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THE COSTS OF REPRODUCTION TO RED DEER HINDS

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SUMMARY

(1) Successful reproduction by red deer (*Cervus elaphus*) hinds reduced the mother's body condition, survival and fecundity during the next breeding season. The effects of successful reproduction on fecundity were modified by population density as well as by the mother's age, and the birth date and sex of her calf.

(2) In contrast, successful reproduction in one year had little effect on the birth weight, survival or growth of any calf produced the following season—apparently because non-breeding (yeld) hinds lost a higher proportion of their body reserves during the winter months than successful breeders (milk hinds).

(3) Although mothers that conceived again in the year following the birth of a calf weaned their calves earlier than those that failed to breed again, this difference had no obvious effect on the survival of the previous calf.

(4) Increases in the size of matrilineal groups of hinds reduced the reproductive performance of their members. This effect should be included among the costs of successful reproduction.

INTRODUCTION

While the costs of reproduction to breeding females are most commonly measured in energetic terms, it is the effect of reproductive success on the future reproductive potential of individuals and their offspring that is the proper currency of cost when optimal life-history strategies are being considered (Pianka & Parker 1975; Gadgil & Bossert 1970; Stearns 1976; Charlesworth 1980). However, evidence of the importance and extent of these effects is rudimentary. Studies of several iteroparous vertebrates have shown that a mother's reproductive success in one year can reduce her chances of survival or her subsequent fecundity (e.g. Lack 1966; Bryant 1979; Koford 1966; Drickamer 1974; Kawai 1969; Tanaka, Tokuda & Kotera 1970; Altmann, Altmann & Hausfater 1978; Wilson, Gordon & Bernstein 1978) though this is not always the case (e.g. Smith 1981). But how does successful reproduction in one year affect the survival and growth of subsequent offspring? Is it possible that successful reproduction also affects the viability of a mother's *previous* offspring in species showing prolonged parental care? And where offspring adopt home ranges that overlap those of their mother and their sibs, does the size of the family group affect the reproductive performance of its members, as has been suggested (Clark 1978)? Clearly all three effects should be investigated before the costs of reproduction to the mother can be calculated.

In this paper, we examine the effects of successful reproduction on mothers and their offspring in an expanding population of red deer (*Cervus elaphus* L.) and investigate some

of the factors affecting these costs. We divide the potential consequences of successful reproduction into four categories:

- (i) effects on the mother's own condition, survival and subsequent fecundity.
- (ii) effects on the growth, viability and reproductive performance of any calf born in the following year.
- (iii) effects on the growth, viability and reproductive performance of any calf reared in the *previous* year.
- (iv) long-term effects on the reproductive performance of members of the hind's matrilineal group.

METHODS

The Rhum deer population

The data used in the analyses described below were collected in the North Block of the Isle of Rhum (Scotland) between 1971 and 1980 (see Fig. 1). The size and history of the Rhum deer population have been described elsewhere (Lowe 1969; Clutton-Brock, Guinness & Albon 1982). All deer using the North Block could be recognized individually either by facial characteristics or from ear tags and collars and we were able to monitor the reproductive performance of all hinds resident in this area since 1971 (Guinness, Albon &

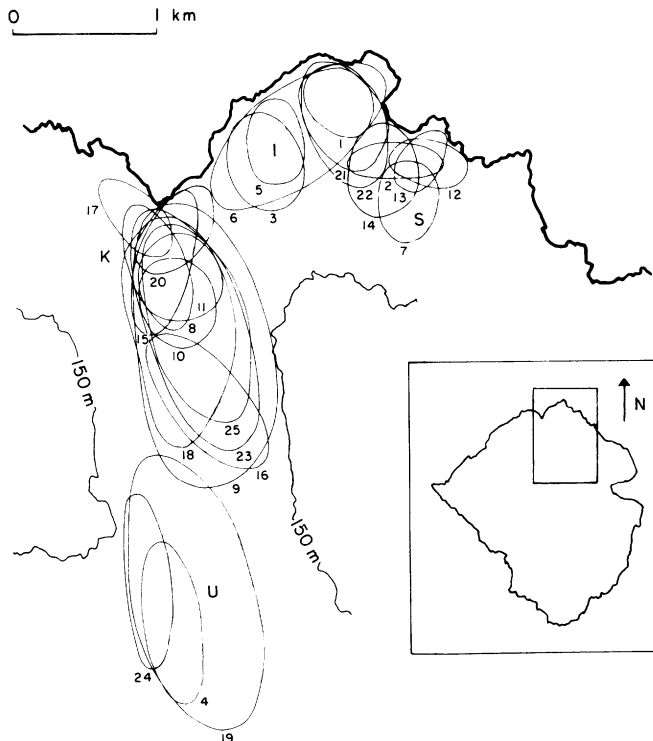


FIG. 1. The study area in the North Block of Rhum. Ellipses (1–25) show the 65% core areas of different matrilineal groups of hinds, which can be divided into four main spatial divisions (U, Upper Glen; K, Kilmory; I, Intermediate Area; S, Samhnan Insir). The core area shown is the smallest area that accounted for 65% of sightings of all members of the matrilineal group between 1973 and 1979.

