Variation in harem size of red deer (*Cervus elaphus* L.): the effects of adult sex ratio and age-structure

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Abstract

The relationships among harem size, adult sex ratio (proportion of males > 5 years in the adult population, i.e. males > 5 years plus females > 2 years) and male age-structure of red deer *Cervus elaphus* was investigated in La Petite Pierre National Reserve (PPNR) in France. We tested whether: (1) increasing adult sex ratio leads to a decrease in harem size along with an increase in the number of harems within a given rut period; (2) whether participation of sub-adult males in mating activities increases with decreasing adult sex ratio, and as the proportion of adult males decreases. Harem size did not vary over the mating period, suggesting a high turnover of harem-holders leading to an increase in the costs of mating for males. Harem size averaged 1.43 ± 0.91 and was lower than harem sizes typically reported for red deer (e.g. > 2.5 in Scotland and Norway). In support of the first prediction, a decrease in harem size and an increase in the total number of harems seen with an increasing sex ratio was observed (harem size $= 2.08 - 1.26 \, [\pm 0.43] \times$ (sex ratio); $r^2 = 0.25$, $F_{1,18} = 6.19$, $P = 0.02$). Both the uniform distribution of females among harem stags and the small harem sizes observed in PPNR might concur to a smaller variance in male reproductive success than previously reported in red deer. Lastly, in partial support of the second prediction, the proportion of sub-adult males observed during the mating season decreased with increasing adult sex ratio and with increasing proportions of adult males. Whether or not the lower proportion of sub-adults seen when competition among mature males increases means that less young males mate, cannot be assessed from our study.

Key words: *Cervus elaphus*, forested habitat, mating tactics, red deer, sexual selection, rutting season, ungulates

INTRODUCTION

The type of mating tactic observed in a given population of mammal depends on the spatio-temporal distribution of oestrous females and on group stability (Orians, 1969; Emlen & Oring, 1977; Clutton-Brock, 1989; Davies, 1991), which are both determined by the distribution of food resources (Geist, 1974; Jarman, 1974; Ralls, 1977). Polygyny (*sensu* Reynolds, 1996) should occur whenever some males have the opportunity to 'economically' prevent other males having access to females (Emlen & Oring, 1977; Clutton-Brock & Harvey, 1978; Davies, 1991). At the population level, the mating system can be defined as the sum of all individual mating tactics (Clutton-Brock, 1989; Reynolds, 1996; Apollonio, Festa-Bianchet & Mainardy, 2000). Mating tactics, however, are remarkably variable among and within populations (Hogg, 1984; Lott, 1990; Thirgood, Langbein & Putman, 1999). They can vary among individuals with age, size (Caro &

Bateson, 1986) or environmental conditions, depending on the relative costs and benefits of the amount of energy allocated to fighting and guarding activities, predation risks (Jarman, 1974; Kalas, Fiske & Sæther, 1995; Goldspink *et al*., 2002) and effective mating success. Alternative tactics (such as kleptogamy) are mostly adopted by subordinate individuals (Byers & Kitchen, 1988; Modig, 1996; for review see Austad & Howard, 1984). Frequent changes of mating tactics according to environmental conditions have led to the concept of optimal mating strategies, which are usually defined by using modelling approaches (Dunbar, Buckland & Miller, 1990; Sandell & Liberg, 1992; Stevenson & Bancroft, 1995).

In polygynous species, annual male mating success is closely associated with fighting success and dominance rank (Buechner, 1961; LeBoeuf, 1974; Clutton-Brock, Guinness & Albon, 1982; Gammell, 2001), and is much more variable among individuals than female mating success (Gibson & Guinness, 1980*a*; Le Boeuf & Reiter, 1988; Rose, Clutton-Brock & Guinness, 1998; Wilson, Olson & Strobeck, 2002). In red deer, the main proximate

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factor that determines the number of offspring fathered and that differentiates successful from unsuccessful males is harem size (Gibson & Guinness, 1980*a*; Pemberton *et al*., 1992), and to a lesser degree harem-holding time, timing of breeding access, and female density (Gibson & Guinness, 1980*b*). External factors, such as the quality of soil characteristics (Kitchen, 1974) or previous use of mating areas by other males (Deutsch & Nefdt, 1992), may also influence male mating success. Because of the high variance in their reproductive success, males of polygynous species compete intensively for mates and are therefore subject to marked sexual selection pressures (Wade, 1979; Sutherland, 1985), leading to strong between-sex differences in morphological, behavioural and demographic traits (Darwin, 1871; Fisher, 1930; for reviews see Alexander *et al*., 1979; Clutton-Brock, Albon & Guinness, 1985; Loison *et al*., 1999).

