Multiple causes of sexual segregation in European red deer: enlightenments from varying breeding phenology at high and low latitude

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Sexual segregation outside the mating season occurs in most species of sexually dimorphic ungulates and has been extensively described in the literature, but the mechanisms causing segregation are still debated. The detailed pattern of sexual segregation throughout the year has rarely been presented for mammals, and no study, to our knowledge, has used latitudinal-related variation in breeding phenology to shed light on the underlying mechanisms. Recent methodological developments have made it possible to quantify separate components of segregation (social, habitat) and activity synchrony in animal groups, but these major improvements have so far been little used. We observed European red deer year round at two widely different latitudes (France and Norway) and tested three different mechanistic hypotheses of segregation related to: (i) predation risk; (ii) body-size-related forage selection; and (iii) activity budget. Habitat segregation peaked during calving in both populations and dropped rapidly after calving. Females with calves were more segregated from males than were females without calves, pointing to a key role of anti-predator behaviour even though large predators are absent in France and extremely rare in Norway. However, at both sites individuals also grouped with their own sex within habitat types (i.e. social segregation), and individuals in mixed-sex groups were less synchronized in activity type than individuals in either unisex male or unisex female groups, suggesting that differences in activity budgets are involved. Social segregation peaked during calving and was lowest during the rut (indicating aggregation) in both populations; these activities occurred one month later in the Northern populations, corresponding well with known differences in breeding phenology. We conclude that latitude-dependent breeding phenology shapes the seasonal pattern of sexual segregation and that sexual segregation in ungulates has multiple causes.

Keywords: social and habitat segregation; predation risk; activity pattern; habitat shelter; *Cervus elaphus*; biogeographical gradient

1. INTRODUCTION

Sexual segregation is common in large herbivorous mammals outside the rutting season (Miquelle *et al.* 1992; Main *et al.* 1996; Bleich *et al.* 1997; Bowyer *et al.* 2002; Ruckstuhl & Neuhaus 2002), especially in temperate regions and when the sexes are dimorphic in size (Mysterud 2000; Ruckstuhl & Neuhaus 2002). However, the causes of sexual segregation are among the most controversial topics in the foraging literature, partly because a formal and consensual definition is lacking, and partly because reported results are highly dependent on the considered methodology and spatio-temporal scale (Bowyer *et al.* 1996; Main *et al.* 1996; Conradt 1998*b*). Sexual segregation can be split into social segregation (sexes live in different social groups) and habitat segregation (different use of habitats) (Bon & Campan 1996; Main *et al.* 1996).

In an attempt at unification, Conradt (1998*b*) proposed a formal and objective definition of sexual segregation by defining segregation as the departure from random association and by allowing the quantification of the social and habitat components of sexual segregation.

Three hypotheses of sexual segregation are generally recognized as the most likely (Main *et al.* 1996; Ruckstuhl & Neuhaus 2002). First, the 'predation-risk hypothesis' (Main *et al.* 1996; Ruckstuhl & Neuhaus 2002) states that anti-predator behaviour shapes sexual segregation because females and especially offspring are more vulnerable to predation than are larger males (Bowyer 1984; Miquelle *et al.* 1992; Bon & Campan 1996; Main & Coblentz 1996; Main *et al.* 1996; Bleich *et al.* 1997). Predictions are that females, especially those with offspring, should choose safe habitats (vegetation cover or escape habitat) even at the expense of forage quality. Segregation should then peak around calving time (table 1).

Second, the 'forage-selection hypothesis' (Clutton-Brock *et al.* 1982; Main *et al.* 1996; Ruckstuhl & Neuhaus

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Table 1. A review of the hypotheses and predictions of sexual segregation addressed in the current study.
(Predictions that were supported by the current study are in bold while predictions that were rejected are in italics.)

hypotheses	predictions						references
	A. habitat quality	B. annual pattern (except rut)	C. latitude: France versus Norway	D. females with and without offspring	E. social segregation (within habitat)	F. male–female synchrony	
1. predation-risk hypothesis	**females in lower-quality habitats**	**more around calving time, or as long as female with offspring**	**earlier in France than in Norway, since calving is earlier**	**more segregation for females with offspring**	*no pattern*	*no pattern*	Bowyer (1984); Main *et al.* (1996)
2. forage-selection hypothesis	*males in lower-quality habitats*	*segregation year round*	*no pattern*	*no difference (if similar sized), but lactating females need more energy*	*no pattern*	*no pattern*	Short (1963); McCullough (1979); Clutton-Brock *et al.* (1982, 1987); Main *et al.* (1996)
3. activity-budget hypothesis	*no pattern*	*segregation year round, as long as activity differs*	*no pattern*	*no difference if similar activity pattern; yes if different activity pattern*	**commonly single-sex groups**	**mixed-sex groups less synchronous**	Conradt (1998*a*); Ruckstuhl (1998, 1999); Ruckstuhl & Neuhaus (2002)

2000, 2002) relates habitat segregation to the sex-specific nutritional requirements that are caused by sexual body-size dimorphism (Watson & Staines 1978; Clutton-Brock *et al.* 1982). Based on interspecific allometric studies showing that large herbivores can survive on a lower-quality diet than can small ones, the Jarman–Bell principle (Bell 1971; Geist 1974; Jarman 1974), we predicted that males should occupy lower-quality habitats year round (Demment & Van Soest 1985; table 1). Another derived hypothesis, 'the scramble-competition hypothesis', focuses on the fact that there is no good reason for males to use low-quality habitat unless females are competitively superior and exclude males at high density (Clutton-Brock *et al.* 1987). Indeed, among grazing ungulates, the smaller sex (females) has a competitive advantage over the larger sex (males) when feeding on short grass swards. This is related to the lower allometric coefficient between incisor arcade breadth and body size compared with the coefficient linking energy demands and body size (Illius & Gordon 1987, 1990). Males may therefore be excluded from mutually preferred vegetation types and forced to feed on low-quality but more abundant diet at high density (Staines *et al.* 1982; Clutton-Brock *et al.* 1987; but see Conradt *et al.* 1999). However, such predictions are valid only when we assume that intraspecific allometry is equivalent to interspecific allometry.