TABLE 1. Number of hinds and stags resident in the North Block of Rhum 1971–1980

Year	Stags		Hinds	
	≥ 1 year old	≥ 1 year old	Milk*	Yeld†
1970/1	—	53	—	—
1971/2	124	60	23	3
1972/3	129	70	24	13
1973/4	141	78	36	8
1974/5	125	90	32	13
1975/6	129	104	38	14
1976/7	130	118	39	17
1977/8	148	127	39	24
1978/9	157	150	50	20
1979/80	135	149	40	42
1980/1	122	157	49	37

* All hinds that produced calves in the previous season and reared them through the summer months (June–September).

† All parous hinds that had either failed to conceive the previous season or had lost their calves during the summer months.

Individuals were counted as residents if they were seen in at least 10% of censuses of the study area during at least 4 months of the year.

Clutton-Brock 1978; Guinness, Clutton-Brock & Albon 1978). Since 1972, the North Block has been censused five times each month and the identity and location of all animals seen has been recorded: individuals are regarded as resident if they are seen in at least 10% of these censuses during any 4 months of the year. Culling in the area was ceased in 1972 and, since 1971/2, the population of hinds resident in the area has risen from sixty animals ≥1 year old to 157 in 1980 (see Table 1). Only after the population reached a density of twenty-five deer/km² in 1975/6 did most aspects of reproductive performance begin to show a noticeable decline (Clutton-Brock, Guinness & Albon 1982), and we consequently refer to the period 1971–1975 as low density and the period 1976–1980 as high density.

During the calving season in May and June, daily censuses of the study area provided records of the dates on which hinds calved as well as of calf mortality (Guinness, Clutton-Brock & Albon 1978; Guinness, Albon & Clutton-Brock 1978). In addition, approximately 80% of calves born to mothers resident in the study area were caught and marked within a week of birth.

Reproductive status of hinds

In any year, only a proportion of hinds calved (see Table 1): of those that failed to do so, the substantial majority had probably failed to conceive during the previous October (Clutton-Brock, Guinness & Albon 1982). Around 15% of mothers lost their calves within 2 weeks of birth and a further 10–20% during the winter, mostly between February and April (Guinness, Clutton-Brock & Albon 1978).

This permitted comparisons to be made between four categories of mothers: (i) those that had not produced a calf and had not suffered the energetic costs of either gestation or lactation (true yields), (ii) those that had lost their calf shortly after birth and had consequently suffered the costs of gestation but not lactation (summer yields), (iii) those that had reared their calves through the summer but lost them in late winter (winter yields), and (iv) those that reared them successfully till the age of one year (milk hinds).

Since both the latter two categories had suffered the heavy energetic costs of lactation while neither of the first two had done so, we combined categories (i) with (ii) and (iii) with (iv), referring to the former as yield hinds and the latter as milk hinds.

In examining the effects of the mother's reproductive status on the growth and viability of subsequent calves (section 2), we retain the terms 'milk' and 'yield' to refer to the mother's reproductive status in the season preceding the next calf's birth. Where we examine the effects of reproduction on any calf reared the *previous* year (section 3), we refer to mothers as either pregnant or non-pregnant depending on whether or not they calved in the season following the calf's birth.

Definition of variables

Variables used in comparisons were defined as follows:

Milk hind: any hind that had produced a calf during the previous breeding season and reared it until it was at least 4 months old.

Yield hind: any parous hind that had either failed to conceive the previous season or had lost her calf between June and October.

Maternal mortality: the probability that the mother will die during the year following the birth of her calf.

Fecundity: the probability of calving among hinds belonging to a particular category.

Conception date: the date on which a calf was conceived estimated by back-dating from its birth date by 234 days for female calves and 236 for male calves. Calves conceived or born before the median date for their year are referred to as early, those conceived or born after this date as late (see Guinness, Gibson & Clutton-Brock 1978).

Birth weight: the weight of the calf at birth calculated for calves caught when ≤ 14 days old, assuming a weight gain of 0.4 kg/day. Calves born below the median birth weight for their year of birth are referred to as light, those born above this weight as heavy.

Mother's age: the age of a hind in years. All individuals were incremented one year on 1st May, immediately prior to the calving season. The ages of most hinds regularly using the study area were known because individual recognition had been maintained since birth but, in a minority of cases, age estimates were based on examination of tooth wear (see Clutton-Brock, Guinness & Albon 1982).

Antler length in yearlings: the length (cm) of the antlers (excluding pedicle) of stags at 16 months old. This measure has been shown to be correlated with the yearling's body weight and body size as well as with his antler size and reproductive success as a mature stag (Clutton-Brock, Guinness & Albon 1982).

Age of first breeding females: the age at which a hind produced her first calf.

Core area: the smallest area of a hind's range that included 65% of all sightings in censuses over a given period. The method used to define this area has been described elsewhere (Clutton-Brock, Guinness & Albon 1982).

Matrilineal group: the total number of a hind's known matrilineal relatives, including her mother, sisters, aunts, nieces, grandmothers and granddaughters. Previous analysis has shown that related hinds occupy overlapping core areas, that they tend to associate with each other and that the frequency of aggression between matrilineal relatives is low (Clutton-Brock, Guinness & Albon 1982).

