (see Gerard et al., 2002), even though olfactory or auditory stimuli may also be involved (Barrette, 1991). In addition, interactions between individuals are necessary to keep group cohesiveness, which implies co-ordinated activities and thus allelo-mimetism (Deneubourg & Goss, 1989). See Box 11.1.

Animals are classically considered to associate at random (Grubb & Jewell, 1966; Geist, 1971; Langman, 1977; Hillman, 1987; Hinch et al., 1990), with grouping depending on food distribution (Lott & Minta, 1983; Lawrence, 1990). However, ecological factors alone cannot account for phenotype assortment according to body size, sex, age or social status (Estes, 1991b; Bon et al., 1993; Villaret & Bon, 1995, 1998; Cransac et al., 1998). Social segregation between sexes is a particular case of social aggregation, as two categories of individuals are found together less often than expected if they were associated at random (Conradt, 1998b). Concerning the mechanism involved, this means that the sexes
Box 11.1 Social mechanisms conditioning group formation and cohesiveness

Social mechanisms conditioning group formations

- No discrimination between individuals
- Discrimination-based fusion (involving attraction/repulsion) depending on:
  - assortive phenotype (sex, age, size) based on activity compatibility (movement, activity budget)
  - social compatibility based on previous encounters

Social mechanisms conditioning group cohesiveness

- Allelo-mimetism
- Symmetrical interactions
- Long-lasting or frequent interactions
- Synchrony in activity budgets
- Co-ordination in movement
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(social classes) can differ in the degree of social attraction to the opposite sex, move at a velocity or/and have activity rhythms that impair association for long periods of time (see also Chapter 10). Social attraction can rely on the activity of animals but also on the capacity to discriminate the sex or age of conspecifics. Experiments have revealed that domestic ungulates were capable of social discrimination between juveniles and adults (Kendrick et al., 1995; Porter et al., 2001). The sexes can be segregated on a large scale, involving high degrees of spatial segregation, or on a small scale. On a small scale, subgroups can be detected within larger groups as occurs between juveniles within female groups (Richard & Pépin, 1990; Gerard et al., 1995). In children, girls and boys may be socially segregated at a smaller scale by being closer to their own gender than expected by chance in a school playground (see Pellegrini et al., 2003; Chapter 12). The local interactions between neighbours generating this small-scale segregation include attraction and repulsion as well as mutual adjustment of activities. Furthermore, the sorting process may be facilitated by simple physical constraints such as crowding of one sex that reduces available space for the other sex. These rules can lead to group splitting and so the promotion of social segregation at a larger scale (see Deneubourg et al., 1991 for an explanation in social insects).

In the following sections, we present some habitat-related mechanisms leading to sexual segregation in heterogeneous environments. We then forward arguments that illustrate the importance of non-ecological mechanisms leading to social and/or spatial segregation at large and small scales in both heterogeneous and homogeneous environment. Lastly, we suggest that unexplored processes such as ‘social amplification’ can produce higher level of habitat or spatial segregation that cannot be obtained if individuals behaved independently of one another.

Habitat choice, parental behaviour, social disturbances and predation risks

In ungulates, males are not implicated in raising young. The reproductive strategy or predation risk hypothesis states that sexual segregation is the consequence of sexual difference in reproductive investment (Chapters 3 and 9). Females’ use of safe habitat is considered as an adaptation to reduce the risk of predation on offspring and as a way to improve females’ reproductive success. However, only a few authors have considered the mechanisms promoting changes of female
behaviour around parturition. The following examples will illustrate the proximate explanation of social and habitat segregation.

