

# Density-related changes in sexual selection in red deer

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## SUMMARY

In sexually dimorphic mammals, high population density is commonly associated with increased mortality of males relative to females and with female-biased adult sex ratios. This paper investigates the consequences of these changes on the distribution of male breeding success, the intensity of competition for females and the opportunity for sexual selection. After the red deer (*Cervus elaphus* L.) population of the North Block of Rum (Inner Hebrides) was released from culling, female numbers rose and male numbers declined, leading to an adult sex ratio of around one male to two females. This change was the result of increased mortality of males relative to females during the first two years of life; of increased emigration rates by young males; and of reduced immigration by males from outside the study area. The increasing bias in the adult sex ratio affected the timing of breeding as well as the distribution of mating success in males. As the adult sex ratio became increasingly biased towards females, the degree of skew in mating success (calculated across all harem-holders) increased, but mature males defended harems for shorter periods and a higher proportion of males held harems. In addition, a higher proportion of calves were fathered by immigrant males and the proportion fathered by males born in the study area declined. These results support the contention that, where high population density is associated with a female-biased adult sex ratio, competition for mates is likely to decline.

## 1. INTRODUCTION

In some polygynous, sexually dimorphic animals, males appear to be at a disadvantage in competition for scarce resources, and mortality from starvation is biased towards males, with the result that populations close to carrying capacity show female-biased adult sex ratios (Clutton-Brock *et al.* 1982). For example, in Soay sheep (*Ovis aries* L.) on St Kilda, males are more likely to die than females in the population crashes that occur every three or four years and, immediately after a crash, there are commonly six mature females to every surviving mature male (Clutton-Brock *et al.* 1991; Grenfell *et al.* 1992). Similarly, in red deer (*Cervus elaphus* L.), the cessation of the annual cull in the North Block of Rum led to higher mortality in immature males (stags) relative to females (hinds), causing an initial male bias in the adult population to change to a strong female bias (Clutton-Brock & Albon 1989; figures 1a and b).

The effects of resource shortage on male survival and on the adult sex ratio have generated speculation concerning the relationship between demography and the intensity of sexual selection. In particular, Geist (1971) has suggested that, as ungulate populations approach carrying capacity, males may be unable to expend as much energy on mating competition, with the effect that the intensity of mating competition and the intensity of sexual selection will decline. Mating competition and the degree of skew in mating success among breeding males may also decline where

adult sex ratios are biased towards females, if the number of females that successful males can defend does not increase in proportion to female numbers. For example, studies of Soay sheep on St Kilda show that, when adult sex ratios are strongly biased towards females, males less than one year old account for a higher proportion of conceptions than in years when adult sex ratios are more even (Stevenson & Bancroft 1995; Pemberton *et al.* 1996).

In this paper, we describe the effects of changes in female density and the adult sex ratio on the distribution of mating success and the opportunity for sexual selection in the red deer population of the North Block of Rum. Our analysis focuses on four main questions: (i) How does increasing density of females affect survival, emigration and immigration rates in the two sexes? (ii) How does increasing density of females affect the timing of the breeding season? (iii) How do changes in the adult sex ratio affect the harem size and the duration of harem holding by individual males? (iv) How do changes in the adult sex ratio affect the proportion of young and mature males that breed and the extent of skew in mating success among males? For the purpose of this analysis, red deer have the advantage that harem-holding males are able to guard their females effectively from marauding, non-territorial males so that visual estimates of mating success (including harem size, mating frequency and related measures) are closely correlated with genetic estimates of mating success (Pemberton *et al.* 1992; Rose 1995).