Analysis

Our analysis concentrated initially on comparisons between the reproductive performance of all milk and yield hinds in our sample and we subsequently sub-divided these categories to examine the effects of maternal age and population density as well as of the sex, birth date and weight of the previous calf. One limitation of overall comparisons was that, as a consequence of local variation in home range quality and population density, some hinds were consistently successful breeders while others were consistently unsuccessful. Since hinds with poor home ranges were less likely to be fecund than those with good ranges, this effect tended to be conservative, reducing the reproductive performance of yield hinds relative to milk hinds and minimizing differences between them.

To avoid this problem, we repeated analyses within hinds, comparing the reproductive performance of particular mothers in years when they were previously yield *v.* those when they had been milk. However, this was only possible when we were considering continuously distributed variables such as birth date and weight, for the life-spans of hinds are too short for comparisons of discontinuous variables (such as fecundity and calf mortality) to be meaningful. In these cases, we repeated our analyses for each of the four divisions of the study area (see Fig. 1), thus removing the principal cause of individual variation.

Frequency data cast into 2×2 contingency tables were analysed using the *G*-test, a statistic analogous to Chi-square (Sokal & Rohlf 1969). Comparisons between individual hinds were made using the Mann-Whitney *U*-test and within individual hinds using the Wilcoxon matched pairs test (Siegel 1956).

RESULTS

(1) How does successful reproduction affect the mother's condition, survival and subsequent fecundity?

Mother's body condition

Previous studies have shown that successful reproduction has a pronounced effect on the mother's body condition during the 6 months following the birth of her calf (Mitchell, McCowan & Nicholson 1976). In milk hinds, rump fat, kidney fat and total carcass weight all remain virtually steady during the course of the summer whereas in yield hinds all three measures show a pronounced increase during the same period (Fig. 2). By October, the difference in body condition between milk and yield is obvious to the experienced observer and yield hinds change into their winter coat earlier than milk hinds (Clutton-Brock, Guinness & Albon 1982).

Mother's survival

The age-specific mortality rate of milk hinds was consistently higher than that of yields during the period of our study (see Fig. 3). Of thirty-seven parous hinds that died between 1974 and 1980 (mostly in late winter or early spring: see Clutton-Brock, Guinness & Albon 1982) only seven (18.9%) were yield during the previous breeding season. Differences in survival between milk and yield hinds were most pronounced among young and old animals.

Subsequent fecundity

Overall, milk hinds showed substantially lower fecundity (68.4%) than yield hinds (89.5%) ($G = 34.4$, d.f. = 1, $P < 0.001$, $n = 562$). The difference in fecundity between milk

Costs of reproduction to red deer hinds

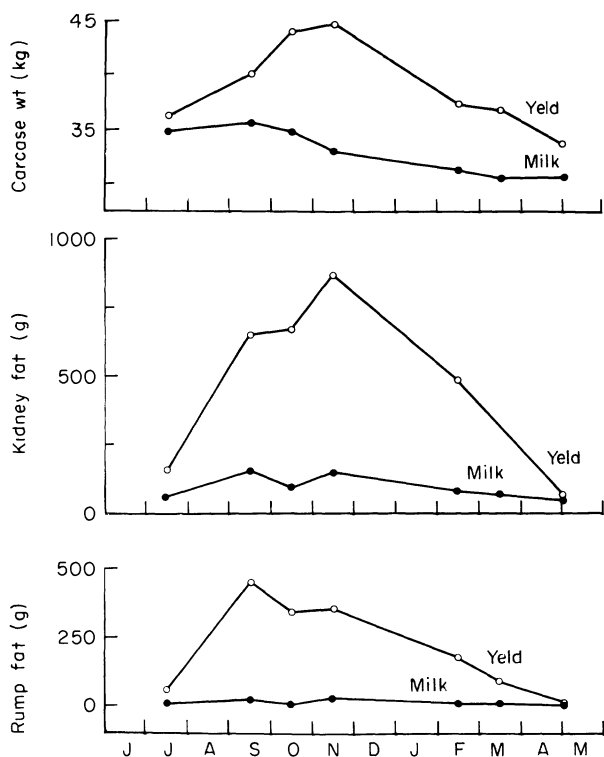


FIG. 2. Changes in carcass weight, kidney fat and rump fat in milk and yield hinds shot on Rhum (from Mitchell, McGowan & Nicholson 1976).

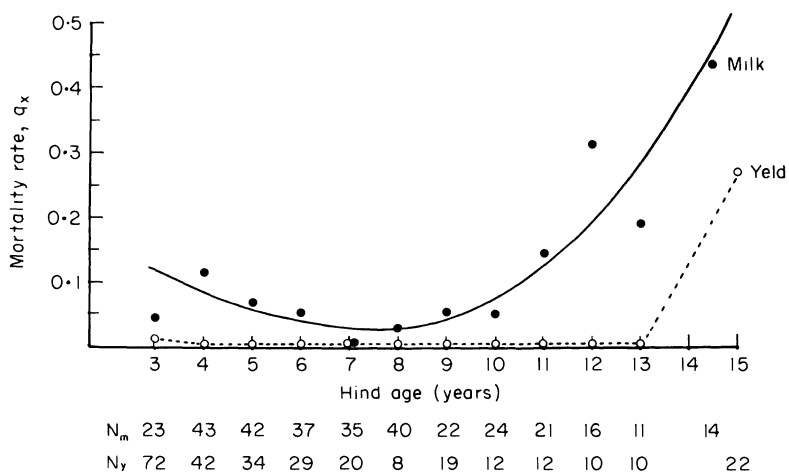


FIG. 3. Age-specific mortality rates in milk and yield hinds. Points show the proportion of milk *v.* yield hinds dying at each age, lines the (smoothed) curves based on these figures. Data from 1974–1980 combined.