In mountain ungulates, females restrict themselves to steep slopes just before parturition, meanwhile non-parturient females and males use better feeding habitats (Shank, 1982; Bergerud et al., 1984). Spatial segregation is less marked when involving females without offspring in mountain and non-mountain areas (Festa-Bianchet, 1988; Miquelle et al., 1992; Bon et al., 1995; Ginnett & Demment, 1999). But the choice of habitat type depends on the local context, including prey and predation types (Ruckstuhl & Neuhaus, 2002). For instance, females with calves in Masai giraffes, *Giraffa camelopardalis tippelskirchi*, and kudu, *Tragelaphus strepsiceros*, avoid woodland habitats and use open habitats probably because higher visibility provides better risk detection (Du Toit, 1995; Ginnett & Demment, 1999). The choice of secure areas around parturition suggests that females are more sensitive to disturbance and predation risks at this period (Frid, 1999; Weckerly et al., 2001). In areas where large predators are scarce or absent, sexual segregation in habitat use vanishes (du Toit, 1995). Berger et al. (2001) showed that naïve female moose, *Alces alces*, experiencing predation on their calves were able very quickly to exhibit anti-predator behaviour. Kohlmann et al. (1996) reported that female Nubian ibex, *Capra ibex nubiana*, with young kids temporarily confined in a predator safe canyon, differ in habitat use from females followed by kids. The former move farther from escape terrain, use better feeding habitat and spent more time feeding than the latter.

However, there is also a much more proximal explanation why females search out particular areas. Increased habitat and spatial segregation is also the consequence of marked modification of parturient females’ social behaviour (Poindron et al., 1988). A few days before parturition or when followed by neonates, females become asocial (Alexander et al., 1979; du Toit, 1995) and aggressive (Gosling, 1969; Cederlund, 1987; Estep et al., 1993) in several ungulate species. By withdrawing from groups, female taruca, *Hippocamelus antisensis*, near parturition segregated by habitat from male and mixed-sex groups commonly found year round (Merkt in Frid, 1999). Miquelle et al. (1992) reported that female moose with offspring seemed to avoid areas already used by other moose. Cliffs and forested areas provide physical obstacles disrupting visual contact and so can be chosen by parturient females as they allow seclusion from conspecifics of both sexes (Cransac et al., 1998) and animals of other species, including men and predators. Seclusion would facilitate the mother-young bonding (Poindron et al., 1988) and
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allow avoiding social perturbations or the possibility of adoption by other parturient females (Arnold et al., 1975). In addition, other physiographic characteristics can be key factors involved in the selection of areas to give birth (see Bon et al., 1995).

Social and habitat segregation is supposed to be determined by gestation and the presence of young. Thus, segregation might peak during the birth season. Behavioural changes around parturition, associability and aggressiveness, are not caused by habitat heterogeneity, although females can use it at that period to satisfy isolation, as discussed earlier. Thus, we can expect social and spatial segregation between parturient, lactating and non-lactating females or males in homogeneous environments. Because the maternal behaviour is hormonally induced, social and habitat segregation should vanish with the end of maternal care and the physiological weaning. If it persists outside the period of maternal care, it is necessary to consider other mechanisms than those invoked by the predation risks hypothesis. It remains also to be explained what causes females to venture farther from safe areas when offspring become older (Bergerud et al., 1984; Bon et al., 1995).

**IS HABITAT SEGREGATION EQUAL TO SEXUAL DIFFERENCES IN HABITAT CHOICE?**

Up to now, with a few exceptions, sexual segregation was mostly attributed to different habitat selection by the two sexes (see Bon & Campan, 1996). However, is habitat segregation necessarily caused by different habitat choices between the sexes? Some authors argued that habitat segregation might result from other mechanisms, such as, for example, social mechanisms (Shank, 1982; LaGory et al., 1991; Bon, 1991).

Social mechanisms involved in segregation

**Social segregation versus habitat segregation**

Conradt (1998b, Chapter 2) proposed an index that allows measuring and comparing the degree of social, spatial and habitat segregation between the sexes. Social segregation here refers to the presence of males and females in single-sex groups, while spatial segregation refers to the use of exclusive quadrates by one sex. Using long-term studies on red deer, *Cervus elaphus*, and Soay sheep, *Ovis aries*, Conradt (1999) showed that the degree of social and spatial segregation was always higher than
habitat segregation. This allowed the author to conclude that at least one part of social segregation cannot result from habitat segregation, and that each component was probably the result of different causes (Bon & Campan, 1996). Social segregation seems to be a rule in social dimorphic ungulates, and independent of the size of populations (Bon et al., 2001), density of males or females (Conradt et al., 1999b) and spatial segregation (Kie & Bowyer, 1999).

