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Factors affecting reproduction in red deer *(Cervus elaphus)* hinds on Rhum

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Summary. In a population of free-ranging red deer hinds on the Isle of Rhum (Inner Hebrides) we investigated relationships between four aspects of reproductive performance (fertility, calf birth weight, birth sex ratio and calving date) and four variables likely to affect the mother's condition: age, reproductive status, home range area and year of calving. Fertility was significantly related to mother's age, reproductive status and home range area as well as to year of calf's birth. Stag calves were heavier than hind calves and birth weight was significantly related to mother's age, home range area and year of (calf's) birth but not to mother's reproductive status. Birth sex ratio did not differ from parity, and was not significantly associated with any of the four variables examined. Birth date was significantly related to the mother's reproductive status, home range area and year of (calf's) birth but not to mother's age or the sex of the calf.

Introduction

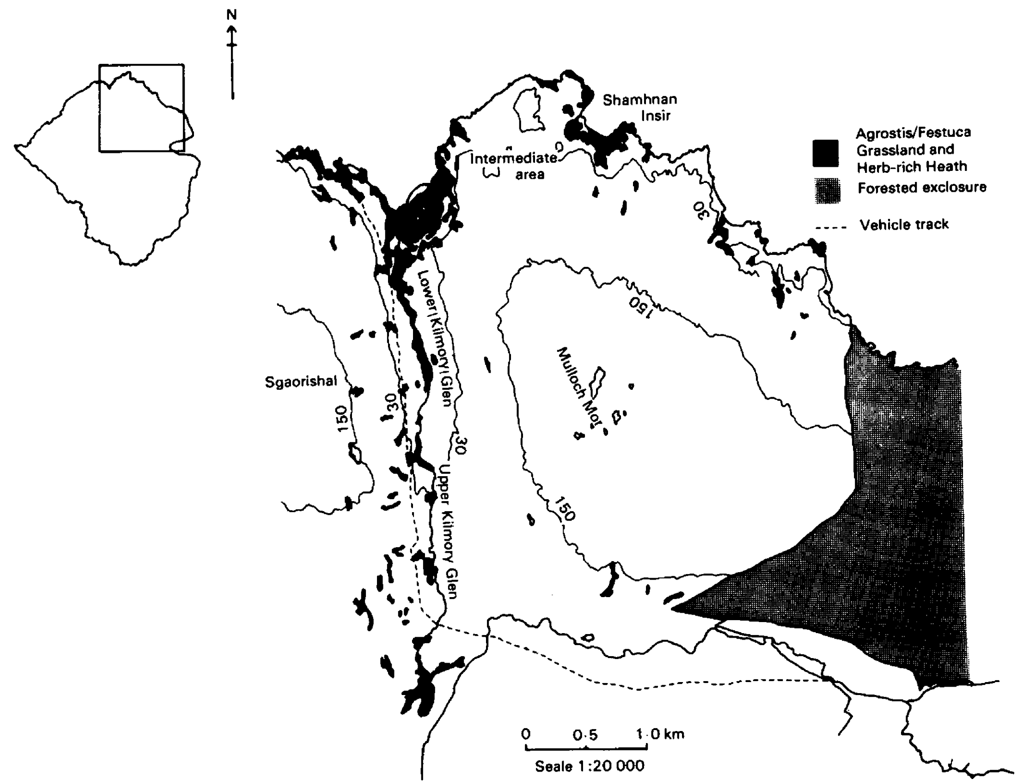
Many studies of ungulates have shown that reproductive performance is related to the mother's reproductive condition or to factors which affect this (Sadleir, 1969; Caughley, 1977). Lower pregnancy rates, lower birth weights and later birth dates tend to occur in (1) old animals compared to young (Sadleir, 1969); (2) mothers that have reared one or more offspring the previous year compared to those which have not (Mitchell, McCowan & Nicholson, 1976); (3) populations in which food supplies are sparse because the animals are living in marginal habitat or population density is high (Mitchell, Staines & Welch, 1977; Staines, 1978); (4) years when food is short compared to those when it is abundant (McCullough, 1971). However, there has so far been little attempt to compare the importance of different factors or to examine the extent to which they interact. In the present study of red deer we considered four aspects of reproductive performance, the frequency of parturition (i.e. fertility), the sex of offspring, birth weight and birth date, and examined relationships between these and mother's age, mother's reproductive status in the previous year, home range area and calf's year of birth.