Variations in adult sex ratio, which are often related to changes in population size (Clutton-Brock, Rose & Guinness, 1997), should lead to variations in the intensity of male–male competition. Although adult sex ratio is generally female-biased in polygynous species (e.g. Clutton-Brock, Guinness *et al*., 1982), two types of population can be distinguished in relation to adult sex ratio. In populations with an adult sex ratio strongly biased towards females, females may aggregate in large harems held by high-ranking males, to avoid harassment by subordinate males (Clutton-Brock, Price & McColl, 1992; Carranza & Valencia, 1999) and leading to high variance in mating success among males. In contrast, in populations with more balanced adult sex ratios, male–male competition is high and male mating success may be impaired by the high energetic demand of female guarding and fighting (Geist, 1982; Skogland 1989). Females may thus be more uniformly distributed among males, which could decrease variance in the mating success of males. In addition, adjustments of male mating tactics related to changes in sex ratio may occur in relation to male age (bison *Bison bison*: Komers, Messier & Gates, 1994; moose *Alces alces*: Solberg & Sæther 1994). Indeed males can reproduce as yearlings (Hogg & Forbs, 1997; Coltman, Festa-Bianchet *et al*., 2002), with a lower risk-to-reward ratio when the sex ratio is female biased (Soay sheep *Ovis aries*: Stevenson & Bancroft, 1995) or when adult males are rare (Squibb, 1985; Singer & Zeigenfuss, 2002). To reproduce as sub-adults, however, may still bear some costs, e.g. young bighorn rams *Ovis canadensis* suffer a higher mortality rate as a consequence of early reproductive activities, when adult rams are scarce (Singer & Zeigenfuss, 2002). One can thus expect a higher investment by sub-adults in reproductive activities either when females are in excess relative to males or when there is a paucity of adult males.

In this study, variations in harem size over the rutting period and the relationships between harem size and population age- and sex-structure were investigated in a red deer population inhabiting a deciduous forest located in north-east France. The following predictions were tested:

Prediction 1. Increasing sex ratio toward adult males should lead to smaller harem sizes, because of higher male–male competition for mating (elk *Cervus canadensis*: Bender, 1996), increasing the energetic demands of fighting and female guarding (Geist, 1982). As a consequence, the number of harems observed during the rut should increase with increasing ratio of males to females, because females should be more evenly distributed amongst harem males than when the ratio of males to females is low. Alternatively, with more males, the harassment level sustained by females may increase (Réale, Boussès & Chapuis, 1996) and they may thus aggregate in large harems, leading to a positive relationship between the proportion of males and mean harem size.

Prediction 2. Young males should invest more heavily in reproduction both when the proportion of adult males decreases (Solberg & Sæther, 1994) and when the average age of males becomes younger (Singer & Zeigenfuss, 2002). It was thus predicted that harem size should decrease and the number of harems should increase when the proportion of adult males increases, because young males are less effective in holding large harems (Ozoga & Verme, 1985) and breeding (Noyes *et al*., 1996), and females are reluctant to mate with the youngest males (Prothero, Spillett & Balph, 1979).