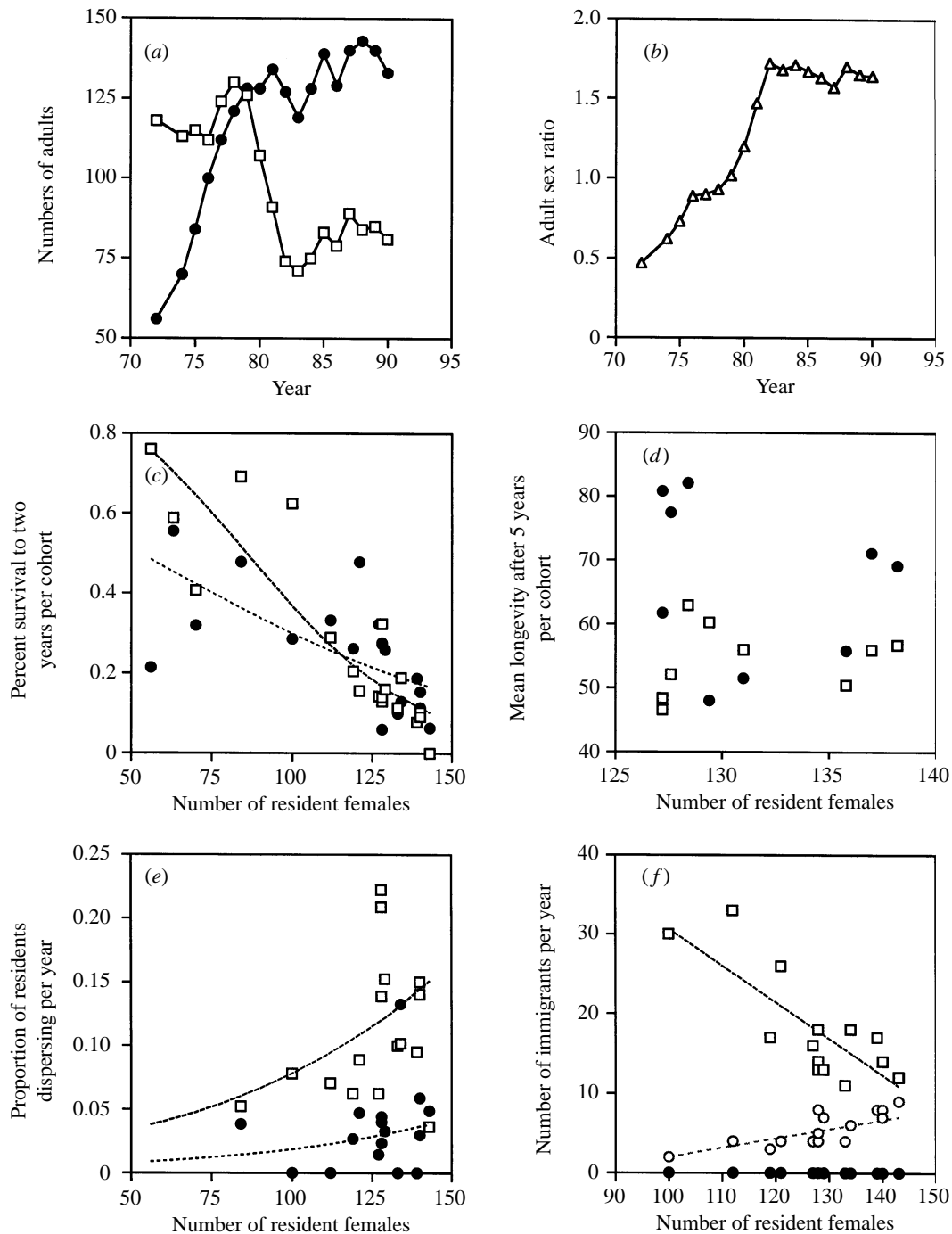


Figure 1. Demographic changes in the North Block of Rum following the cessation of culling in 1972. (a) Numbers of adults ( $\geq 2$  years) of each sex resident in the study area, 1972–95:  $\square$  males,  $\bullet$  females. (b) The sex ratio (females:males) of resident adults ( $\geq 2$  years) ( $\triangle$ ). (c) Percentage survival to 24 months for members of each cohort of calves:  $\square$  males,  $\bullet$  females. (d) Mean longevity of males and females reaching two years calculated across surviving members of each cohort:  $\square$  males,  $\bullet$  females. (e) Proportion of natal males ( $\square$ ) and females ( $\bullet$ ) of 2–6 years emigrating (permanently) from the study area each year. (f) Number of animals of all ages immigrating into the study area per year as permanent residents ( $\square$  males,  $\bullet$  females) or rut immigrants (males only,  $\circ$ ), immigrating temporarily during the rut.