After a control of predators in an enclosed population of white-tailed deer, *Odocoileus virginianus*, Kie and Bowyer (1999) reported that spatial segregation decreased at high density of deer, whereas the level of social segregation was unchanged. As a consequence of higher spatial overlap between the sexes, dietary differences were lower than at moderate density and diet impoverished more in females than males. This is inconsistent with a prediction of the scramble competition hypothesis (see Chapter 2) that females actively or passively exclude adult males from preferred areas (Bleich et al., 1997; Romeo et al., 1997). In their study, Kie and Bowyer (1999) also rejected the social factors hypothesis, namely, that social segregation was driven from males avoiding costly social interactions linked to female proximity in mixed-sex groups. This hypothesis has been criticized because sexual interactions are dependent on sexual hormones that are produced seasonally, and so it is unlikely to apply outside the mating period (Main et al., 1996). However, this does not exclude the relevance of other social mechanisms.

Social segregation based on age or social status

More rarely considered, age is a factor that is implied in the degree of sexual segregation (Bon et al., 1993; Bon & Campan, 1996). Yearling males are most often observed in female groups while the oldest ones are rarely associated with females outside the rut (Nievergelt, 1967; Geist, 1971; Bon & Campan, 1989; Festa-Bianchet, 1991; Miquelle et al., 1992; Ruckstuhl, 1998; Ruckstuhl & Festa-Bianchet, 2001). Bon et al. (2001) found a gradient of social segregation linked to male age in Alpine ibex, *Capra ibex*, even when spatial segregation was low in winter, rendering ecological mechanisms a very unlikely cause of social segregation. Age difference was also found to be an important factor of social and spatial segregation among males splitting up into groups of similar-aged individuals (Bon et al., 1993; Villaret & Bon, 1995, 1998).

Social segregation within the sexes is not only observed as a function of age, but may also be dependent on events occurring early in
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ontogeny. Jewell (1986) reported that castrated Soay sheep males not only formed groups of their own but also used distinct home ranges. They socially and spatially segregated from entire males and females (see also Ruckstuhl et al., submitted). It is likely that the lack of male hormones that is implicated in the male-like behaviour influenced the nature of interactions and levels of behaviour of early castrated males. As a consequence, these males set up a social network among themselves, which made them socially segregated from non-castrated males and females.

The assumption that aggregation is based on a general interattraction between conspecifics must be modulated because the force of attraction may vary during ontogeny. When ageing, individuals seem to be less sociable in some populations of European mouflons (Ovis aries), bighorn sheep, chamois (Rupicapra rupicapra) and isard (R. pyrenaica) (Pfeffer, 1967; Geist, 1971; Shank, 1985; Richard-Hansen, 1992; Hass & Jenni, 1993). According to Shank (1985: 122), social and spatial segregation of old male chamois is a trade-off between dependence on feeding resources and a ‘need for solitude’, reflecting social intolerance. However, old animals might more often be alone because they are less sociable or because they lack similar-aged peers (Villaret & Bon, 1998). When available, old non-reproductive buffaloes were reported to group together, apart from younger males (Sinclair, 1977). Population density and hence the probability of meeting conspecifics is also a factor contributing to the chance of both sexes to be found alone (Fig. 11.2; see also Gerard & Loisel, 1995 and Gerard et al., 2002 for a discussion on mechanisms underlying aggregation).

**BEHAVIOURAL MECHANISMS INDEPENDENT OF HABITAT HETEROGENEITY**

Recently, new hypotheses were proposed, suggesting that sexual segregation may be explained by different mechanisms, including movement or spatial behaviour, activity budgets, and social behaviour (Bon & Campan, 1996; Conradt, 1998b; Ruckstuhl, 1998; Bon et al., 2001). These hypotheses differ notably from previous ones in the sense that they do not depend upon habitat heterogeneity, and that they propose mechanisms that can produce social and eventually spatial segregation in heterogeneous but also in homogeneous environment. If social segregation is observed in controlled and homogeneous habitats, observers have either not detected an ecological heterogeneity that animals do detect, or non-ecological mechanisms are at work.
From individual mechanisms to collective patterns

Figure 11.2 Proportion of observations corresponding to alone individuals during census of groups in two populations of Alpine ibex, Bargy and Sous-Dine, according to the sex and male age. Bargy population contained c. 120 adults while Sous-Dine population only 27 adults. Data from the mating and the birth periods were omitted because males are often alone during the rut and females less social at parturition. Males were found more often alone when getting older in both populations. Note, however, that the probability of being found alone in both sexes is higher in the smaller than the larger population. Numbers in brackets correspond to the total number of observations of groups (lone individuals included).