METHODS

Study area

The Petite Pierre National Reserve (PPNR) is a 2800-ha forest located in north-east France (48.5°N, 7°E) in the Vosges Mountains, at a mean elevation of 300 m. The climate is continental with oceanic influences (mean January and July temperatures are 0.6 °C and 18.4 °C, respectively. Trees cover most of PPNR, and consist of a mosaic of silver fir *Abies alba*, douglas-fir *Pseudotsuga douglasii*, Norway spruce *Picea abies* and European beech *Fagus sylvatica* trees. The understory includes patches of hairy wood-rush *Luzula pilosa*, brambles *Rubus fruticosum*, juniper *Juniperus* sp. and bracken *Pteridium aquilenium*. Roe deer *Capreolus capreolus* and wild boar *Sus scrofa* were also present in the reserve and all 3 ungulates were hunted, based on quotas for both species of deer or freely for wild boar. Annual hunted numbers during the last 10 years averaged 35 red deer, 50 roe deer and 100 wild boar. This annual culling stabilized the PPNR red deer population, with management aimed at maximizing the number of adult males. To achieve this, hunters inside the reserve were allowed to harvest only antlerless animals and yearling males after 1975. As a result, over the last 2 decades, the adult sex ratio measured as the proportion of adult males in the population (i.e. the number of adult males divided by the total number of adult individuals of both sexes following Clutton-Brock & Albon, 1989; Clutton-Brock & Parker, 1992) increased and the average age structure of males became older. In

France, the rutting season of red deer usually covers the last 2 weeks of September and the first week of October (Malgras & Maillard, 1996). Two main periods can be defined in this population in relation to deer density: a high-density period before 1983 and a low-density period from 1983 to present (for details see Bonenfant *et al*., 2002). These changes in density, age-composition and adult sex ratio were used as an experimental manipulation of the population structure (Sinclair, 1989).

Data collection

Rutting censuses have been carried out in the PPNR every year since 1979 and were originally designed to estimate the number of roaring males inside the reserve. During the third week of September and the first week of October, 50 observers counted and identified all deer seen, for sex and age classes at 25 different observation sites, with particular attention paid to open areas. Each deer was age-classified as calf, yearling and adult (i.e. 2 years of age and older) for females and as calf, yearling, sub-adult (adult younger than 5 years of age) and adult (5 years of age and older) for males. The distinction between sub-adults and adult males was made by experienced wildlife managers in relation to deer morphology and relative antler size (see Crampe, Gaillard & Loison, 2002 for a similar approach on isard *Rupicapra pyrenaica*). In particular, sub-adults have a narrower neck (owing to the partial development of muscles), lack a long-haired and dark-brown mane and have smaller antlers and body size compared with adult males. Each observation site was chosen to minimize the risk of disturbing the deer while maximizing the chances of observations. The spatial distribution of observation sites within the reserve was thus defined based upon both their use by red deer and vegetation height (i.e. short vegetation allowing long distance sightings was favoured). The size, composition and number of groups were recorded during 3 h before darkness and 3 h after first light the next morning. To reduce the occurrence of double counts, marked animals (see Bonenfant *et al*., 2002) were used to identify harems. Observers recorded the timing and direction of mobile deer groups, which were then compared with the observations made on adjacent areas. When this procedure indicated double counting in 2 neighbouring areas, groups were recorded only once. From 1979 to 1999, the mean number of harems observed annually was 86.4 ± 29.8, with a range of 41–148.

Temporal variation in harem size

Following Clutton-Brock, Guinness *et al*. (1982), harem size was defined as the number of adult females defended by an adult male at a given time. A harem is thus composed of at least 1 female and 1 male. To ensure that counts performed on different dates over the course of the rut were consistent, whether a temporal trend occurred in harem size was tested first using a 1-way ANOVA. Harem size was log-transformed and entered as the response variable in the model, and count order as the factor (whether it was the first or second counting session performed by managers during the breeding season). Model assumptions (residual normality) were checked using Cook's distance and graphical dispersion of residuals (Venables & Ripley, 1994).

Distribution of females among harem-holder males with changing sex ratio

Mean harem size and the number of harems observed in a given year were regressed on adult sex ratio during the rut at PPNR using an ANCOVA-like procedure, density (high *vs* low) being included in the model as a factor. Density was entered in the model because of its known effect on group size in ungulates (Wittenberger, 1981) and its potential confounding effects on adult sex ratio (Clutton-Brock, Rose *et al*., 1997). Our definition of sex ratio did not include yearling and sub-adult males and thus allows for the bi-maturation process (*sensu* Wiley, 1974) in red deer, i.e. a delayed age of social maturity in males compared with females. Similar analyses with the same variables (sex ratio and density) were conducted to investigate the effect of adult sex ratio on the number of sub-adult males (used as the response variable) observed during the rutting season in PPNR in breeding areas. The number of harems and the number of sub-adults are count variables, which are Poisson distributed. A weighted log-linear model was therefore considered the most suitable statistical framework to test our hypotheses (McCullagh & Nelder, 1983; for an application see Baldi, Albon & Eston, 2001). **Q1**