Third, the 'activity-budget hypothesis' (Ruckstuhl 1998; Ruckstuhl & Neuhaus 2000, 2002) states that between-sex differences in activity pattern may lead to social segregation (bighorn sheep, *Ovis canadensis* (Ruckstuhl 1998); red deer, *Cervus elaphus* (Conradt 1998*a*; Conradt & Roper 2000); see Ruckstuhl & Neuhaus (2002) for a review of 22 ruminant species). Indeed, differences in activity budget would make it difficult for females and males to stay in mixed-sex groups owing to the increased cost of synchrony to maintain group

cohesion (Jarman 1974; Côté *et al.* 1997). The 'activity-budget hypothesis' predicts: (i) that segregation should occur all year round (except during the rut); and (ii) that mixed-sex groups should be less synchronized in their activity than single-sex groups outside the rutting season (table 1).

Although breeding phenology (i.e. the timing of calving and rutting) is likely to be the driving force behind the temporal pattern of sexual segregation, the interplay between latitude-dependent breeding phenology and sexual segregation has not yet, to our knowledge, been investigated. Mammalian breeding phenology is expected to be delayed at high latitudes (Bronson 1989) and the most likely mechanism for the delayed optimal time of calving (and rutting) in northern ungulates is low temperatures leading to later plant phenology (Albon & Langvatn 1992). Several studies dealing with sexual segregation have considered data from all seasons (e.g. Miquelle *et al.* 1992; Villaret *et al.* 1997; Cransac *et al.* 1998; Bon *et al.* 2001), but all except Cransac *et al.* (1998), who presented monthly estimates for mouflon sheep (*Ovis gmelini*), provided the segregation estimates on a coarse time-scale. High-resolution temporal patterns of sexual segregation covering the full year have therefore rarely been presented for ungulates, and previous studies have never taken advantage of methodological improvements that allow separation of the social and habitat components of segregation (Conradt 1998*b*).

In this study, we analyse social and habitat segregation in two red deer populations living at contrasting latitudes (49° N in France and 63° N in Norway) and therefore differing in their breeding phenology (a three to four week difference; R. Langvatn and F. Klein, unpublished results; figure 1) taking advantage of the recent methodological advancements (Conradt 1998*b*). The predictions that we aimed to test are summarized in table 1. Whatever the
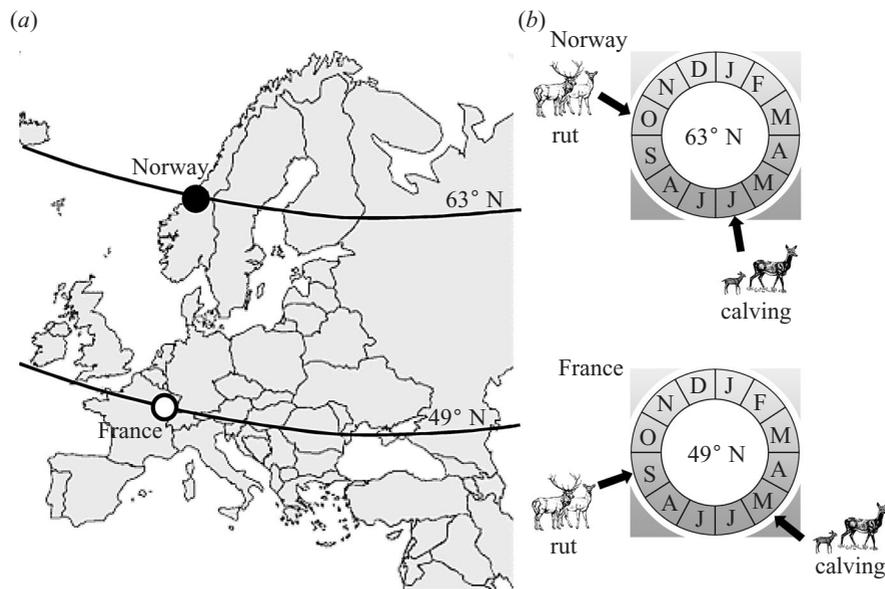
Figure 1. (*a*) Location map and (*b*) breeding phenology of European red deer at high (Norway, 63° N) and low (France, 49° N) latitudes. Rutting and calving occur one month earlier in France than in Norway.

underlying mechanisms of sexual segregation (table 1), we expect that delayed breeding phenology at high latitude (Bronson 1989) should induce an equivalent temporal delay in the social and habitat segregation pattern.