TABLE 2. (a) Area-specific and (b) age-specific fecundity of milk and yield hinds, 1971–1980 (sample sizes shown in brackets)

(a) Area	Milk	Yield†
Upper Glen (U)*	76.6 (47)	100.0 (14)
Kilmory (K)	68.1 (138)	94.1 (68)
Intermediate area (I)	71.3 (101)	87.7 (57)
Samhnan Insir (S)	60.7 (84)	82.7 (52)
(b) Age (years)	Milk	Yield†
4	51.5 (33)	85.7 (7)
5	57.7 (52)	95.0 (40)
6	60.0 (50)	93.1 (29)
7	72.1 (43)	91.7 (24)
8	84.6 (39)	93.8 (16)
9	65.1 (43)	80.0 (5)
10	88.0 (25)	83.3 (18)
11	76.7 (30)	80.8 (10)
12	86.4 (22)	90.9 (11)
13	72.2 (18)	100.0 (8)
14	43.8 (16)	78.3 (23)
Total	68.4 (371)	89.5 (191)

* Areas refer to the four main concentrations of hinds shown in Fig. 1.

† Does not include first breeders.

and yield hinds was accentuated when figures were calculated separately for each of the four parts of the study area (Table 2). This was a consequence of the fact that hinds using Kilmory enjoyed consistently higher fecundity than those at Samhnan Insir, where food was less abundant (see Clutton-Brock *et al.* 1982).

The effect of successful reproduction on subsequent fecundity was most pronounced among young and old hinds (Table 2(b)): young milk hinds (4–6 years old) and old animals of over 14 years were substantially less likely to produce calves the following year than animals of 7–13 years ($G = 15.56$, d.f. = 1, $P < 0.001$; $G = 7.423$, d.f. = 1, $P < 0.01$ respectively, whereas fecundity among yield hinds did not differ between age groups.

The date on which a hind produced her calf apparently influenced her probability of calving again the following year (Fig. 4). The later a hind conceived in the previous year, the less likely she was to conceive again the following breeding season (Fig. 4). Linear regression indicated that fecundity declined by 1% for every day's delay in the conception date of the previous calf.

As we have described elsewhere (Guinness, Albon & Clutton-Brock 1978; Clutton-Brock, Albon & Guinness 1981) rearing male calves had a greater effect on their mother's subsequent reproductive performance than rearing female calves: mothers of male calves were significantly less likely to be fecund the subsequent year than mothers of female calves and rearing a male calf retarded the subsequent conception date to a greater extent than rearing a female calf. This was apparently because mothers suckled male calves more frequently than female calves. The alternative explanation that this effect was a consequence of the greater birth weight of male calves (see Clutton-Brock, Albon & Guinness 1981) appeared unlikely since mothers that produced and reared heavy-born calves were no less likely to calve again the following year than those that had reared light-born calves (Table 3).

Costs of reproduction to red deer hinds

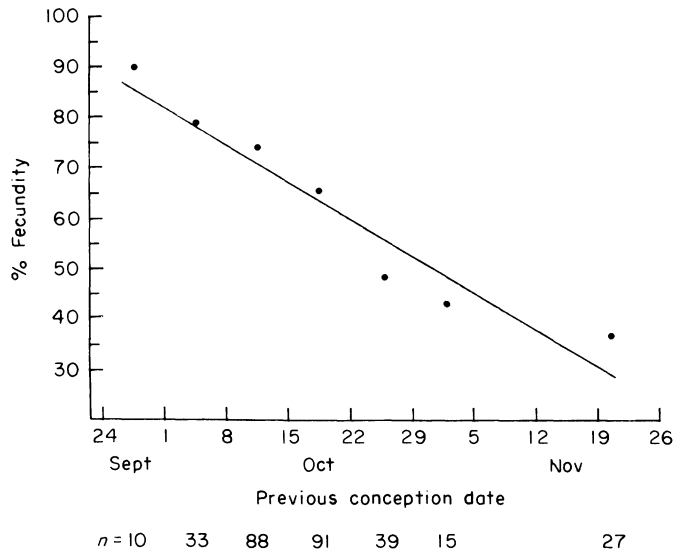


FIG. 4. The effect of conception date on fecundity in the following year among milk hinds. Conception date was calculated by subtracting the mean gestation length for male calves (236 days) and female calves (234 days) from the known birth date for the calf. Fecundity declined in milk hinds as conception date increased: $r = -0.960$, $F_{1,5} = 58.60$, $P < 0.01$, $Y = 90.24 - 1.04x$.

TABLE 3. The effect of birth weight of calf on fecundity in the following season

	Low density 1971-1975		High density 1976-1980		Overall	
	Light*	Heavy	Light	Heavy	Light	Heavy
% fecundity	80.0	81.3	52.5	57.3	60.0	63.6
Sample size	30	32	80	89	110	121

* Calves were categorized as heavy or light depending on whether or not they were above or below the median birth weight for their sex in their year of birth.