Population age structure and harem distribution

Antler size correlates poorly with age in cervids. Therefore, age was either assessed from the marking of newborn fawns or a from a post-mortem inspection of cementum layer (Hamlin *et al*., 2000; Festa-Bianchet *et al*., 2002). In the PPNR only 20% of the population was marked, so it was not possible to know the age structure of the population exactly. Thus the proportion of sub-adults among males was used as a proxy for the age structure of males. In polygynous ungulates, sex ratio is frequently reported to correlate with the age structure of the population. The proportion of young males in a population is usually higher when the adult sex ratio is female-biased (Mysterud, Coulson & Stenseth, 2002). Consequently, the link between sex ratio and age structure was tested with a non-parametric Spearman's rank-correlation test (Sokal & Rohlf, 1981). Our second prediction that the proportion of sub-adult males should affect both harem size and the number of harems held by adult males, was tested by successively entering sex ratio, age structure and the first order interaction term in the model involving a weighted Poisson regression with a gamma error distribution (McCullagh & Nelder, 1983). The effect of each variable entered in the model
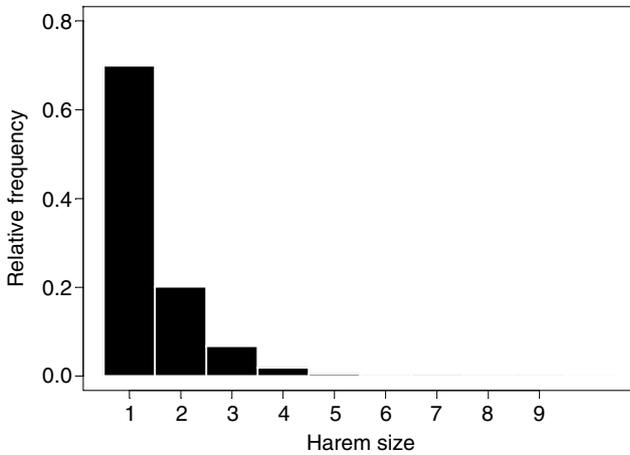
Fig. 1. Distribution of red deer *Cervus elaphus* harem sizes (number of adult females, i.e. 2 years of age and older) defended by an adult male (i.e. > 4 years of age) in La Petite Pierre National Reserve, France ($n = 1850$).

was tested with likelihood ratio tests using a backward selection procedure (Searle, 1971). All statistical analyses were performed using SPlus software (Venables & Ripley, 1994) and the level of rejection of a null hypothesis set at $\alpha = 0.05$.

RESULTS

Temporal variation in harem size

Whether harem sizes varied in time and between count sessions (morning and evening) was tested first. No trend over the rutting season in the number of females per harem could be detected. Mean harem sizes were 1.93 ± 1.18 for the first count *vs* 1.39 ± 0.07 1 week later ($F_{1,795} = 0.20, P = 0.65$). Thus, mean harem size does not depend on observation dates and time, and interannual comparisons are reliable. Pooling all 21 years, mean harem size averaged 1.43 ± 0.91 ranging from 1 to 9 (Fig. 1) with a median harem size of one female.