## 2. METHODS

All data used in this analysis were collected in the 12 km<sup>2</sup> North Block of Rum (Inner Hebrides, Scotland), between 1972 and 1990 (Clutton-Brock *et al.* 1982). Since 1972, all the deer living in the North Block have been identified as individuals, using natural variation or artificial marks (Clutton-Brock *et al.* 1982). Most females born in the study area remain there throughout their lives, whereas around 12% of males

disperse to other parts of the island, usually between the ages of two and six years. In addition, between two and six mature males have immigrated temporarily into the study area each mating season (rut), subsequently wintering in other parts of the island.

Animals were considered to be resident in the study area if they were seen in at least 10% of censuses in any 4-month period. Residents were considered to have dispersed if they fell below this level and did not return. Female red deer

typically mate only once per oestrus, and give birth to a single calf the following May or June (Clutton-Brock *et al.* 1982). During the annual rut in October, the entire study area was censused daily (by FEG) to provide data on the number of days females spent in the harems of particular males, as well as opportunistic data on oestrus observations and copulations. Approximately 80% of neonates are caught, weighed, sexed, marked and, since 1982, sampled for genetic analysis.

Our estimates of the mating success of different stags were based on observations of the harem size of 304 stags that rutted in the study area between 1972 and 1990. For each calf born in the study area, the conception date was estimated by backdating by 235 days (the population mean gestation period, Guinness *et al.* 1978) from the calf date of birth. For an 11-day period centred on the estimated conception date (i.e.  $\pm$  one standard deviation of the gestation period), we identified each male in whose harem the mother was seen, and calculated the total number of days that each of those males was seen with the mother. A comparison of behavioural and genetic estimates of paternity in this population has demonstrated that the probability of paternity increases with the number of days that a male holds the mother during the 11-day period, and that a male holding a female for six or more days during this period has at least 90% probability of being the father (Pemberton *et al.* 1992). Unless the female was observed to have been in oestrus, the paternity of the calf was awarded to the male that held the female for the longest period during the 11-day period. In cases where the hind was in oestrous and in a harem, the paternity was awarded to the harem-holding male irrespective of the total number of days that he held the female, as oestrus observations proved to be particularly reliable indicators for paternity (Pemberton *et al.* 1992). However, these data were only available for relatively few hinds. For individual males, annual mating success was the sum of paternities awarded in this fashion for each separate mating season.

Other measures used in this analysis were as follows:

1. Population density: the number of females two years and older resident in the study area in a given year.
2. Survival: the percentage of animals in each cohort of calves that survived to different ages. The date of death of most individuals dying in the study population was known to within a month (Clutton-Brock *et al.* 1982).
3. Adult sex ratio: the ratio of resident adult females two years and older:resident males of the same age, calculated in March.
4. Number of animals immigrating/emigrating: the number of individuals that joined the study population each year, using the criteria described above. Temporary immigrants were males that were resident outside the study area but defended harems in the study area between September and November. Permanent immigrants were animals resident in the study area who had been born outside it.
5. Conception date: the estimated conception date for each female that gave birth in each year, calculated by subtracting the mean gestation length of 235 days (Guinness *et al.* 1978) from the date of birth of each calf. The annual mean conception date was calculated across all females that gave birth each year. This and other measures of the timing of reproduction were expressed as the number of days since 15 September each year.
6. Age classes: most females conceived for the first time when they were between three and four years old and reached full body weight around four years; males were fertile in their second year of life but continued growing until the age of five or six years (Clutton-Brock & Albon 1989). Calves were animals of  $\leq 12$  months; yearlings were animals of 12–24 months and, in some analyses, were combined with calves to form a juvenile category; adults were all animals  $\geq 2$  years old. Young males were 2–5 years old and mature males were  $> 5$  years old.
7. First and last day of harem-holding: in each year, we identified the first and last day on which each male was seen defending a harem. The population first day of harem-holding and last day of harem-holding were the means of these dates, calculated across all males in each age class in each year.
8. Harem size: the mean number of females seen per day with each male during the breeding season (15 September–15 November). Harem size for each age class in each year was the mean of these values calculated across all harem-holding males in that age class.
9. Number of days holding a harem: the mean number of days during the breeding season on which each male was seen defending a harem. Number of days holding for each age class for each year was the mean of these values for all harem-holders in that age class.
10. Mating success (MS): the mating success of each age class each year was calculated as the mean number of matings by all harem-holding males, including males that held females but were not awarded the paternity of a calf.
11. Immigration status: nats were animals born in the study area; immigrants were animals born outside the study area who subsequently became residents there; temporary immigrants were animals resident outside the study area for most of the year who immigrated temporarily during the rut. For analyses which included data on both individual age and immigration status, it was necessary to restrict the data to the 1976 and later ruts, as we did not know the origin of mature stags which participated in earlier ruts.