2. MATERIAL AND METHODS

(a) *Study areas*

In Norway, the study area is situated in the western mid-part of the country (5156 km²; centred around 63° N), well within the core area for red deer (Mysterud *et al.* 2001), and consists of 12 municipalities in the counties Møre og Romsdal (four) and Sør-Trøndelag (eight). Red deer in this area comprise two of five defined populations of red deer (populations three and five; e.g. Mysterud *et al.* 2002). The deer habitat ranges in altitude from sea level to *ca.* 750 m and consists mainly of pine forest (*Pinus sylvestris*) with pockets of mixed deciduous forest (dominated by *Betula* sp., *Populus tremula* and *Sorbus aucuparia*), open heather (*Calluna vulgaris*) and agricultural land. Red deer occasionally also use areas above the tree line (mainly when foraging at night-time during the summer), which range in altitude between 500 and 700 m depending on the distance to the coast. The climate is strongly seasonal (mean January and July temperatures are –2.2 °C and 12.9 °C, respectively). Median calving date is 16 June and median date of ovulation is *ca.* 15 October (Langvatn *et al.* 2004; figure 1). Natural predators are very scarce and include golden eagles (*Aquila chrysaetos*) and lynx (*Lynx lynx*), both being capable of killing calves only. Human hunters annually cull red deer from 10 September to 15 November.

The French study area is La Petite Pierre National Reserve, located in northeast France (28 km²; 49° N) in the Vosges Mountains, at a mean elevation of 300 m. The habitat is mainly forested, with trees covering *ca.* 85% of the total area. The heterogeneous canopy consists predominantly of a mixture of silver fir (*Abies alba*), Douglas fir (*Pseudotsuga douglasii*), Norway spruce (*Picea abies*) and European beech (*Fagus sylvatica*). The climate is continental with oceanic influences (mean January and July temperatures are 0.6 °C and 18.4 °C, respectively) leading to warm winters and cool summers. Most calves are born in

mid-May, while the rutting activity peaks in late September (F. Klein, unpublished results). Thus, the breeding phenology is approximately one month earlier in France than in Norway (figure 1). Natural predators are absent but a limited number of red deer are culled annually from 15 November to 30 January (Bonenfant *et al.* 2002).

(b) *Red deer data*

In Norway, observations consist of three different types. In early spring (March and April), deer were observed primarily on farmland by research personnel in vehicles and by farmers (from observations on their properties). All year, research personnel on foot observed deer in all types of terrain, but with variable intensity. Hunters recorded groups of red deer in the period 10 September to 15 November (also in all types of terrain). Altogether, research personnel, farmers and hunters determined the age (according to three classes: calf, yearling and adult) and sex of red deer in 2045 groups (group size of between 1 and 56) from 4 January to 25 December in the years 1956–1984 and classified habitat into one of five types (table 2).

In France, managers and research personnel from the Office National de la Chasse et de la Faune Sauvage performed all observations year round either on foot or by car. Altogether, 1912 groups (including observations of single animals) were recorded from 2 January to 30 December from 1980 to 1999. The sex and the age (calf versus adult) of each individual in a sighted group were determined. Field observers also recorded whether the females did or did not have a calf at heel (the status 'unknown' was assigned whenever the motherhood relationship was not formally established). Finally, the habitat occupied by each group was assigned to one of the seven different types (table 2).

(c) *Statistical analyses*

(i) *Definition of segregation, aggregation and synchronization coefficients*

The study of the interplay between habitat segregation and social segregation (grouping with their own sex regardless of habitat) has only recently been made possible. Conradt (1998*b*) developed an index of sexual segregation that is independent of

Table 2. Description of the habitat types found in Norway and France.

habitat type	description
Norway	
pine forest	open pine (*Pinus sylvestris*) forest with blueberry (*Vaccinium myrtillus*) and heather (*Calluna vulgaris*) in the field layer
mixed forest	a mix of deciduous (*Betula* sp., *Populus tremula* and *Sorbus aucuparia*), spruce (*Picea abies*) and pine (*Pinus sylvestris*) forest with juniper (*Juniperus communis*) and willow (*Salix* sp.) in the field layer; dense forest type
heather land	open dry glens (no trees) with *Calluna vulgaris* dominating the field layer
above tree line	treeless land at 500–700 m altitude; willow, blueberry and crowberry (*Empetrum nigrum*) in the field layer
agricultural land	Timothy (*Phleum pratense*) and other grass species farmed as winter feed for cattle and sheep
France	
agricultural land	open fields of corn, sugar beet or alfalfa; these standing crops are non-fenced and freely available to deer
meadows	open fields of grass species farmed mainly for fodder production and summer feed for cattle
regeneration	typical colonizing vegetation with birch (*Betula pendula*), juniper (*Juniperus communis*), hawthorn (*Crataegus* sp.) and brambles (*Rubus* sp.) following clear-cut events (exploitation or Lothar storm): less than 4 m in height but providing very good sheltering and resting habitats to deer
plantation	young-stage (shoots less than 5 years old) and still-not-exploited deciduous (beech, hornbeam, oak), coniferous (spruce, fir) or mixed forest; semi-open to dense forest type
pole plantation	closed uniformly distributed forest type consisting of Douglas fir (*Pseudotsuga douglasii*) or Norway spruce (*Picea abies*) forest from 5 to 15 years old; poorly developed field and shrub layer
timber-tree	a mix of deciduous oak (*Quercus* sp.), hornbeam (*Carpinus betulus*), beech (*Fagus sylvatica*) spruce and pine forest with juniper (*Juniperus communis*); the field layer is composed of blueberry (*Myrtillus* sp.) and mosses, brambles or hairy wood-rush (*Luzula pilosa*) and bracken (*Pteridium aquilinum*) following the dominant timber-tree species; dense forest type
regenerating timber-tree	identical to timber-tree habitat except for an additional and intermediate layer of young growing poles (mainly beech, hornbeam, spruce and fir); dense forest type