The population density of hinds in the study area modified the effect of successful reproduction on subsequent fecundity (Fig. 5). As population density increased, the fecundity of milk hinds declined while that of yield hinds was unaffected. This was partly because increased population density accentuated the effects of the mother's age: at high population density, differences in fecundity between milk and yield hinds were more pronounced among old animals (≥ 14 years old) and young animals (≤ 6 years old) than when population density was low (Table 4).

As well as influencing the probability of subsequent conception, rearing a calf affected the timing of conception and parturition. More milk hinds calved after the median birth date in each year ($G = 7.81$, d.f. = 1, $P < 0.01$: Table 5) and, overall, milk hinds calved 4 days later than yields. Again, a slightly greater effect was observed when comparisons were made within individual hinds: individuals calved, on average 7 days later when they had reared a calf the previous year compared to years in which they had not done so (Guinness, Gibson & Clutton-Brock 1978).

Like fecundity, conception date was influenced by the sex of the previous calf reared: on average, hinds calved around 11 days later in years following the successful rearing of a

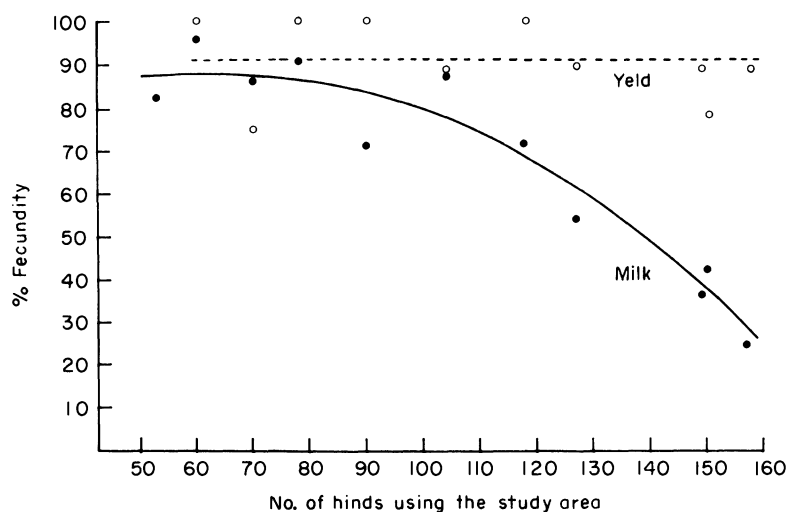


FIG. 5. Fecundity of yield and milk hinds plotted against the number of hinds (>1 year old) using the North Block between 1971 and 1981. Yield hinds: regression $F_{1,8} = 2.499$, NS (dashed line fitted through the mean, 91.0). Milk hinds: regression equation, $Y = 57.228 + 0.947x - 0.0072x^2$, $F_{2,8} = 47.86$, $P < 0.001$; $r^2 = 0.922$. Reduction in sums of squares due to inclusion of x^2 , $F_{1,8} = 9.540$, $P < 0.02$. For sample sizes see Table 1.

TABLE 4. Effects of population density on the fecundity (%) of milk hinds of different ages (sample sizes shown in brackets)

Age (years)	Low density 1971-1975		High density 1976-1980		Overall	
	Milk	Yield	Milk	Yield	Milk	Yield
4-6	75.0 (60)	92.0 (25)	42.7 (75)	94.1 (51)	57.0 (135)	93.4 (76)
7-13	91.0 (89)	95.0 (20)	67.7 (130)	87.5 (72)	77.2 (219)	89.1 (92)
14+	75.0 (4)	100.0 (6)	33.3 (12)	70.6 (17)	43.5 (16)	78.3 (23)
Total	84.3 (153)	94.1 (51)	57.1 (217)	87.9 (140)	68.4 (370)	89.5 (191)

TABLE 5. The effects of the mother's reproductive status on the birth date of her subsequent calf

	Low density 1971-1975		High density 1976-1980		Overall	
	Milk	Yield	Milk	Yield	Milk	Yield
% calving after median birth date in year	51.2	35.1	59.2	42.9	55.8	41.0
Median deviation from median birth date in year	+0.55	-3.67	+1.87	-3.83	+1.61	-2.54
Sample size	86	37	120	119	206	156

TABLE 6. Effect of calving date on calving date the following year

Date of previous birth:	Low density 1971-1975		High density 1976-1980		Overall	
	Early*	Late	Early	Late	Early	Late
% calving late the next year	52.8	53.8	48.3	65.5	49.6	61.7
Median deviation from median birth date in year	+2.00†	+1.78	+0.39	+4.00	+0.50	+2.40
Sample size	36	26	87	55	123	81

* Calving date was categorized into earlier than the median date for the year *v.* later than the median date for the year.

† All values are positive because consecutive calving tends to become progressively later.