Relationships were analysed using multiple linear and generalized linear models in Genstat (Version 5.3, Genstat Committee 1993). In analyses of demographic variables we plot relationships with the number of resident females, as previous analyses suggest that measures of survival and fecundity are affected principally by female density (Clutton-Brock & Albon 1989). We use skew (Sokal & Rolf 1981) in mating success as the principal index of variation in mating success within each year. In analyses of variation in the breeding success of males we plot measures directly against the adult sex ratio, as this is likely to influence the intensity of mating competition among males.

### (a) Analysis

Continuously distributed response variables were analysed using multiple linear regression models. Initially, the 'maximal' model was fitted to the data; this included all the measures and interaction terms to be considered as explanatory variables. Each explanatory variable was then dropped from the model, unless this significantly reduced the variance explained by the model (tests of significance will be discussed below). Once no more variables could be dropped without reducing the variance explained, variables that were previously dropped were reinstated to confirm their non-significance; the most parsimonious but adequate model is termed the 'minimal' model. After the minimal model was constructed, the significance of terms was tested using  $F$  ratios (Sokal & Rohlf 1981), and these models were used to set the appropriate regression lines in figures. A regression with two explanatory variables  $X_1$  and  $X_2$  has the equation  $Y_R = a + \beta_1 X_1 + \beta_2 X_2$ , where  $\beta_1$  and  $\beta_2$  measure the average change in  $Y_R$  for a one unit change in each  $X$  variable. For

measures that were probabilities, such as survival, logistic models were employed and these were used to set the appropriate regression lines in figures. The logistic equation,  $e^z/(1+e^z)$  estimates the probability of an event occurring, with  $z = a + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_n X_n$ , where  $\beta$  represents a regression coefficient. As for standard linear models, the maximal model was reduced until the most adequate minimal model was reached. In logistic modelling, the significance of a term is measured by a change in the 'deviance', which is distributed approximately as  $\chi^2$ , with degrees of freedom equal to the change in residual degrees of freedom.

### 3. RESULTS

#### (a) *Changes in survival and the sex ratio*

After the cessation of culling in 1972, the number of resident females in the study area rose rapidly, stabilizing after 1980 (Clutton-Brock *et al.* 1985). The number of mature males initially increased, but then declined after 1980 ( $F_{1,37} = 26.21$ ,  $p < 0.001$ ; figure 1a), so that, after 1972, the adult sex ratio became progressively biased towards females, stabilizing after 10 years (figure 1b).

These changes were associated with reductions in the survival of immatures of both sexes ( $\chi^2 = 111.8$ , d.f. = 2,  $p < 0.001$ , figure 1c). However, as previous analyses have shown (Clutton-Brock & Albon 1989), the survival of immature males decreased significantly more than the survival of immature females ( $\chi^2 = 13.4$ , d.f. = 1,  $p < 0.001$ , figure 1c). No significant decrease in adult longevity after five years was observed in either sex (males  $F_{1,16} = 0.09$ ,  $p = 0.77$ ; figure 1d).