Harem size and number of harems with varying adult sex ratio

In support of the first prediction, a negative relationship was found between adult sex ratio and the mean number of females held by a harem holder. Over the range of adult sex ratio that the PPNR population experienced, harem size could be predicted linearly from sex ratio (Fig. 2) by the following equation: mean harem size = 2.08–$1.26 [\pm 0.43] \times$ [adult sex ratio] ($r^2 = 0.25, F_{1,19} = 6.191, P = 0.020$). Density did not influence the slope of the relationship between adult sex ratio and harem size ($F_{1,17} = 0.005, P = 0.940$) nor did it affect the intercept ($F_{1,17} = 0.630, P = 0.430$). As further support for the first prediction, total number of harems increased with
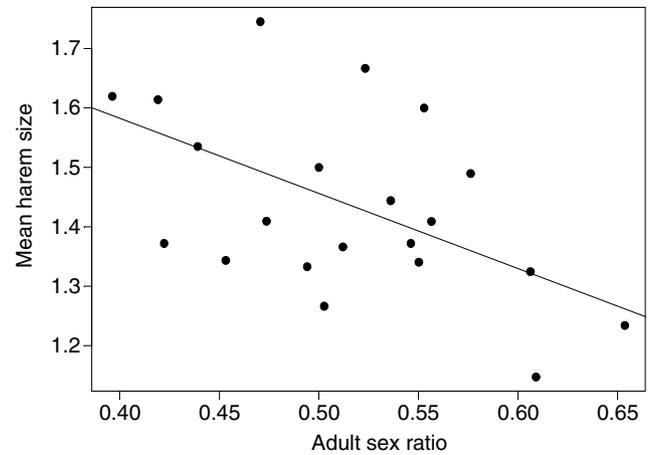

Fig. 2. Mean harem size as a function of adult *Cervus elaphus* sex ratio (i.e. number of males > 4 years of age divided by the number of males > 4 years of age plus the number of females at 2 years of age or older) for red deer during the rut in La Petite Pierre National Reserve, France. Mean harem size = $2.08 - 1.26 [\pm 0.43] \times$ [adult sex ratio]; $F_{1,19} = 6.19, P = 0.02, r^2 = 0.25$).
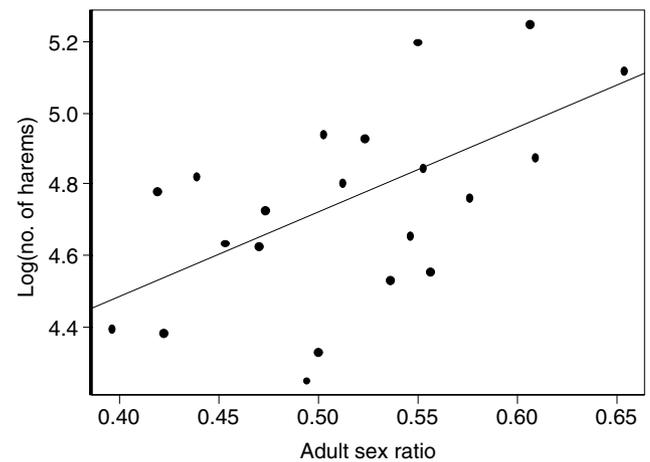

Fig. 3. Log-linear relationship between the number of harems observed and the adult *Cervus elaphus* sex ratio (i.e. number of males > 4 years of age divided by the number of males > 4 years of age plus the number of females at 2 years of age or older) during the rut for red deer in La Petite Pierre National Reserve, France (Ln (number of harems) = $3.53 + 2.37 [\pm 0.30] \times$ (adult sex ratio); likelihood ratio test: $\chi^2 = 61.69$, d.f. = 1, $P < 0.0001$ explaining 34.9% of the deviance).

increasing sex ratio. The relationship between sex ratio and the total number of harems counted (Fig. 3) was described by the following equation: Ln (number of harems) = $3.53 + 2.37 [\pm 0.30] \times$ (sex ratio) (likelihood ratio test: $\chi^2 = 61.69$, d.f. = 1, $P < 0.0001$; the regression lines accounted for 34.9% of the deviance).

Population age structure and harem distribution

As expected for polygynous ungulates (Mysterud *et al.*, 2002), a negative correlation was found between adult sex
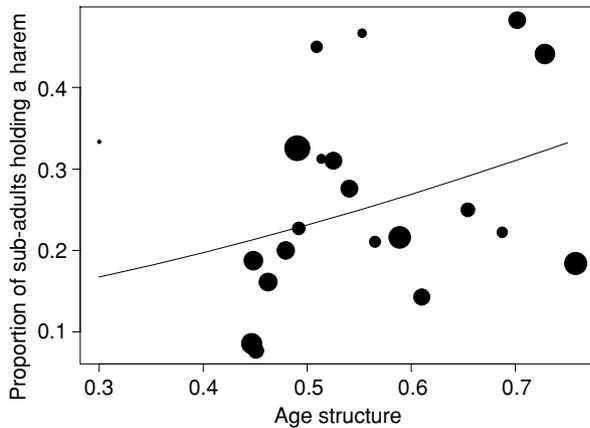
Fig. 4. Logistic regression of the proportion of sub-adult *Cervus elaphus* males that are harem holders on the population age-structure, approximated by relative abundance of sub-adults among males ($n = 561$, likelihood ratio test: $\chi^2 = 4.835$, d.f. $= 1$, $P = 0.027$ explaining 12.1% of the deviance). Dot size is proportional to the total number of sub-adult males (harem holder and non-holder) counted during the rut.