TABLE 7. Effects of birth weight of calf on the birth date of any calf born in the following year

Weight of previous calf:	Low density 1971-1975		High density 1976-1980		Overall	
	Light*	Heavy	Light	Heavy	Light	Heavy
% calving late the following year	68.4	36.4	56.9	43.8	59.7	41.9
Median deviation from median birth date (days) of calf in the following year	+3.67	-1.50	+3.40	-0.30	+3.00	-0.62
Sample size	19	22	58	64	77	86

* Birth weight was categorized into lighter than the median weight for the year *v.* heavier than the median birth weight for the year.

male calf than in years following the successful rearing of a female calf (Clutton-Brock, Albon & Guinness 1981). At high population density, hinds that calved late in one year also tended to calve late in the following year ($G = 4.063$, d.f. = 1, $P < 0.05$: Table 6) though there was no tendency for the difference in calving date between milk and yield hinds to increase as population density rose ($r_s = 0.204$, $N = 9$, NS). Calving date was also related to the birth weight of the previous calf: overall, hinds calved later after years in which they had successfully reared a light-born calf than after years when they had successfully reared a heavy-born calf ($G = 4.359$, d.f. = 1, $P < 0.05$: Table 7).

(2) *How does successful reproduction affect the growth and viability of any calf born the following year?*

Birth weight of subsequent calf

There was no consistent difference in birth weight between the calves of milk and yield hinds when variation in birth weight between years was taken into account (Table 8). Overall, mean birth weights for calves born to milk and yield hinds were $6.75 \text{ kg} \pm 1.30$

TABLE 8. The effects of the mother's reproductive status on the birth weight of any calf born the following year

	Low density 1971-1975		High density 1976-1980		Overall	
	Milk	Yield	Milk	Yield	Milk	Yield
Mean birth weight (kg)	6.80	7.01	6.72	6.61	6.75	6.70
±S.D.	1.38	1.49	1.25	1.30	1.30	1.34
Sample size	66	23	98	88	164	111

TABLE 9. Factors affecting calf mortality

(a) The effects of the mother's reproductive status on the survival of calves during their first year of life

	Low density 1971-1975		High density 1976-1980		Overall	
	Milk	Yeld	Milk	Yeld	Milk	Yeld
% calf mortality	26.4	29.8	27.5	41.2	26.9	38.0
Sample size	125	47	120	119	245	166

(b) Differences in survival between calves born to milk *v.* yeld hinds occupying different parts of the study area (see Fig. 1) 1976-1980 (High density)

	Upper Glen		Kilmory		Intermediate area		Samhnan	Insir
	Milk	Yeld	Milk	Yeld	Milk	Yeld	Milk	Yeld
% mortality in first year of life (%)	16.7	28.6	26.7	38.5	36.4	45.5	25.0	44.4
Sample size	7	18	52	45	33	33	27	24

and $6.70 \text{ kg} \pm 1.34$, respectively. Similar results were obtained within individual hinds: in a sample of forty-one for which data were available, only twenty-three (56%) produced heavier calves when they had been yeld the previous season.

Suckling behaviour and association frequency

An analysis of a sample of suckling bouts involving 119 calves of 1-30 weeks old revealed no significant differences in the duration of suckling bouts involving the calves of milk and yeld hinds: mean bout length for milk hinds was $81.7 \text{ s} \pm 28$ compared to $80.9 \text{ s} \pm 27.3$ for yelds at 8 weeks (Cockerill 1982). Nor did the frequency with which calves associated with their mothers differ between the offspring of milk and yeld hinds (Cockerill 1982).

Calf mortality

There was no tendency for the calves of milk hinds to be more likely to die during their first year of life than those of yeld hinds (Table 9(a)). In fact, during the latter half of the study when population density was high, the calves of yeld hinds were significantly more likely to die during their first year of life than those of milk hinds ($G = 4.982$, d.f. = 1, $P < 0.05$). The direction of this effect was consistent within all the four main divisions of the study population though differences within each area did not attain statistical significance (Table 9(b)).

Calf growth (males)

The general rule that dimorphic characteristics show low growth priorities (Huxley 1932) suggests that antler development should be particularly sensitive to variation in

TABLE 10. The effects of the mother's reproductive status on the antler development (at 16 months of age) of male calves born in the subsequent year

	Low density 1971-1974		High density 1975-1978		Overall	
	Milk	Yeld	Milk	Yeld	Milk	Yeld
% male yearlings with antlers longer than the median*	56.3	37.5	48.9	46.2	51.9	42.9
Sample size	32	16	45	26	77	42

* Values calculated for each cohort and then combined.

nutrition. However, there was no tendency for the sons of yeld hinds to show greater antler development at 16 months than those of milk hinds (Table 10), nor did this analysis show any difference when it was repeated for individual hinds.

Age at first breeding (females)

In red deer hinds, body weight exerts a strong influence on the age at first breeding (Hamilton & Blaxter 1980). However, there was no evidence that the daughters of yeld hinds were more likely to conceive for the first time at a younger age than those of milk hinds. As in the case of calf mortality, a trend in the reverse direction was apparent and, in the sample overall, the daughters of milk hinds were more likely to calve as 3 year olds than those of yeld hinds ($G = 4.35$, d.f. = 1, $P < 0.05$: Table 11). Sample size was too small to allow us to repeat this analysis within the four diversions of the study area.

(3) How does successful reproduction affect the growth and viability of any calf born the previous year?