Trends also occurred in dispersal and immigration rates. As population density rose, the proportion of 2–6-year-old animals that dispersed to take up home ranges in other parts of the island increased ( $\chi^2 = 8.4$ , d.f. = 1,  $p < 0.01$ ; figure 1e). At all densities, males were more likely to disperse than females ( $\chi^2 = 64.3$ , d.f. = 1,  $p < 0.001$ ). While there was no significant interaction between female density and the sex of dispersing animals, in some years when female numbers were high, a substantial proportion of 2–6-year-old males dispersed (figure 1e). As resident female numbers rose, the number of males immigrating permanently into the study area declined ( $F_{1,13} = 22.61$ ,  $p < 0.001$ ; figure 1f), but there was an increase in the number of mature males (>5 years) immigrating temporarily into the study area during the rut ( $F_{1,16} = 4.5$ ,  $p = 0.049$ ; figure 1f). During the same period, no females immigrated into the study population (figure 1f).

#### (b) *Changes in the timing of breeding*

Rising female numbers were associated with a progressive change in the timing of breeding. As the number of resident females increased, the mean date of conception changed from 12 October to 21 October ( $F_{1,17} = 12.51$ ,  $p = 0.003$ ). This was associated with later dates of harem-holding by males; the mean first day on which males of all ages were seen holding harems changed on average from 28 September to 13 October ( $F_{1,35} = 19.89$ ,  $p = 0.001$ ; figure 2a). At all densities, young males started holding later than mature males ( $F_{1,34} = 19.51$ ,  $p < 0.001$ ), but male age interacted with

female density so that, when female density was high, the first day of harem-holding for young males became later, relative to that for mature males ( $F_{1,33} = 11.0$ ,  $p = 0.002$ ). The mean last day of harem-holding also became later overall ( $F_{1,35} = 15.7$ ,  $p < 0.001$ ; figure 2b), but was more strongly affected by rising female numbers in young than mature males ( $F_{1,33} = 8.4$ ,  $p < 0.001$ ).

#### (c) *Changes in harem holding*

As female numbers rose and the sex ratio became progressively biased, the proportion of resident males that held harems during the mating season increased ( $\chi^2 = 104.3$ , d.f. = 1,  $p < 0.001$ ) and the mean age of harem-holding males declined ( $F_{1,16} = 11.60$ ;  $p = 0.004$ ). Changes in the proportion of young and mature holding harems are shown in figure 2c, changes in the mean age of harem holders in figure 2d.

Both mean and median harem size showed no significant change as the density of hinds increased and the sex ratio became biased towards females (mean:  $F_{1,34} = 3.6$ ,  $p = 0.067$ ; median:  $F_{1,16} = 0.70$ ,  $p = 0.416$ ), though maximum harem size increased from 25 to 34 hinds ( $F_{1,16} = 5.63$ ,  $p = 0.031$ ). In addition, there was a non-significant tendency for the size of harems held by young males to increase (figure 2e). The number of days for which individuals defended harems declined as hind numbers rose and the sex ratio became biased towards females ( $F_{1,34} = 11.5$ ,  $p = 0.002$ ; figure 2f).

#### (d) *Changes in the distribution of mating success*

As female numbers rose and the sex ratio became progressively female-biased, the mean mating success of males holding harems declined ( $F_{1,29} = 5.7$ ,  $p = 0.029$ ; figure 3a). However, the overall skew in mating success (calculated across all males that held harems) increased ( $F_{1,15} = 5.51$ ,  $p = 0.034$ ; figure 3b). This was not because of any increase in maximum mating success, which did not change significantly as the adult sex ratio became progressively biased ( $F_{1,15} = 0.00$ ,  $p = 0.99$ ). Instead, the increase in skew was apparently caused by an increase in the number of relatively unsuccessful males and the proportion of matings each year that were attributed to males with low mating success increased ( $\chi^2 = 7.34$ , d.f. = 1,  $p < 0.001$ , see figure 3c).