Materials and Methods

Study area

All data were collected on the North Block of the Isle of Rhum (Inner Hebrides) between 1971 and 1976. Both the study area and the island have been described elsewhere (Lowe, 1969: Clutton-Brock & Guinness, 1975). The study area was divided into four parts (see Text-fig. 1). (1) Upper Kilmory Glen (3 km^2) extended from the mid-point of Kilmory Glen to the watershed at the southern end. (2) Lower Kilmory Glen (2·86 km^2) was the area from the mid-point of Kilmory Glen northwards to the sea and included the western face of Mullach Mor and the eastern face of Sgaorishal. (3) The Kilmory/Shamhnan Insir watershed (referred to as the Intermediate area, 1·96 km^2) extended from the eastern edge of Kilmory Bay eastwards to the edge of Shamhnan Insir itself. (4) Shamhnan Insir (1·35 km^2) extended from the immediate environs of the bay southwards to the top of Mullach Mor.

Population density was highest at Shamhnan Insir (18·5 hinds/km^2) and lowest in Upper Kilmory (4·3/km^2). Lower Kilmory and Shamhnan Insir included relatively large areas of *Agrostis/Festuca* and herb-rich grassland (Ferreira, 1970) which the animals strongly selected: 16·7% and 13·3% of their respective areas were covered by these vegetation types while comparative percentages for Upper Kilmory and the Intermediate area were 1·67 and 1·30 (figures calculated from Ferreira, 1970). The overall population density and the number of hinds/ha of grassland were higher at Shamhnan



Text-fig. 1. Map of the study area on Rhum, showing the distribution of *Agrostis–Festuca* and herb-rich grasslands. Contour lines show height above sea level in metres.

Insir than Lower Kilmory. Circumstantial evidence suggests that food availability was lower at Shamhnan Insir: standing crop on the herb-rich grassland was generally lower in this area (T. H. Clutton-Brock, unpublished data) and winter calf mortality was higher (Guinness, Clutton-Brock & Albon, 1978b).

Animals

The numbers of stags, hinds and calves which used the study area in each year (1971–1976) are shown in Table 1: figures were taken from census counts of the area which were repeated 5 times each month. Since 1974, the deer in the study area have not been culled; the stag population remained approximately constant while the hind population increased by 48 animals.

The following information was obtained.

Fertility, i.e. the proportion of hinds $\geqslant 3$ years of age which gave birth to calves. Whether or not a hind calved in a particular year was determined by close observation of individual hinds during the calving season (see below).

Age of dam. The ages of all hinds using the study area were known, to an accuracy of ± 1 year for older animals, from maintaining recognition of them since they were yearlings, from ear tags used

Table 1. The numbers (calculated at the end of April) of stags, hinds ⩾1-year-old and calves using the four parts of the study area in different years

Year	Deer	Upper Kilmory	Lower Kilmory	Intermediate area	Shamhnan Insir	Total
1972	Stags	26	65	5	18	114
	Hinds	8	19	18	14	59
	Calves	5	7	8	3	23
1973	Stags	21	65	10	20	122
	Hinds	9	22	20	15	66
	Calves	6	12	10	8	36
1974	Stags	30	67	13	17	127
	Hinds	8	26	17	18	69
	Calves	3	11	8	8	30
1975	Stags	29	60	7	16	117
	Hinds	9	30	21	20	80
	Calves	5	16	6	6	33
1976	Stags	25	68	7	10	110
	Hinds	11	35	28	22	96
	Calves	3	13	8	9	33
1977	Stags	19	70	12	16	117
	Hinds	13	40	29	25	107
	Calves	6	14	9	7	36

in a previous study or from tooth wear and other physical characteristics (see Guinness, Gibson & Clutton-Brock, 1978a). The ages given in the text are those of the dam at the time of giving birth; e.g. an animal which became pregnant when she was a 2-year-old and calved the following June was recorded as a 3-year-old. This usage differs from that of Mitchell (1973) who measured fertility before calving and therefore classified animals according to the year in which they conceived. In analyses involving interactions between mother's age and other variables, the age categories have been grouped as 3–4 years, 5–7 years, 8–10 years and ⩾ 11 years.

Status of dam in the year before the breeding season. Three classes of hinds were recognized: immature yeld (hinds which had never bred); yeld, i.e. 'true' yeld (mature hinds which had not given birth the previous year) and summer yeld (hinds which had borne a calf but had lost it before the end of the first September); and milk, i.e. winter yelds (hinds which had borne a calf and lost it between October and May: the majority of such calves died between February and April) and 'true' milk (animals which had successfully reared a calf the previous year). The rationale for this classification was that true yeld and summer yeld hinds had not suffered the nutritional strain of rearing a calf through the winter whereas both winter yeld and milk hinds had done so.