ratio and the proportion of sub-adult male deer observed during the reproductive season ($r_s = -0.572$, $n = 21$, $Z = -2.564$, $P = 0.010$). There were no significant relationships between density and age structure ($Rs = -0.077$, $N = 21$, $z = -0.339$, $P = 0.737$) or density and sex ratio ($r_s = -0.086$, $n = 21$, $z = -0.38$, $P = 0.708$). The highest proportion of young males was found when sex ratio was the most biased toward females. However, in contradiction to our second prediction, neither the proxy of population age structure we used ($\chi^2 = 0.197$, d.f. $= 1$, $P = 0.667$) nor the interaction term between sex ratio and age structure ($\chi^2 = 0.006$, d.f. $= 1$, $P = 0.935$) had any effect on mean harem size. With more sub-adults counted on the breeding site, we did not find a higher average proportion of sub-adult harem holders ($26 \pm 1.8\%$; LRT: $\chi^2 = 0.936$, d.f. $= 1$, $P = 0.333$). In comparison with the number of harems recorded during this 21 year-long study, the number of sub-adult males seen defending females was fairly low and averaged 9 ± 5 per year. The proportion of sub-adult males holding a harem decreased linearly on the logit scale as their relative abundance among males decreased: logit (proportion of sub-adults that were harem holders) $= -2.207 + 2.012$ $[\pm 0.912] \times$ (proportion of sub-adults among the males) (LRT: $\chi^2 = 4.835$, d.f. $= 1$, $P = 0.027$, $n = 561$; Fig. 4).

An increase of number of harems as the average age of males became younger was also predicted. Our results showed this occurred only when the adult sex ratio was below 0.5 (age structure × sex ratio interaction: $\chi^2 = 6.630$, d.f. $= 1$, $P = 0.010$). Above this sex ratio, the sign of the slope reversed and the number of harems during mating decreased (Fig. 5). Our second prediction was thus only partially supported by our data. By entering both sex ratio and age structure in the model of number of harems seen, it seemed that the effect of sex ratio was dependent on the age structure. When the proportion of sub-adult males is at the maximum observed in PPNR (> 55% of total male number), no relationship between sex ratio and the number of harems could be detected. However, as shown by Fig. 5, the lower the proportion of sub-adults, the steeper the increase of the number of harems with sex ratio.

DISCUSSION

Harem size, harem distribution and sex ratio

Mean harem size was shown to be negatively influenced by the proportion of males present during the rut. This observation supports previous studies relating adult sex ratio to mean harem size in several distinct populations of elk (Bender, 1996), in feral horses *Equus caballus* (Kaseda & Khalil, 1996) and in semi-domesticated reindeer *Rangifer tarandus* (Roed *et al.*, 2002). Despite the range of sex ratio of elk in Bender's (1996) study, which was similar (0.16–0.38) to that of red deer in our study (0.4–0.6), the decrease in mean harem size was of a lower magnitude in red deer (regression slope -1.45) than in elk (regression slope -46.3). Such a large difference could be explained by: (1) the interpopulation level of analysis in Bender's (1996) study contrasting with our intrapopulation level of investigation; (2) the different definition of harem used: harem encompassed bulls, calves and females in Bender's (1996) study. Alternatively, when sex ratio approached balance or became biased toward males (Skogland 1989), males would be expected to switch from harem defence to individual female defence. Indeed, the energetic demands required to hold a large harem when adult sex ratio is high exceed the reproductive advantages of holding such a large harem (Geist, 1982). The better post-rut condition of males when sex ratio is balanced (0.5) compared to when females are in excess (Bender, 1996) might support a shift from a harem defence to a tending mating tactic (defence of a single female in oestrus), with much less agonistic interactions among males at high than at balanced sex ratios (J. M. Gaillard, pers. obs. on elk). However, opposite patterns have been observed in male Dall's sheep *Ovis dalli* and Bighorn (Singer & Zeigenfuss, 2002), for which intrasexual competition, at least for adult males, was less intense when the population was biased toward females. Such discrepancies may be accounted for by the influences of adult sex ratio on reproductive effort and tactics that could depend on the average mating tactic of males (Yoccoz *et al.*, 2002). On the other hand, with an increasing proportion of males among adults, females may encounter higher levels of harassment and disturbance (Réale *et al.*, 1996), which could prevent most mating males from herding numerous females, while a few males would be highly successful by holding few large harems (see also Kaseda & Khalil, 1996).