Changes also occurred in the proportion of calves fathered by immigrant males (figure 3d). As female numbers rose and the sex ratio became progressively biased, the distribution of matings across resident, permanent and temporary immigrant males changed significantly ( $\chi^2 = 15.5$ , d.f. = 2,  $p < 0.001$ ). The proportion of matings achieved by resident stags born in the study area declined, the proportion of calves sired by temporary immigrants showed no change, and the proportion of calves fathered by permanent immigrants increased. The effect of changes in the sex ratio differed significantly between permanent immigrants and natal residents ( $\chi^2 = 10.98$ , d.f. = 48,  $p < 0.001$ ). Despite these changes, resident stags born in the study area always achieved the majority of paternities, followed by permanent immigrants then temporary immigrants ( $\chi^2 = 389.0$ , d.f. = 2,  $p < 0.001$ ).

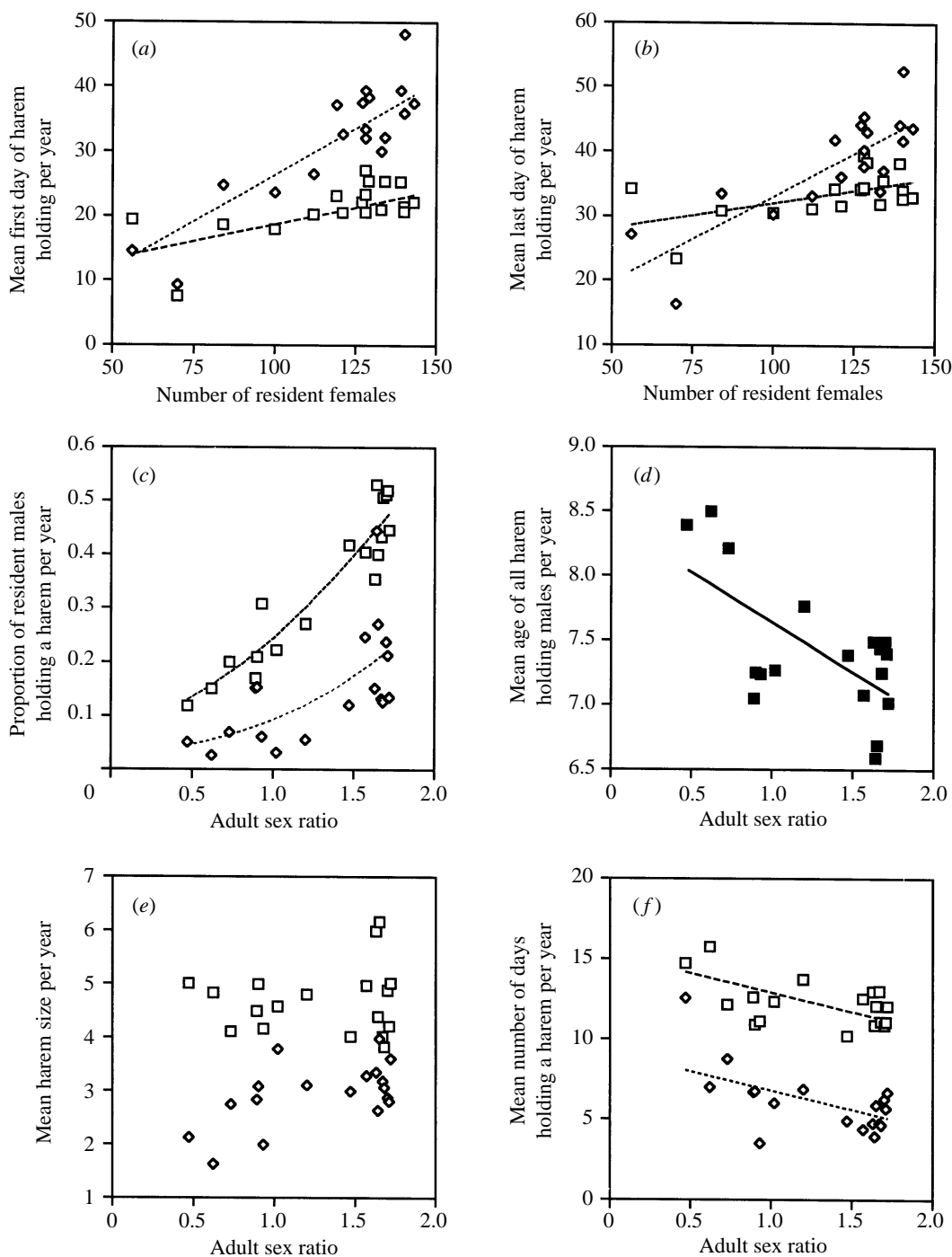


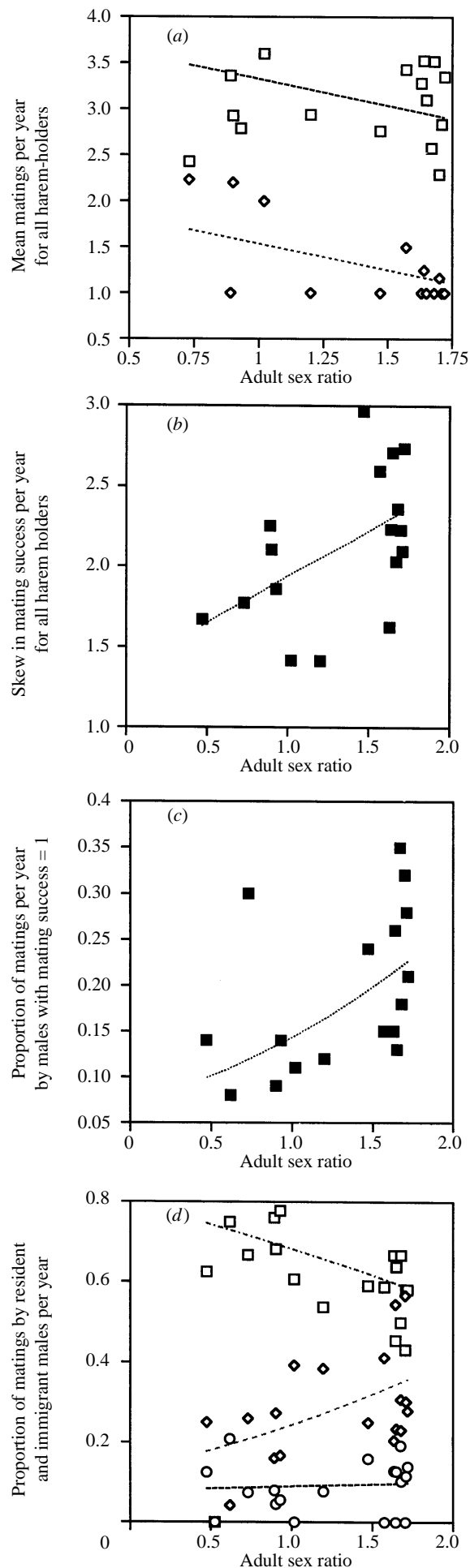
Figure 2. Changes in the timing of the rut with increasing numbers (for males of 2-5 (◇) and >5 years (□)). (a) Mean date of first day of harem-holding (see §2) (b) Mean date of last day of harem holding (see §2). (c) Proportion of resident males holding harems. (d) Mean age of harem holders (calculated across all ages). (e) Mean harem size. (f) Mean number of days per season on which individuals held harems.

As there was a decrease in the number of males immigrating permanently (see above), this represents an increase in the per capita success of immigrant stags ( $F_{1,16} = 20.91, p < 0.001$ ).