The activity budget hypothesis

Recently, it has been proposed that sexual dimorphism in body size could lead to sexual differences in activity budgets in ungulates (Conradt, 1998a; Ruckstuhl, 1998; Chapters 2 and 10). One basic prediction of the activity budget hypothesis is that, because of their smaller size, higher energy requirements and lower efficiency in processing forage, females would spend more time feeding than males (Ruckstuhl, 1998; Ruckstuhl & Neuhaus, 2000; see also Ruckstuhl & Neuhaus Chapter 10). The resulting asynchrony in activity is considered a major constraint for mixed-sex groups to be maintained, resulting in social segregation.

The activity budget hypothesis predicts segregation without implying differences in forage selection. It is theoretically possible to find social segregation without habitat/spatial segregation: both sexes can form separate groups, use overlapping ranges in which they can exploit the same habitat patches at different times (Francisci et al., 1985) or at the same time without mixing. The activity budget hypothesis
assumes that to stay together, the individuals belonging to the same
groups must share similar activity rhythms allowing activity synchrony.
Allelo-mimetism is implicit to activity synchrony, i.e. when individuals
in a group exhibit patterns of individual activity that would not occur
if individuals were independent (Deneubourg & Goss, 1989). The hypo-
thetical possibilities of animals meeting and having similar activity
rhythms are illustrated in Fig. 11.3(a) and (b). Consider a population
of individuals with two states, active and inactive, and independent
from each other in their activity. A stable group will depend upon
the probability of two individuals to be synchronized in order to stay
together. If the activity budgets differ too much between both ani-
imals (as suggested to occur between females and males in dimorphic
species), the probability of staying for a time longer than a bout of
activity or inactivity is unlikely (Fig. 11.3(a)). If two animals having
the same activity rhythm meet, the probability of associating for a last-
ing period will depend on both individuals being in the same phase
(Fig. 11.3(b)). This probability would be higher for same-sex than for
opposite-sex animals. However, synchrony in activity between the sexes
is possible if males and females do not vary too much in activity bud-
gets, and if at least one sex adjusts its activity rhythm to that of the
other sex. Although we do not know how overall activity synchrony
in a group is achieved, it can be assumed that having the same activ-
ity as surrounding animals can result in a high degree of overall syn-
chrony. It is not necessary for individuals to adjust their behaviour
to the entire group. In most ungulate species, groups are unstable
in size and composition (Marchal et al., 1998). However, data obtained
from wild populations indicate that activity synchrony in single-sex
groups is higher than expected by chance (Côté et al., 1997; Ruckstuhl,
1999). This suggests that animals belonging to groups of the same sex
are either synchronized by the same external releaser or possess the
same internal clock. It is more parsimonious thinking that individu-
als with activity budgets not too different can tune their activity to
each other through interactions (Fig. 11.3(c)), such as allelo-mimetism
allowing to be in phase. Ramírez Ávila et al. (2003) have shown that
interactions between oscillators that differ in their intrinsic period
enable individuals to adopt the same period. This individual ability
could lead to clustering of individuals having similar activity periods,
and social segregation between individuals having dissimilar periods.
Note that the possibility for individuals to aggregate based on simi-
lar activity period and interaction does not mean that all groups are
synchronized.
(a) Individual animals with different rhythms

(b) Individuals with the same but unsynchronized rhythm

(c) Individuals with similar rhythm, and which can synchronize activity to each other through interaction

Figure 11.3 Hypothetical cases of meeting between two individuals and possibility of activity synchrony: (a) both individuals exhibit distinct or (b) similar activity rhythms without possibility of synchronization and (c) both individuals can synchronize their activity.
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Dispersal behaviour