Harem size, harem distribution and age structure

In many polygynous mammalian species, males mature physiologically as early as 1.5 years of age, but they do
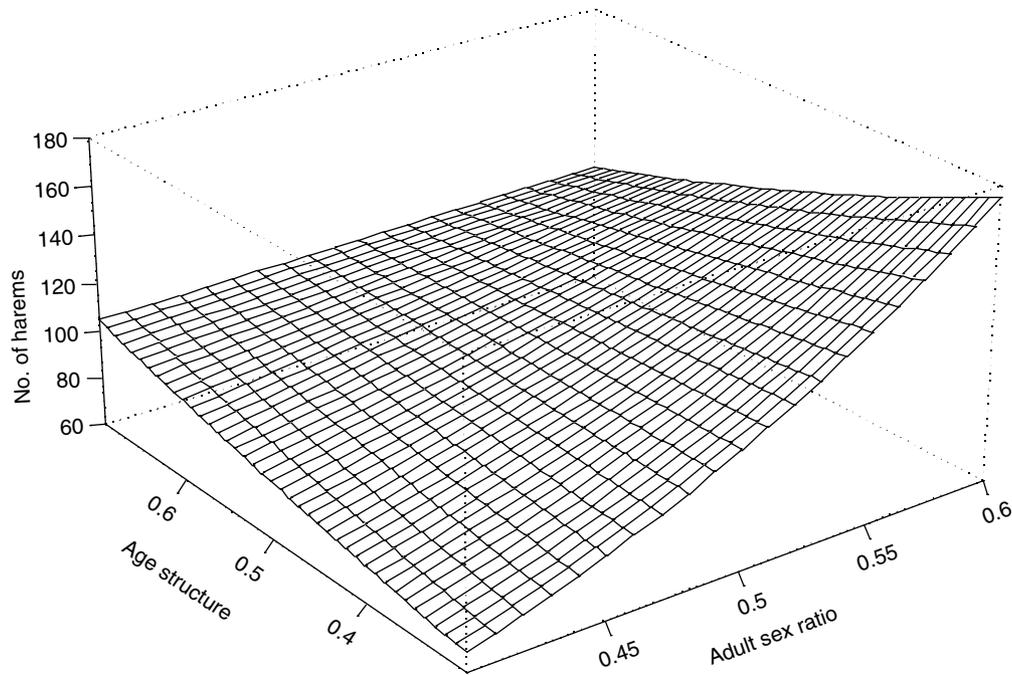
Fig. 5. Interactive effects among adult sex ratio, age-structure and number of harems observed during the rut in the red deer *Cervus elaphus* population of La Petite Pierre National Reserve, France. Adult sex ratio was calculated as the number of males > 4 years of age divided by the number of males > 4 years of age plus the number of females at 2 years of age or older. The age structure was approximated by the proportion of sub-adults (< 4 years of age) among the males.