population sex ratio, population density and group size. We therefore calculated the magnitudes of both the social segregation, SC_{social} (equation (2.1)), and the habitat segregation, $SC_{habitat}$ (equation (2.2)), components of sexual segregation following Conrad (1998*b*) for each month of the year (whenever sample sizes were greater than 30 group observations) and for each female reproductive status (with or without a calf at heel). All segregation coefficients can take values between 1 (total segregation) and –1 (total aggregation). Individuals of both sexes can be said to associate randomly if SC_{social} is not statistically different from 0. We assessed synchrony within three group types (mixed groups, only-female groups and only-male groups) using a similar coefficient to the segregation coefficients proposed by Conrad (1998*b*) (equation (2.3)).

$$SC_{social} = 1 - \frac{N}{XY} \sum_{i=1}^{k} \frac{x_i y_i}{n_i - 1}. \tag{2.1}$$

In equation (2.1), x_i is the number of males in the ith group, y_i is the number of females in the ith group, n_i is the group size of the ith group ($n_i = x_i + y_i$), k is the number of groups with at least two animals, X is the total number of males sampled (excluding solitary animals), Y is the total number of females sampled (excluding solitary animals) and N is the total number of males and females sampled.

$$SC_{habitat} = 1 - \frac{M}{ZW} \sum_{i=1}^{l} \frac{z_i w_i}{m_i - 1}. \tag{2.2}$$

In equation (2.2), z_i is the number of males in the ith habitat type, w_i is the number of females in the ith habitat type, m_i is the number of males and females in the ith habitat type ($m_i = z_i + w_i$), l is the number of habitat types that are used by

at least two animals, Z is the total number of males sampled, W is the total number of females sampled and M is the total number of males and females sampled. Contrary to the calculation of social segregation, when calculating $SC_{habitat}$ solitary individuals are included.

$$SynC = 1 - \sum_{h=08.00}^{20.00} \frac{N_h}{N} \frac{N_h - 1}{A_h R_h} \sum_{j=1}^{k_h} \frac{a_{h,j} r_{h,j}}{n_{h,j} - 1}. \tag{2.3}$$

In equation (2.3), N is the total number of animals observed, N_h is the number of animals observed in hour h of the day, A_h is the number of animals observed foraging in hour h of the day, R_h is the number of animals observed resting in hour h of the day, $n_{h,j}$ is the total number of animals observed in hour h of the day in the jth group, $a_{h,j}$ is the number of animals observed foraging in hour h of the day in the jth group and $r_{h,j}$ is the number of animals observed resting in hour h of the day in the jth group.

Standard errors are not readily available from the original definition of the segregation coefficients by Conrad (1998*a*,*b*). Consequently, we could not perform basic statistical inference and hypothesis testing. We thus computed standard errors by bootstrapping the segregation-coefficient estimators (Efron & Tibshirani 1993). We replicated the analysis 1000 times with randomly selected subsamples of our data and used the bootstrap mean as an unbiased estimator of segregation coefficients (Efron & Tibshirani 1993). Under the assumption that the SC distribution is correctly approximated by a normal distribution, computation of standard errors allowed us to test biological hypotheses and to compare observed segregation coefficients with a theoretical value of 0 (i.e. the null hypothesis that males and females aggregate at random). A null hypothesis was not

rejected when two 95% confidence intervals (CI) overlapped or when the theoretical value lay within the 95% CI.

(ii) *Testing the seasonal pattern of segregation between groups*

Comparisons of temporal patterns were investigated with simple correlations of monthly SC estimates in the two populations. According to the recommendation of Conradt (1998*b*) to use non-parametric statistics we used Spearman's rank correlation test (Sokal & Rohlf 1995) to compare within-year variations in SC between Norway and France and to test for a difference in the variation of SC over time between females with and without a calf at heel. Similarly, we compared the mean SCs of red deer in the two countries with a Mann–Whitney *U*-test (Sokal & Rohlf 1995).

(iii) *Differentiating habitat use by sex*

Between-sex differences in habitat use were investigated within a generalized linear model framework (McCullagh & Nelder 1989). Because the response variable is the number of individuals counted, we used a Poisson regression and a gamma error distribution. Factors entered in the model were 'habitat type' (a five- and seven-modality factor for Norway and France, respectively), 'time' (12 levels from January to December) and 'sex' (two modalities: male and female). As we were interested in the relative use of each habitat type by each sex, i.e. the proportion of males and females found in each habitat over time, third- and second-order interactions including the factor 'habitat type' were the only terms of interest. All statistical analyses were performed by using the S-PLUS statistical package (Venables & Ripley 1999).