The impact of sexual differences in dispersal behaviour on social and spatial segregation has rarely been examined (Bon & Campan, 1996). In dimorphic ungulate species, as in many mammals, juvenile females usually settle in or near their maternal or natal range while males often disperse from their natal group or area (cervids: Clutton-Brock et al., 1982; Bunnell & Harestad, 1983; Nelson & Mech, 1984; Cederlund et al., 1987; Cederlund & Sand, 1992; Höizenbein & Marchinton, 1992; wild sheep: Festa-Bianchet, 1986; Dubois et al., 1994). Based upon long-term radio-tracking of mouflons, Dubois et al. (1993) found two categories of two- to three-year-old males regarding their dispersion outside their rut. Some males still used their natal range, while most of them gradually dispersed until using non-maternal and stable ranges. Even when males and females spatially overlapped, they were still socially segregated (Dubois et al., 1993). The difference in spatial dispersion between males and females often results in males using a higher diversity of habitats (Ordway & Krausman, 1986; Villaret et al., 1997).

Motion behaviour

Dimorphism in body size can also be at the origin of other differences in behaviour, such as motion. Larger or powerful individuals probably walk or move more rapidly than smaller individuals, or travel a larger distance per unit time. If so, group splitting and spatial segregation, or structuring at a small scale, can arise even if the individuals in the population, whatever their size, do not differ in their habitat choices (Gueron et al., 1996; Couzin & Krause, 2003). Ruckstuhl (1998) found that bighorn ewes and rams had the same step rate per unit time, but ewes dedicated more time to walking, had longer walking bouts and travelled larger distances than rams. Miquelle et al. (1992) also reported that in moose females and subadult males moved more during the feeding periods than large males. On the other hand, Michelena et al. (2004) have shown experimentally that merino rams, when placed within the same pastures were walking twice as rapidly than ewes within the same pastures. However, no social segregation at a large scale was found since both sexes were together in a single group for several weeks. During the eight-week experiment, males were more often found in the front of the group than females. Same-sex pairs of nearest neighbours were significantly more frequent than mixed-sex ones, which might result from higher step rates in males than in females. However, when sheep
of both sexes were distributed at random within the group, pairs of nearest neighbours of same sex still outnumbered opposite-sex pairs. These results suggest a high level of inter-sex attraction, explaining the lack of social segregation at a large scale, compensating for the difference in activity budget and moving velocity between the sexes, and higher intra-sex than inter-sex affinity accounting for the social segregation at a small scale.

The social affinity hypothesis

Mechanisms proposed to explain social segregation in children, and data collected on behavioural development and social interactions in other mammal species inspired the social affinity hypothesis (Bon & Campan, 1996; Bon et al., 2001). Jacklin and Maccoby (1978) suggested that the differences in the level of activity (Eaton & Enns, 1986) and in how both sexes get socially involved could lead to problems of social matching between girls and boys (see Pellegrini & Long, 2003 for a recent discussion). They proposed the notion of behavioural incompatibility that Legault and Strayer (1991) extended by defining it as ‘a set of differences in the overall composition of behavioural repertoire’ to account for social segregation between the sexes in children. Bon and Campan (1996) argued that sexual differences in behaviour and social motivation lead to behavioural and social incompatibility, and thus social segregation between different sex-age classes in social ungulates. Behavioural compatibility would be necessary for social cohesion to occur.