#### 4. DISCUSSION

In many dimorphic ungulates, mortality among males is higher than among females when conditions

are harsh or food availability is low (elk: Anderson 1958; Flook 1970; Peek *et al.* 1967; mule deer: Klein & Olson 1960; Robinette *et al.* 1957; reindeer and caribou: Banfield 1954; wildebeest: Talbot & Talbot 1963; tsessebe: Child *et al.* 1972; and Soay sheep: Clutton-Brock *et al.* 1991). This study provides a detailed example of this trend. This is thought to be attributable to the faster growth rates and larger body size of males, which raise their nutritional requirements



above those of females, increasing the relative susceptibility of males to starvation (Clutton-Brock *et al.* 1982, 1985, 1987). The cessation of culling of red deer in the North Block of Rum in 1972 was followed by an increase in the number of resident females and a progressive bias towards females in the adult sex ratio, which changed from 0.47 to 1.72 females per male. This occurred partly because mortality rose more rapidly in immature males than females (no consistent changes occurred in the longevity of males or females reaching maturity), and partly because the proportion of natal males emigrating increased while the number of males immigrating into the study area decreased (figures 1e and f). Increases in the number of females in the study area were associated with changes in the timing of the rut. As the number of females rose, conception dates and the timing of harem-holding by stags became progressively later, though at all stages young stags were more likely to father calves late in the rut (figure 2).