3. RESULTS

Social segregation was higher overall than habitat segregation, indicating that individuals grouped with their own sex within large-scale habitat types (monthly estimates of $SC_{social} > SC_{habitat}$: Norway: $\chi^2 = 8.67$, d.f. = 1, $p = 0.003$; and France: $\chi^2 = 8.67$, d.f. = 1, $p = 0.003$; figure 2). Habitat segregation was most pronounced and significantly different from 0 only during calving time (figure 2*b*). Habitat-use analyses selected the same model in both countries including the third-order interaction among habitat, time and sex (Norway: $\chi^2 = 87.984$, d.f. = 39, $p < 0.0001$; France: $\chi^2 = 307.877$, d.f. = 72, $p < 0.0001$). At this time (June) in Norway, adult females stayed in sheltered deciduous forest (64%, $n = 69$, agricultural land excluded; figure 3*a*), while males occupied high-altitude non-forested areas recently free from snow (57%, $n = 21$, agricultural land excluded; figure 3*b*). Correspondingly, female deer in France stayed in closed and mostly sheltered habitat (timber-tree 81%, $n = 132$; figure 3*c*), while the males used open habitat such as agricultural lands and meadows (20%, $n = 13$) or plantation (37%, $n = 25$) during the calving time (May) (figure 3*d*). Social segregation varied extensively throughout the year, showing a peak during the calving time immediately followed by a return to values similar to those prior to calving and then a drop below 0 during the rut (indicating aggregation) in both red deer populations (figure 2*a*). Sexes were consistently more segregated in France than in Norway outside the rutting season (September and October; figure 2*a*). Females with a calf at heel were more segregated from

males than were females without a calf at heel in both populations especially during the calving season (Wilcoxon signed-rank test for paired data: Norway: $Z = -2.096$, $p = 0.036$, $n = 6$; and France: $Z = -2.392$, $p = 0.016$, $n = 12$; figure 4). Mixed-sex groups were less synchronized in activity than only-male and only-female groups outside the rutting season (figure 5). The pattern of sexual segregation (both social and habitat) was delayed by one month in the northern populations, corresponding well with the known delay in breeding phenology (the correlations between social segregation of both populations without and with correction for the time delay in breeding phenology were, respectively: $r^2 = 0.713$, $Z = 2.354$, $p = 0.018$, $n = 11$; and $r^2 = 0.867$, $Z = 2.864$, $p = 0.004$, $n = 11$; figure 1). In the rutting season, males and females in France aggregated only weakly and less than in Norway ($\chi^2 = 10.83$, d.f. = 1, $p = 0.001$; figure 2*a*). French and Norwegian stags held on average the same number of hinds during the rutting season (mean ± s.e. of 1.6 ± 0.08 and 1.5 ± 0.07 females per male, respectively).

4. DISCUSSION

We have shown that the annual cycle of sexual segregation is closely related to breeding phenology by reporting for the first time, to our knowledge, a temporal delay in annual sexual-segregation pattern in the same species at two different latitudes. Although the annual cycle was predicted by the predation-risk hypothesis, several other predictions of the activity-budget hypothesis were also supported. Therefore, the pattern of sexual segregation has multiple causes and the different hypotheses are not mutually exclusive, but rather explain different aspects of the complex pattern of sexual segregation (summarized in table 1).

(a) *The predation hypothesis and evidence based on breeding phenology*

The predation-risk hypothesis has received massive support in explaining sexual segregation in ungulates: females with young often select safer habitat even at the expense of forage quality (Bergerud *et al.* 1984; Francisci *et al.* 1985; Shank 1985; Festa-Bianchet 1988; Berger 1991; Miquelle *et al.* 1992; du Toit 1995; Main & Coblentz 1996; Main *et al.* 1996; Bleich *et al.* 1997; Villaret *et al.* 1997). In our study, social segregation and habitat segregation peaked when calves were newborn and probably most prone to predation, and was delayed in Norway compared with France, demonstrating the utility of accounting for breeding phenology in sexual-segregation studies. Females stayed in more sheltered habitat, while at the same time males used habitat of superior nutritional quality in Norway (Albon & Langvatn 1992) and France. It is somewhat surprising that the predation-risk hypothesis was the main determinant of sexual segregation, as red deer predators (mainly wolves and bears) have been scarce or completely absent both in east France (Breitenmoser 1998) and Norway (Swenson *et al.* 1995, 1998) during the past 100 years, or approximately 13 red deer generations (generation time of 7 years; Clutton-Brock *et al.* 1982). Witnessing the ghost of past predation after so long suggests that evolution of optimal behaviour in ungulates has been very strongly influenced by predators (Byers 1997).
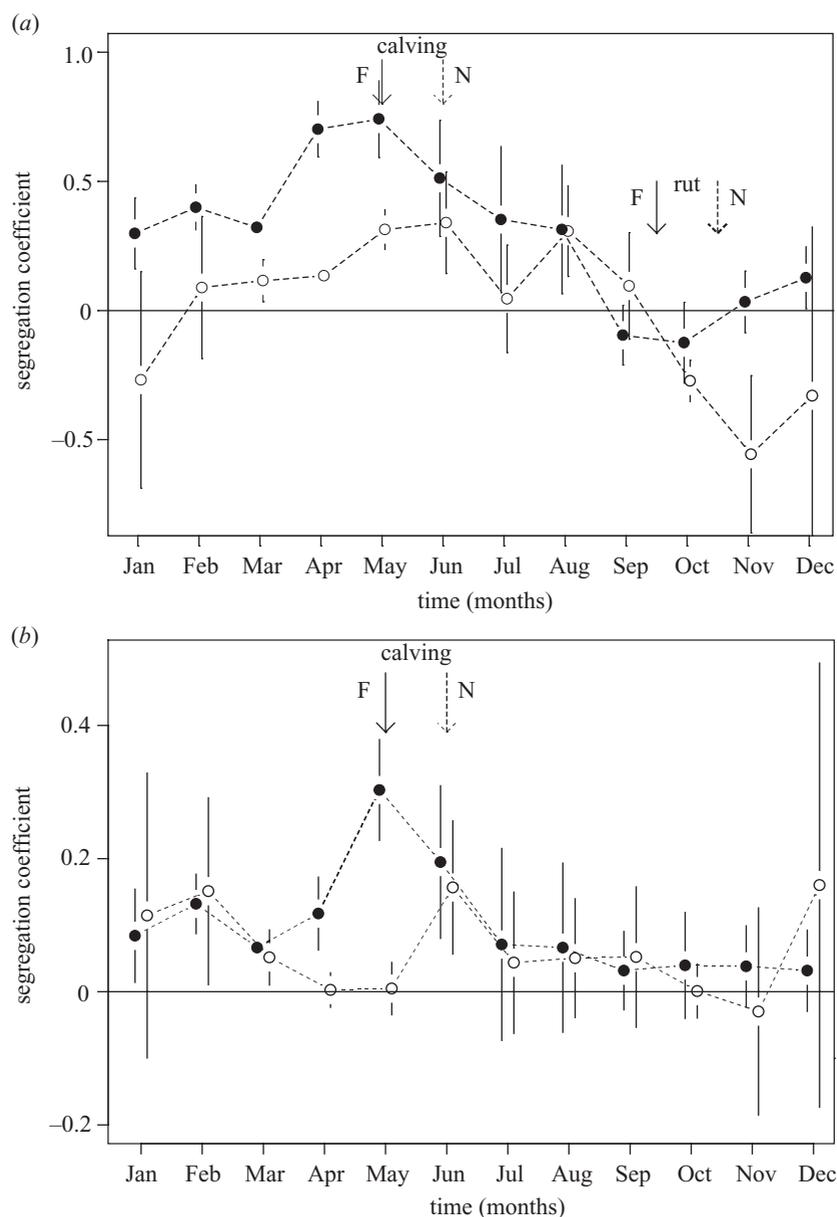
Figure 2. Monthly sexual segregation in Norwegian (N) (open circles) and French (F) (filled circles) red deer (mean ± 95% CI) as calculated by the segregation coefficients in Conradt (1998*b*) and disentangled into the components of (*a*) social and (*b*) habitat segregation.