Home range of dam. This was the part of the study area usually occupied by the mother (see above).

Date of birth of calf. Calving was associated with an increase in udder size (Guinness, Lincoln & Short, 1971; Blaxter, Kay, Sharman, Cunningham & Hamilton, 1974), with a reduction in body size and with a variety of behavioural changes (Clutton-Brock & Guinness, 1975). As soon as these had been seen, we attempted to locate the hind and her calf. When the hind disappeared from her usual range and was later found with a calf we assumed that the birth had occurred on the day after she was last seen in her usual home range (see Clutton-Brock & Guinness, 1975). For all years except 1973 the date of birth was assessed for 95% of calves. Hinds which were not pregnant were identified by body shape and absence of a distended udder (Guinness *et al.*, 1971; Blaxter *et al.*, 1975).

Weight of calf at birth. The calves were caught with a long handled net, weighed and marked with ear flashes and/or an expanding collar. For calves marked within 24 h of birth, the weight at marking

was taken as the birth weight. For those marked ≤12 days after calving, we assumed a weight gain of 0·40 kg/day (see Youngson, 1971; Mitchell, 1971) and extrapolated back to find the birth weight of the calf.

Year of birth of each calf. Because population density was rising (Table 1), inter-year differences were confounded with density changes. Where sample size was too small to examine differences between years, we have examined whether differences existed between the first half of the study (1971–1973) when population density was relatively low and the second half (1974–1976) when it had increased (see Table 1).

Analyses

Data were drawn from a total of 91 breeding hinds. Our sample of calves was too small to allow us to analyse individual relationships and births from different hinds have been considered together, assuming each birth to be a statistically independent event. Sample size was too small to permit multi-variate statistics involving more than three variables at a time. For normally distributed variables, analyses of variance were used and for skewed distributions the Kruskal–Wallis test (Siegel, 1956). For frequency data, we employed G tests (Sokal & Rohlf, 1969) and used repeated tests to analyse relationships between three specific variables at a time. These tests were to show (i) whether two variables were significantly related or were statistically independent of each other, and (ii) whether two variables interacted in their effect on a third (see Sokal & Rohlf, 1969). Throughout the text, the terms 'independence' and 'interaction' are used in their specialized, statistical sense. Although we quote percentage figures in conjunction with the results of G tests in the text, tests were always carried out on frequencies.

Results

Fertility

Fertility varied with age, as found by Mitchell (1973) for a large sample of hinds collected from Rhum. No 2-year-old calved; 3-year-old hinds showed lower fertility than 4-year-olds ($G = 5{\cdot}228$; d.f. $= 1$; $P < 0{\cdot}05$); 4-year-olds showed lower fertility than animals of 5–10 years ($G = 5{\cdot}024$; d.f. $= 1$; $P < 0{\cdot}05$); and there was a non-significant trend to reduced fertility in hinds aged >12 years (Table 2).

Table 2. Mean percentage fertility among hinds allocated to eight age classes

	Age (years)							
	3–4	5–6	7–8	9–10	11–12	13–14	15–16	17–18
No. of hinds	66	62	56	42	29	14	4	2
% Fertility	61·7	83·7	87·5	92·9	93·5	87·5	80·0	0

As in previous studies of the red deer population of Rhum (Lowe, 1969; Mitchell, 1973), milk hinds showed lower fertility (82·2% overall) than yelds (95·5% overall) ($G = 8{\cdot}42$; d.f. $= 1$; $P < 0{\cdot}01$). However, this difference was smaller than that found in two previous studies (48·1%: Lowe, 1969; 55·6%; Mitchell, 1973). This difference between the three studies was highly significant ($G = 42{\cdot}72$; d.f. $= 1$; $P < 0{\cdot}001$; $G = 16{\cdot}07$; d.f. $= 1$; $P < 0{\cdot}001$ respectively), and was due to the lower fertility of the milk hinds studied by Lowe (1969) and Mitchell (1973). Although the data of Lowe (1969) and Mitchell (1973) were based on counts of corpora lutea, rather than of calves born as in the present study, twins are rare in red deer, suggesting that the difference in fertility between the studies was at least as great as these figures indicate.