In mammals, sexual differences are found in levels of motor activity (Holekamp & Sherman, 1989) and type of behaviour (Cheney, 1978; Sachs & Harris, 1978; Moore, 1985; Meaney, 1988) from an early stage of life. In dimorphic ungulates, social behaviour and morphology mature more gradually in males than in females, long after reaching sexual maturity (Geist, 1968, 1971; Grubb, 1974; Jarman, 1983; Rothstein & Griswold, 1991; Shackleton, 1991). Juvenile males are more often engaged in rough-and-tumble or pseudo-sexual plays, while females are more often engaged in locomotor play and also spend more time in feeding activities than males (Bon & Campan, 1996). The difference between the sexes in the amount of interactions still persists into adulthood (Le Pendu et al., 2000). Owing to the differences of social motivation, behavioural style and morphology, females could avoid or be indifferent to male social interactions. Although mixed-sex groups of mouflons were infrequent, Le Pendu et al. (2000) found a high rate
of inter-sex interactions, initiated by males over two years old when males and females co-occurred at attractive feeding sites. Males interact much more frequently than females in sheep, even when the latter are involved in the interactions (Michelena et al., 2004). Several authors have argued that females avoid interacting with dominant males (see Bon & Campan, 1996). Weckerly et al. (2001) found that Roosevelt elk (Cervus elaphus roosevelti) females displayed slightly higher aggression rates in mixed-sex groups when males were more prevalent, possibly as a consequence of females approaching one another when avoiding males. Female and mixed-sex groups also walked away when approached by male groups exceeding six individuals. Because females avoided only large male groups, Weckerly et al. (2001) concluded that this social mechanism is unlikely to account for high degrees of social segregation.

From a physiological point of view, behavioural dimorphism in social behaviour and dispersal between the sexes is induced by perinatal androgens (Hinde, 1974; Goldfoot et al., 1984; Moore, 1985; Meaney et al., 1985; Holekamp & Sherman, 1989). For example, Jewell (1986, 1997) showed how castrated Soay lambs formed self-contained groups, avoided interacting with other sheep and used ranges distinct from ewes and rams as adults (see also Clutton-Brock et al., 1982). These results indicate how physiological mechanisms and the type of behavioural style can affect social and spatial segregation. The social affinity hypothesis thus predicts that grouping will probably occur between animals of the same sex and age (Bon et al., 2001). Yet, even if groups persist when individuals share the same motivation to associate, they may contain individuals with very dissimilar behaviour such as females and offspring. This is made possible because of the shared motivation to stay together and because individuals can carry out their maintenance activities within such groups.

**SYNERGY BETWEEN DIFFERENT MECHANISMS**

All populations occurring in the wild face a certain degree of heterogeneity in their habitat. How an individual animal chooses its home range will depend on some basic or vital requirements, but also on phenotypic constraints or cognitive abilities.

Habitat segregation is most often considered as the result of an active choice or compromising between conflicting factors. However, it is worth noting that an experimental design is necessary to ascertain
that females and males differ in habitat choice. For instance, Morton (1990) demonstrated experimentally that habitat segregation observed in the hooded warbler (*Wilsonia citrina*) was founded on sexually distinct preferences of physical characteristics of habitat. However, Desrochers (1989) showed that male and female black-capped chickadees were segregated by habitat because males excluded females from preferred microhabitats. Such demonstrations remain scarce for ungulates. Pérez-Barbería and Gordon (1999) carried out an experiment with Soay sheep and showed that both sexes preferred high quality to low quality grazing patches. However, contrary to the predictions of the forage selection hypothesis, females spent more time foraging on the low quality swards than males.

The activity budget and the social affinity hypotheses do not exclude the contribution of mechanisms linked to reproduction or ecological factors to sexual segregation, but they state that differences in behaviour and social motivation are basic mechanisms of social segregation. Food quality and distribution, predation risks (Jarman, 1974) but also population density and habitat openness are causal factors of animal grouping (Barrette, 1991; Gerard et al., 1995, 2002). In the wild, it is difficult to set apart the impact of ecological factors from that of social factors and we argue that sexual segregation probably involves several mechanisms. The question of synergy or antagonism between different mechanisms, in particular social and ecological ones, is poorly documented (Bon & Campan, 1996). To illustrate the importance of this topic, we present a model where slight differences in habitat use between the sexes can be amplified by social attraction (see Appendix 11.1 for details of the model).

Finally, we would like to point out that experimental studies are needed to test non-ecological mechanisms in controlled habitat, with the underlying idea that a better knowledge of behavioural/cognitive mechanisms and interactions between individuals will provide new insight into aggregation and segregation dynamics. We also recommend considering the quantitative aspect and interplay of mechanisms, and the dynamics of social and spatial structures that are difficult to tackle if one only considers the individual’s perspective.