not reach social maturity before the age of 5 or even 7 years (red deer: Clutton-Brock & Albon, 1989). In sheep, several studies have shown that yearling males may serve as much as 15% of the females (Hogg & Forbes, 1997 in bighorn; Coltman, Bancroft *et al.*, 1999 in Soay sheep). Sub-adult males may benefit from higher access to reproduction when the sex ratio becomes more biased toward females, as suggested for moose (Solberg & Sæther, 1994) and Dall's sheep (Stevenson & Bancroft, 1995). In PPNR, being a harem holder as a sub-adult male seemed to depend slightly on their relative proportion of occurrence in the male population. Despite an amount of explained deviance equal to 12.1%, this relationship can still be regarded as biologically meaningful (Møller & Jennions, 2002), but this suggests that holding a harem for sub-adult is likely to be affected by other factors. Because of the very dense vegetation cover found in PPNR (tree cover is > 80%), most cryptic behaviours of sub-adult males could not be observed, and therefore alternative strategies such as kleptogamy may have been overlooked. Without any support from genetic studies (e.g. Stevenson & Bancroft, 1995; Coltman, Bancroft *et al.*, 1999), it is only possible to conclude that sub-adult males may be more involved in reproduction when females were more numerous than males. However, we could not confirm that they indeed increase their reproductive success by doing so.

Mean harem size did not vary with changes in age structure, but the number of harems seen increased with the proportion of young males. Because density was not correlated with population age structure and sex ratio, a possible effect of increased number of females was

discarded as an explanation of more sub-adult males in rutting activities. These observations confirm instead the inability of sub-adults to form large harems (Ozoga & Verme, 1985) even when competition from older males is low. At least in PPNR, adult males outcompete sub-adults rapidly at defending a harem, this pattern being more pronounced with high adult sex ratios. Such a result supports the occurrence of a low-risk mating tactic exhibited by young ungulates that are not socially mature, as reported by Jarman (1983) for several species. Besides, emigration could also offer a way for young males to avoid the higher costs of reproduction associated with increasing sex ratio or density (Bonenfant *et al.*, 2002). However, in contrast to adult males, young red deer might face the most intense competition for mating when the adult sex ratio was the most biased towards females because of their increased opportunity to access to reproduction, as reported by Singer & Zeigenfuss (2002) on bighorn sheep.

Limitation of the sex ratio

In their review, Kvarnemo & Ahnesjö (1996) advocated using the operational sex ratio (OSR: number of males ready to mate divided by the number of males plus the number of females ready to mate) instead of the widely used standard sex ratio because OSR correctly predicts the direction and the intensity of sexual selection (Andersson 1994; Kvarnemo & Ahnesjö, 1996). However, OSR calculation requires knowledge of the observed sex ratio, the time spent in mating activities, the number of

reproductive attempts during the breeding season and the time elapsed from gamete production to weaning (Clutton-Brock & Parker, 1992), which were not known for our red deer population. It was thus supposed that the length of gestation and of the breeding and weaning season for an individual are constant from year to year in both sexes (Lincoln & Guinness 1973; Clutton-Brock, Guinness *et al*., 1982) and that changes in the OSR of our red deer population is well described by changes in our measure of adult sex ratio (for a similar approach see Stevenson & Bancroft, 1995).

Potential effects on sexual selection

The mean harem size in PPNR was much lower than usually reported for red deer. For instance a mean harem size of 3.4 was found on Rum Island, Scotland (Clutton-Brock, Guinness *et al*., 1982) and 2.77 was found in Norway (Langvatn, 1977), both of which also showed higher variance in harem size. These differences may be the result of the lower density of deer and the higher forest cover in PPNR compared to Rum (Willson & Pianka, 1963). Consequently, density and vegetation cover might affect male mating tactics through modifying both female distribution and group size (Emlen & Oring, 1977; Clutton-Brock, 1989).

Overall, harem size has been shown to be a reliable proxy of male reproductive success for synchronized breeding and non-promiscuous species (Gibson & Guinness, 1980*a,b*; Pemberton *et al*., 1992; Coltman, Bancroft *et al*., 1999) such as red deer. In our study, because females were more evenly distributed among males, we would expect decreased variance in male reproductive success as the adult sex ratio increases. Differential variance in reproductive success between sexes is a prerequisite for sexual selection to occur (Arnold & Wade, 1984; Andersson, 1994). Thus, smaller harem sizes associated with lower variance in the reproductive success of males might reflect a lesser strength of sexual selection on males as the adult sex ratio increases (Payne 1979; Wade, 1979; Sutherland, 1985).

Acknowledgements

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