Suckling behaviour and association frequency

Hinds that became pregnant during the October rut, weaned their calves of the previous season between November and January whereas those that failed to conceive continued to suckle their calves until the following summer (Table 12). Probably as a result, the offspring of mothers that failed to conceive associated with them more frequently than those of pregnant mothers (Guinness, Hall & Cockerill 1979).

TABLE 11. The effects of the mother's reproductive status on the age at first breeding of her daughters

	Low density 1971-1974		High density 1975-1978		Overall	
	Milk	Yeld	Milk	Yeld	Milk	Yeld
% calving at 3 years	58.6	25.0	12.1	6.7	33.9	14.8
Sample size	29	12	33	15	62	27

TABLE 12. Last observed dates on which pregnant and non-pregnant hinds were seen to suckle their (previous) calves

		Pregnant	Non-pregnant
1975/6	Median	28 October, 1975 (19)	16 July, 1976 (4)
1976/7	Median	1 November, 1976 (18)	5 July, 1977 (10)
1977/8	Median	27 October, 1977 (17)	13 June, 1978 (18)

Last observed suckling dates inevitably underestimate the date of weaning. The table shows the median date of last suckling calculated across all calves that survived their first 3 months of life, sample sizes in brackets. Hinds were assumed to have failed to conceive in the autumn rut if they did not bear a calf the following year.

Mortality and growth

Hinds which conceived again during the October following the birth of a calf were no more likely to lose the first calf during the winter months than those that did not conceive again and continued to suckle their calf of the previous year (Table 13). In addition, their daughters were no less likely to calve as 3 year olds (Table 14), and their sons were no less likely to show superior antler development as yearlings (Table 15) than those of mothers who failed to conceive. Unfortunately, our data are not yet adequate to investigate differences within individuals.

(4) *Does successful reproduction have long-term effects on the reproductive performance of members of a hind's family group?*

As we have shown in previous papers, red deer hinds adopt home ranges and core areas overlapping that of their mother while son's disperse from the mother's range between the ages of 2 and 3 years (Clutton-Brock, Guinness & Albon 1982). Under these circumstances, it would seem likely that the food available to a hind and her mature daughters, as well as their reproductive performance, may decline as the size of the family unit grows (Clark 1978) and such effects could be among the most important costs of

TABLE 13. Effects of the mother's reproductive status on the survival of the *previous* calf during the winter (October–April)

	Low density 1971–1975		High density 1976–1980		Overall	
	Pregnant	Non- pregnant*	Pregnant	Non- pregnant	Pregnant	Non- pregnant
% calf, mortality during first winter (Oct–Apr)	7.0	16.7	14.5	16.1	10.7	16.2
Sample size	129	24	124	93	253	117

* Hinds were assumed to have failed to conceive in the autumn rut if they did not bear a calf the following year.

TABLE 14. Effects of the mother's reproductive status on the age at first breeding of female calves born in the *previous* year

	Cohorts				Overall	
	1971–1974		1975–1978		Pregnant	Non- pregnant
	Pregnant	Non- pregnant	Pregnant	Non- pregnant	Pregnant	Non- pregnant
% calving at 3 years	44.2	50.0	14.3	11.8	32.4	21.7
Sample size	43	6	28	17	71	23

TABLE 15. Effects of the mother's reproductive status on the antler development (at 16 months of age) of male calves born in the subsequent year

	1970–1974		1975–1978		Overall	
	Pregnant	Non- pregnant	Pregnant	Non- pregnant	Pregnant	Non- pregnant
% of male yearlings with antlers longer than the median*	57.4	38.5	43.4	60.7	50.5	53.7
Sample size	54	13	53	28	107	41

* Values calculated for each cohort and then combined.

reproduction. However, it would be over-optimistic to hope to demonstrate an effect of each successful breeding attempt on the reproductive performance of other group members and our analysis concentrates on investigating whether or not reproductive performance declines as the size of matrilineal groups increase.

The size of matrilineal groups in our study area varied from two to ten breeding hinds as a consequence of variation in group size at the onset of the study, of differences in the proportion of males produced and of variation in reproductive success. Analysis of records for forty-three hinds whose reproductive success had been monitored over at least 6 years showed that individuals belonging to groups of above average size produced fewer calves per year than those belonging to groups of below average size ($Z = 2.594$, $P < 0.01$: Table 16), an effect which was found within all four sub-divisions of the study area. In addition, across different matrilineal groups (see Fig. 1) there was a positive relationship between the first and second halves of the study period and the extent to which the mean reproductive success of their members fell ($r_s = 0.360$, $t_{23} = 1.853$, $P < 0.05$ one-tailed).

The lower reproductive success of members of large groups was partly a consequence of an increase in their age at first breeding (only 47% of them bred for the first time as 3 year olds, compared to 79% of hinds belonging to small groups), but differences in calf mortality were also involved: male calves born to hinds belonging to large groups were more likely to die during their first and second years of life than those born to hinds belonging to small groups ($G = 12.60$, d.f. = 1, $P < 0.001$; $G = 10.19$, d.f. = 1, $P < 0.01$ respectively). No similar effects were found among female calves (Table 16).