**APPENDIX 11.1**

Let us consider a population of solitary animals (there are no interactions between individuals whatever their sex), composed of two
Table 11.1 Probability of individual males or females moving between habitats A and B, depending on whether they are solitary or social.

<table>
<thead>
<tr>
<th></th>
<th>Solitary</th>
<th></th>
<th>Social</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Probability of moving from A to B</td>
<td>Probability of moving from B to A</td>
<td>Probability of moving from A to B</td>
</tr>
<tr>
<td>Males</td>
<td>$\alpha_M$</td>
<td>$\beta_M$</td>
<td>$\alpha_M/(1 + M_A)^*$</td>
</tr>
<tr>
<td>Females</td>
<td>$\alpha_F$</td>
<td>$\beta_F$</td>
<td>$\alpha_F/(1 + F_A)^*$</td>
</tr>
</tbody>
</table>

* $M_A$ and $M_B$ ($F_A$ and $F_B$) are respectively the total numbers of males (females) in habitats A and B. $M = M_A + M_B$ and $F = F_A + F_B$ are the total subpopulations of males and females.

At each timestep, any female on habitat A or B has the probabilities $\alpha_f$ and $\beta_f$ to move from A to B and from B to A, depending on the characteristics of habitats A and B (Table 11.1). Accordingly, the number of females moving from A to B is $\alpha_f F_A$ and from B to A is $\beta_f F_B$. At the equilibrium, the number of individual females moving from A to B equals that moving from B to A. This can be written:

$$\alpha_f F_A = \beta_f F_B \quad \text{or} \quad \alpha_f F_A = \beta_f (F - F_A)$$

It is then easy to find that:

$$F_A = \frac{\beta_f F}{(\alpha_f + \beta_f)}$$

If $f_A$ is the proportion of females in A ($F_A/F$) and $f_B$ their proportion in B ($F_B/F$) and we define $r_f = \alpha_f/\beta_f$, then:

$$f_A = \frac{1}{(r_f + 1)} \quad \text{and} \quad f_B = 1 - f_A$$

Similarly the fraction of males in habitat A is:

$$m_A = \frac{1}{(r_M + 1)} \quad \text{and} \quad m_B = 1 - m_A$$
Figure 11.4  Theoretical fractions of animals in two distinct habitats, A (circles) and B (squares) as a function of population size $F$. White symbols correspond to solitary individuals, and black symbols to social individuals. For example, if solitary females have a small individual preference for habitat A, the proportion of females $f_A$ in habitat A will remain to 0.54 and in habitat B $f_B$ to 0.46. If males’ preference for habitat B equals females’ preference for habitat A, then the proportion of males will be such that $m_B = f_A$ and $m_A = f_B$. In the case of social species, with the same individual preference for habitat A than solitary animals, the proportion of females (males) will however increase with the female (male) population size. This figure shows how social interaction may amplify the initial individual habitat choice and, in the case of different individual habitat choice between the sexes, how the degree of habitat segregation increases with the population size of females and males.

Whatever the size of the female subpopulation, the proportion of females in habitats A and B at the equilibrium will depend on the relative preference of females for habitats A ($\alpha_A$) and B ($\beta_A$) and so on the value taken by $r_F$. If there is no preference for any habitat in both sexes, then $r_F = r_M = 1$, and there are proportionately as many females and males in both habitats ($f_A = f_B = 0.5$ and $m_A = m_B = 0.5$) leading to a lack of habitat segregation between the sexes. If females prefer the habitat A and males prefer the habitat B, then $\alpha_F < \beta_F$, $\alpha_M > \beta_M$, $f_A > m_A$ and $f_B < m_B$. For example, consider the initial population is composed of individual females with a ratio $r_F = 0.86$, leading to a slight preference for A, then $f_A = 0.54$ and $f_B = 0.46$ (Fig. 11.4). The greater the difference between the ratio $r_F$ and $r_M$, the greater will be the habitat segregation between the sexes.
Social individuals

Let us consider now the case of a social species composed of subpopulations of females and males of size $F$ and $M$ with an intra-sex attraction and no inter-sex attraction or repulsion. The probability of individual animals moving from habitat A to B (B to A) is the same as earlier but, in this case, as the number of same-sex individuals in the same habitat increases (e.g. A), the probability of leaving this habitat decreases for any individual (see Table 11.1; $n = 1$) as:

$$\frac{\alpha_F}{(1 + F_A)} \quad \text{and} \quad \frac{\beta_F}{(1 + F_B)}$$

The proportions of females in habitats A and B are also independent of what occurs for males, if there are no limits in space available (no indirect competition).