(b) *Females with and without young: a role for lactation or predation?*

Females caring for young may segregate from males as well as other females according to all the three segregation hypotheses, but the detailed temporal pattern can be used to distinguish between the three possibilities. Energetic needs are highest when the females lactate because the production of milk is extremely costly (Sadleir 1969; Loudon 1985; Robbins 1993). Lactating females can therefore have a different activity budget from other females (Ruckstuhl & Neuhaus 2002). Females with calves were more socially segregated from males than were females without calves. In addition, earlier studies reported that females with young tend to form groups on their own in several ungulate species (bison, *Bison bison* (Rutberg 1984; Komers *et al.* 1993), and chamois, *Rupicapra rupicapra* (Pérez-Barbería & Nores 1994)). But, if sexual segregation is caused by females grazing on high-quality pastures to compensate for energy loss to lactation, then segregation should be high (though gently decreasing) during the entire period of intensive lactation (*ca.* 80 days for red deer; Clutton-Brock *et al.* 1982) and not only during calving. Both social and habitat segregation, as well as the segregation difference between reproducing and non-reproducing females, dropped dramatically the month after calving, long before females stop lactating, which is supposed to last for at least six months in red deer (Clutton-Brock *et al.* 1982). In addition, reproductive females in charge of their offspring have been shown to use low-quality habitat in several different species (Edwards 1983; Bowyer *et al.* 1999). Therefore the sexual-segregation peak we observed in spring in both populations (figure 2) cannot be accounted for by sexual differences in forage selection or activity budget caused by lactation alone, and is likely to be related to the anti-predator behaviour.
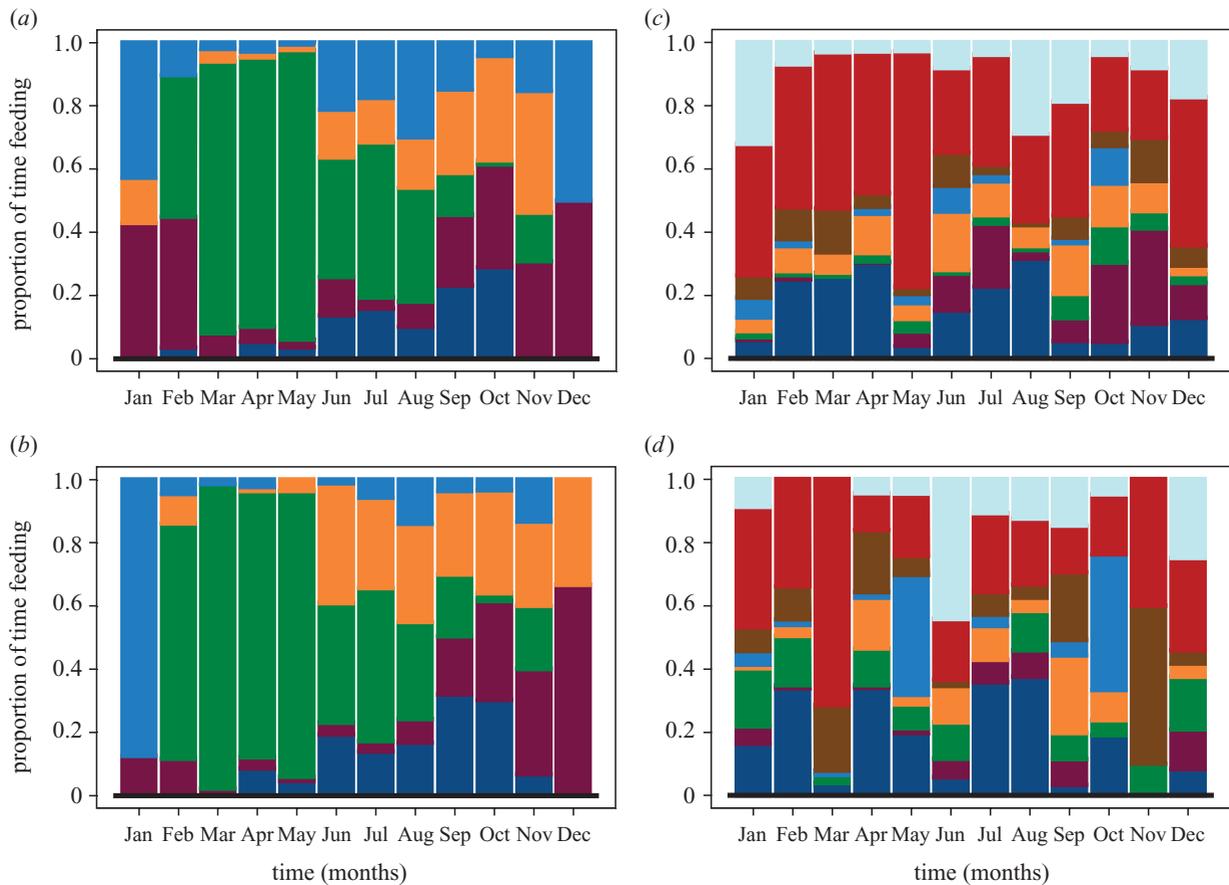
Figure 3. Proportions of different habitat types used each month by male and female red deer in Norway and France. (*a*) Norway habitat use, females; (*b*) Norway habitat use, males (dark blue, pine forest; dark red, mixed forest; green, heather land; orange, above tree line; mid-blue, agricultural land); (*c*) France habitat use, females; and (*d*) France habitat use, males (dark blue, agricultural land; dark red, human buildings; green, meadows; orange, regeneration; mid-blue, plantation; brown, pole plantation; mid-red, timber-tree; light blue, regenerating timber-tree).