Our results suggest that the intensity of direct competition for mates declined as female density increased and the adult sex ratio became biased towards females. Thus, the mean age of males holding harems declined (figure 2d) and the proportion of young and mature males present in the study area that held harems increased (figure 2c). These changes were probably caused both by the increase in the availability of females and by a decline in the capacity of males to hold harems; the number of days for which individual males held harems declined as the adult sex ratio became progressively biased towards females (figure 2f). In contrast, the degree of skew in mating success among harem holders increased as the sex ratio became progressively biased towards hinds (figure 3b) because, at high density, an increased number of inferior males managed to hold harems, raising the proportion of males with low mating success (figure 3c).

Changes also occurred in the relative mating success of resident and immigrant stags. As female numbers rose, the mating success of permanent immigrants increased relative to that of residents (figure 3d). The most likely explanation of this trend is that the phenotypic quality of residents declined with increasing female density, while immigrants raised in other areas of the island where female numbers were maintained below carrying capacity showed superior growth and were consequently more successful in competition for females during the rut. Our previous research has shown that indices of male growth (including antler length) decline rapidly as population density increases (Clutton-Brock *et al.* 1982; Clutton-Brock & Albon 1989).

Figure 3. The distribution of mating success calculated across all males at different (adult) sex ratios: ■ all males, □ mature males, ◇ young males. (a) Mean mating success per year for all harem-holding males. (b) The skew in mating success per year, for all harem-holders. (c) The proportion of matings per year attributed to males responsible for a single mating (success = 1). (d) Proportion of matings attributed to natal residents (□), permanent immigrants (◇) and temporary immigrants (○), at different hind densities.

Our results have two main implications. First, the study suggests that the tendency for resource-limited ungulate populations to show female biases is caused by changes in the balance of immigration and emigration among males as well as by sex differences in survival. Second, our results emphasize the distinction between changes in the opportunity for sexual selection and changes in the intensity of competition between males. Our analysis suggests that the intensity of competition for mates declined at high population density: the average age of harem-holders declined (figure 2*d*) and a higher proportion of males held harems (figure 2*c*). However, these changes were associated with an increase in the degree of skew in mating success (figure 3*b*) rather than with a more even distribution of mating success as we had anticipated. Inspection of the distribution of individual values shows that the rise in skew was a consequence of an increase in the number of relatively unsuccessful males with low mating scores and maximum mating success showed no consistent change with increasing female numbers.

If competition for mating opportunities declines as populations approach carrying capacity and the sex ratio becomes female-biased, this provides a possible explanation of the widespread tendency for secondary sexual traits (such as antler or horn size) to show a low growth priority and to decrease to a greater extent than other traits when resource availability is low (Huxley 1931; Clutton-Brock *et al.* 1982). In many long-lived animals where population size is relatively stable, the ecological conditions that individuals encounter as juveniles are likely to be similar to those they face as adults. Where population density is high and resources are scarce, young males are likely to face increased costs of developing secondary sexual characters combined with reduced benefits in adulthood. This can be expected to favour the evolution of a greater sensitivity to resource shortage in the development of secondary sexual characters than in other traits.

These results are also relevant to the management of red deer and other ungulates. Red deer populations are commonly managed to maximize the number of mature males that can be culled each year. Where female numbers are permitted to rise to ecological carrying capacity, both the sustainable cull of mature males and the size of animals culled will decline (Clutton-Brock & Loneragan 1994). In addition, selection in populations maintained at ecological carrying capacity may be likely to favour early development and a reduction in the size of secondary sexual traits. As we have argued elsewhere (Clutton-Brock & Loneragan 1994), it may be necessary to control female density to maximize both the number and the quality of males that can be culled each year.

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