These results suggested that the more daughters a mother reared successfully, the lower their reproductive performance was likely to be. However, one other explanation had to be considered. Since the core areas of different matrilineal groups overlapped extensively (see Fig. 1), it was possible that members of large groups showed low reproductive success because the number of *unrelated* animals using their core area was higher than for members of small groups—in which case this effect should not be incorporated in any calculation of the costs of individual reproduction. However, when the number of calves reared per year by each of the forty-three hinds in our sample was regressed on the total frequency with which (a) members of her matrilineal group, (b) members of other

TABLE 16. Reproductive performance of hinds belonging to large *v.* small matrilineal groups (1971–1980)

	Members of large groups	Members of small groups
Median number of calves born per individual per year	0.695	0.847
Inter-quartile range	0.571–0.845 (16)	0.778–0.900 (16)
Median number of calves reared to 1 year old per individual per year	0.500	0.675
Inter-quartile range	0.333–0.625 (22)	0.600–0.752 (20)
% male calves dying in first year of life	36.4 (118)	16.2 (117)
% female calves dying in first year of life	22.1 (95)	24.1 (87)
% male yearlings dying	22.7 (75)	6.5 (98)
% female yearlings dying	9.1 (75)	9.3 (66)

Sample sizes shown in brackets. These vary between comparisons because complete data were not available for each individual.

matrilines were seen in her core area over the entire period of observation, it was related only to the former value ($r = -0.343$, $t = 2.249$, d.f. = 38, $P < 0.05$, $y = 8.130 - 0.0033x$; $r = 0.091$, $t = 0.503$, d.f. = 38, NS).

DISCUSSION

Our analysis emphasized the extent to which consistent individual differences in reproductive performance can confuse attempts to measure the costs of breeding. Hinds occupying poor quality home ranges were more likely both to be yeld and to show low reproductive performance than those occupying high quality ranges. Comparisons which ignored these differences inevitably underestimated the effects of breeding on reproductive performance and, in several cases, even indicated that the subsequent reproductive performance of milk hinds was superior to that of yelds. The most satisfactory approach in such cases is to compare values for the same individual under different circumstances and where this is impossible, negative results must be interpreted with caution (see Smith 1981). Estimates of the costs of breeding based on comparisons of the subsequent reproductive performance of breeders *v.* non-breeders is always likely to underestimate the true costs of reproduction to the individual.

Successful reproduction depressed the mother's subsequent condition, survival, fecundity and conception date but there was no evidence that it reduced the birth weight, growth or survival of any calf produced the following season. Why should this have been the case? The most likely answer is revealed by close inspection of seasonal changes in body condition in milk and yeld hinds (see Fig. 2). Although there were pronounced differences in condition between milk and yeld hinds in October (when conception occurred) these dwindled during the course of the winter and had almost disappeared by the following spring. This was because yeld hinds lost most of their fat during the winter months and showed a rapid decline in body weight whereas milk hinds, which entered the winter with little body fat, showed a smaller decline in weight.

The reasons for the rapid decline in the condition of yeld hinds were not obvious, though there is some evidence that similar trends may occur in domestic ungulates: ewes undernourished during pregnancy show a positive correlation between fatness at mating and fat loss during pregnancy (J. Milne pers. comm.). A possible functional explanation of this trend is that animals in poor condition reduce their metabolic rate to a greater extent than those in good condition, trading a reduction in weight loss for some other disadvantage, such as reduced ability to escape predators. However, evidence is not yet available to test this hypothesis.

Although mothers which failed to become pregnant in the October rut weaned their previous calves later than mothers that conceived, the study provided no evidence that their calves were more likely to survive or to show superior growth. However, our sample is as yet too small to repeat this analysis within individuals and it is possible that individual differences in reproductive performance could disguise any effects of pregnancy on the survival and growth of previous calves.

In contrast, the total number of female offspring that hinds reared had an important influence on the reproductive performance of the members of their matrilineal group—which declined as group size rose. Additional evidence for this effect in red deer is provided by the observation that calf/hind ratios decline as group size increases among red deer on the Scottish mainland (Mutch, Lockie & Cooper 1976). Moreover, a negative relationship between the size of matrilineal groups and the reproductive performance of

their members has been found in some other mammals (Downhower & Armitage 1971; Hoogland 1981). The increased mortality of young males compared to young females is found in many species of dimorphic ungulates under conditions of food shortage, and may be a consequence of their reduced fat reserves and faster growth rates (Clutton-Brock, Guinness & Albon 1982).

The negative relationship between group size and reproductive performance has implications in a variety of areas of ecology. It indicates that population regulation occurs at the level of the group, which is likely to contribute to population stability (see Lomnicki 1979). It suggests that in mammals forming matrilineal groups, parental investment in daughters extends after weaning, providing a possible explanation for the occurrence of male-biased birth and weaning sex ratios (Clutton-Brock, Albon & Guinness 1981; Clutton-Brock, Guinness & Albon 1982). And it predicts that, in matrilineal breeding systems, selection is likely to favour mothers that produce male-biased sex ratios in the first half of their life-span and female-biased ones in their later years.

Finally, our results indicate that the costs of reproduction vary widely and are strongly affected by many extrinsic factors—such as population density, the size of the mother's matrilineal group and the quality of the home range—as well as by a variety of intrinsic factors, including the sex, birth date and weight of the calf. This emphasizes the need for models of optimal life-history strategies (Stearns 1976) to incorporate cost functions that vary with the circumstances in which the animal finds itself.

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