(c) *Social segregation*

Sexual segregation was long thought to be a by-product of different habitat selection by females and males (Clutton-Brock *et al.* 1987), even though some studies reported segregation despite small differences in habitat use between the sexes (Cransac *et al.* 1998; Ruckstuhl 1998). Sexual segregation regardless of habitat (i.e. social segregation; Conradt 1998*a*) has since been documented conclusively (Conradt 1999; Conradt *et al.* 1999, 2001), providing an intuitively appealing mechanism (Conradt 1998*a*; Ruckstuhl 1998) and taking advantage of recent advances in methodology (Conradt 1998*b*). Our study confirms that a large proportion of sexual segregation is accounted for by social segregation (figure 2) and that mixed-sex groups were less synchronized than only-male and only-female groups outside the rutting season (figure 5). Different optimal activity budgets in males and females is the most likely mechanism explaining the component of sexual segregation that is not explained by habitat segregation (Ruckstuhl & Neuhaus 2002).

(d) *Lack of evidence for the 'forage-selection' hypothesis*

We found no support for the 'forage-selection' hypothesis in accordance with other recent results (Conradt 1999; Conradt *et al.* 1999), although red deer are one of the most dimorphic ungulate species (more dimorphic

than the 20% threshold needed for sexual segregation to occur; Ruckstuhl & Neuhaus 2002) and several empirical studies provide evidence for males having higher energy needs than females. However, the Jarman–Bell principle was coined at the interspecific level to explain variations in energy requirements and differences in diet selection between the African elephant (*Loxodonta africana*) and dik-dik (*Madoqua kirki*) and more recently between the cow (*Bos taurus*) (750 kg) and Thomson's gazelle (*Gazella thomsoni*) (20 kg) (Wilmshurst *et al.* 2000). The reasoning might be ill founded to explain sexual segregation at an intraspecific level, with some 50 kg weight difference (Conradt *et al.* 1999). At this level, local environmental conditions and individual quality rather than evolutionary constraints might shape energy needs.