At the equilibrium, the number of individual females $f_A$ moving from A to B equals the number $f_B$ moving from B to A, so that:

$$\frac{\alpha_F F_A}{(1 + F_A)} = \frac{\beta_F F_B}{(1 + F_B)}$$

or:

$$\alpha_F F_A (1 + F_B) = \beta_F F_B (1 + F_A)$$

$$\alpha_F F_A - \beta_F F_B + F_A F_B (\alpha_F - \beta_F) = 0$$

As $F_B = F - F_A$, we obtain:

$$\alpha_F F_A - \beta_F (F - F_A) + F_A (F - F_A) (\alpha_F - \beta_F) = 0$$

$$(\alpha_F - \beta_F) F_A^2 - (\alpha_F + \beta_F + F (\alpha_F - \beta_F)) F_A + \beta_F F = 0$$

Dividing by $F^2$, we obtain:

$$((\alpha_F - \beta_F) f_A^2 - (\alpha_F + \beta_F + (\alpha_F - \beta_F)) f_A + \beta_F) = 0$$

If $\alpha_F = \beta_F$, or $r_f = 1$ then $f_A = f_B = 0.5$ whatever the total population $F$. If $\alpha_F < \beta_F$ or $r_f < 1$:

$$f_A = 0.5(D + \sqrt{D^2 - 4E}) \quad \text{and} \quad f_B = 1 - f_A$$

and if $\alpha_F > \beta_F$ or $r_f > 1$:

$$f_A = 0.5(D - \sqrt{D^2 - 4E}) \quad \text{and} \quad f_B = 1 - f_A$$

with:

$$D = 1 + \frac{r_f + 1}{(r_f - 1)F} \quad E = \frac{1}{(r_f - 1)F}$$
Taking into account the intra-sex attraction and \( r_F \neq 1 \), the proportion of females \( f_A \) and \( f_B \) will evolve as a function of the total subpopulation \( F \). For instance, if we set \( r_F = 0.86 \) (as in the case of solitary animals), that is to say a small preference of females for habitat A, we can see that \( f_A > 0.54 \) and grows with \( F \) (Fig. 11.4), which can be assimilated as an effect of amplification. For large value of \( F \), all the females will be in habitat A (\( f_A \approx 1 \)) and environment B is neglected. In contrast, if \( r_F > 1 \), we will observe an amplification of the preference for the environment B.

If the males have the same preference for habitats A and B, and the same degree of attraction among each other as females, the habitat segregation is nil. Besides, if males have a small and steady individual preference for habitat B (\( \beta_M = \alpha_I \)), then the proportion of males in habitat B increases with the number of males found in this habitat and the degree of habitat segregation between the sexes will increase with the increasing size of female and male subpopulations respectively in habitats A and B. The curves of \( f_A \) and \( f_B \) are symmetrical if \( F = M \). This model shows how habitat segregation may be amplified by social interactions and the population size of females and males, despite no modification of individual habitat choice (\( r_F \) and \( r_M \) constant).

It is also possible to show that the disequilibrium of proportions of females in habitats A and B can be theoretically obtained without initial differences of habitat preference, i.e when \( r_F = 1 \). This may occur if the probability for individual animals to move from A to B (B to A) are very sensitive to the number of individuals in the habitat A (B) and for example decreases with the square of the population (see Table 11.1, \( n = 2 \)):

\[
\frac{\alpha_F}{1 + F_A^2} \quad \text{and} \quad \frac{\beta_F}{1 + F_B^2}
\]

In this case, most of the individuals are in habitat A (\( f_A \approx 1, f_B \approx 0 \)) or in environment B (\( f_A \approx 0, f_B \approx 1 \)). The selection of the habitat A or B is a random process and each environment has an equal probability to be selected.