(e) *Geographical variation in the red deer social system*

The latitudinal-related variation in segregation, probably linked to breeding phenology, was not the only geographical variation in the social organization of red deer. Sexes were generally more socially segregated in France than in Norway outside the rutting season. Norwegian red deer's extensive use of agricultural land may lead to the formation of mixed foraging groups in a small space, which split up once they are back in their natural habitat. This will decrease the social-segregation estimates
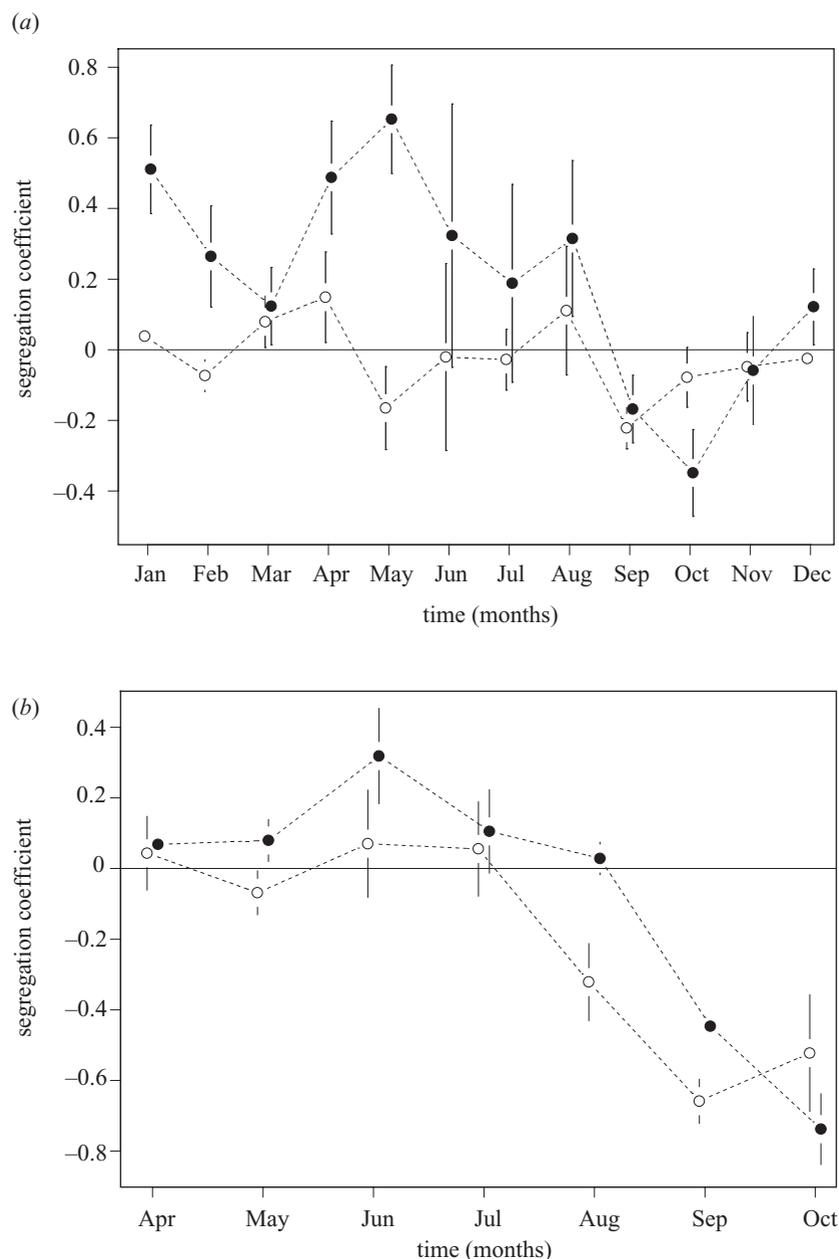
Figure 4. Monthly sexual segregation (social component, mean ± 95% CI) in red deer hinds with (filled circles) and without (open circles) a calf at heel in (*a*) France and (*b*) Norway.

compared with those for France, where much less farmland is available for the deer in the forested area studied. Our study of red deer in France and Norway also contrasts with the most well-known one on the Isle of Rum, Scotland, where prime-aged males hold large harems in open terrain (Clutton-Brock *et al.* 1982). Mating systems in mammals are related to the spatio-temporal distribution of oestrus females (Emlen & Oring 1977; Clutton-Brock 1989), which in turn is closely linked to food-resource distribution. The small number of hinds held by stags in our study compared with red deer on Rum (Clutton-Brock *et al.* 1982) implies a largely different mating system in forested areas from that in more open areas (e.g. Calef & Van Camp 1987). The common male mating strategy in our two forested study areas seems to be the tending of one or two females. The weaker aggregation in France than in Norway during the rut suggests that French males moved between female groups more often than did

Norwegian males (and therefore were observed more often alone). Indeed, male mating strategy in European red deer seems to be highly flexible (Carranza *et al.* 1995).

5. CONCLUSION

We conclude that latitude-dependent breeding phenology drives an annual cycle of sexual segregation, which peaks during calving and drops during the rut, and that the segregation peak in spring is probably caused by a shelter-seeking anti-predator strategy in female European red deer at both high and low latitudes. Sexual segregation is mainly driven by social segregation and not by habitat segregation. We further suggest that a sexual difference in optimal activity budgets is a likely mechanism for the social part of sexual segregation in red deer, and that sexual segregation in ungulates hence has multiple causes.
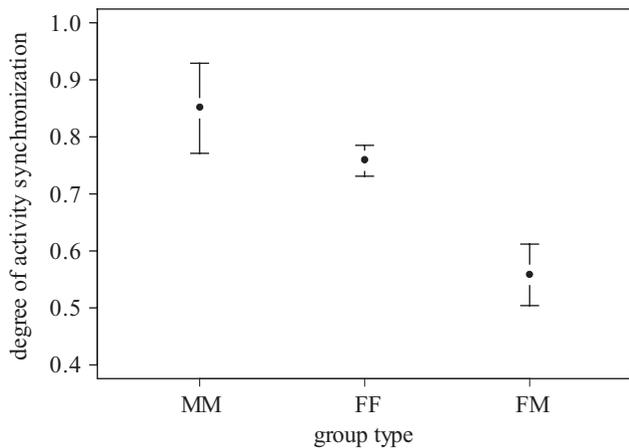
Figure 5. Synchronization coefficients for Norway (mean ± 95% CI) according to the kind of group: only-female (FF), only-male (MM) and mixed-sex (FM) groups. Mean values (with associated s.d.): MM: 0.850 (0.079); FF: 0.758 (0.027); and FM: 0.558 (0.054).

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