In all years except 1973 there was a tendency for the proportion of yeld hinds to be higher among animals which had reared a male calf in the previous year (7·1–36·4% between years with a mean of

22·9%) than in those which had reared a female calf (0–26·7% with a mean of 13·4%). Differences in fertility between the two groups were significant (Wilcoxon Matched Pairs Signed Ranks Test; T = 2; $n = 7$; $P < 0{\cdot}05$). There was no evidence of any interaction between mother's age and home range area or between mother's status and home range area and fertility (see Table 3). However, mother's status may interact with age: 4-year-old milk hinds were less likely (61·5%) to be fertile than older animals (95·7%) (G = 23·673; d.f. = 1; $P < 0{\cdot}001$). Hinds using Kilmory were more fertile than the rest of the population (G = 4·082; d.f. = 1; $P < 0{\cdot}05$) and those using Shamhnan Insir were less fertile (G = 4·123, d.f. = 1, $P < 0{\cdot}05$; see Table 4). These differences were evidently not the product of inter-area differences in the ages of hinds (see Table 3) and could not have been produced by inter-area differences in reproductive status: although rather more yeld hinds occurred at Shamhnan Insir, the effect of this should be to enhance and not depress fertility (see above). The difference in fertility between Kilmory and Shamhnan Insir occurred because 3-4-year-olds at Shamhnan Insir tended to show low fertility: 4-year-old milk hinds were never observed to calve in Shamhnan Insir while 5–10-year-olds at Kilmory showed particularly high fertility. Despite the fact that area differences primarily affected young animals, there was no significant interaction between fertility, home range area and mother's age, or between fertility, mother's home range and mother's status.

Table 3. Comparisons (by 3-way G tests) for (a) fertility, dam's home-range area and dam's age and (b) fertility, dam's reproductive status and dam's home-range area

	G	d.f.	Probability
(a) Area × fertility independence	11·404	3	$P < 0{\cdot}01$
Area × age independence	10·620	9	$P > 0{\cdot}3$
Fertility × age independence	32·606	3	$P < 0{\cdot}001$
Area × age × fertility interaction	11·962	9	$P > 0{\cdot}1$
Area × age × fertility independence	66·592	24	$P < 0{\cdot}001$
(b) Area × fertility independence	5·876	3	$P > 0{\cdot}1$
Area × status independence	7·748	3	$0{\cdot}1 > P > 0{\cdot}05$
Fertility × status independence	3·434	1	$0{\cdot}1 > P > 0{\cdot}05$
Area × status × fertility interaction	1·348	3	$P > 0{\cdot}7$
Area × status × fertility independence	18·406	10	$P < 0{\cdot}05$

Table 4. Percentage fertility of deer (across years) in the four parts of the study area

	Area			
	Upper Kilmory	Intermediate	Lower Kilmory	Shamhnan Insir
No. of hinds	46	76	101	64
% Fertility (range)	82 (50–100)	79·5 (66–82·5)	86·3 (71–100)	73·7 (45·5–88·5)

The overall proportion of adult hinds calving varied between years from 72 to 92% (G = 15·332; d.f. = 5; $P < 0{\cdot}01$), being 72% in 1971 (N = 41), 92% in 1972 (N = 51), 80% in 1973 (N = 56), 92% in 1974 (N = 62), 72% in 1975 (N = 67) and 78% in 1976 (N = 80). These changes were evidently not the product of differences in either age distribution or reproductive status, and were not correlated with changes in population density.

Sex of calf

Sex ratio was slightly biased towards males in the population as a whole, although the trend was not significant: of a total of 254 calves born between 1971 and 1976 whose sex was identified, 138 (54·3%) were males ($G = 1{\cdot}902$; d.f. = 1; $P > 0{\cdot}1$). None of the factors examined had a significant effect on calf sex ratio (Table 5) and there was no evidence that interactions between variables obscured variation in the sex ratio. Contrary to traditional belief, there was no significant tendency for yeld hinds to produce male calves.

Calf weight

The weights of calves were similar to those obtained by Lowe (cited by Mitchell, 1971) from the island as a whole; and were 6·90 kg (6·76 kg: Mitchell, 1971) for stag calves and 6·44 kg (6·35 kg: Mitchell, 1971) for hind calves. Differences in calf weight between the sexes were just significant ($t = 2{\cdot}064$; d.f. = 167; $P < 0{\cdot}05$).

Birth weights of calves differed significantly according to the age category of the dam (Table 6: $F = 15{\cdot}585$; d.f. = 5,163; $P < 0{\cdot}001$). Mean calf weight increased with mother's age from first breeding to a peak in animals of 9–10 and subsequently declined.

Table 5. Birth sex ratio in different groups of red deer calves

	Calves		
	Males	Females	% males
Age of mother (years)			
3	13	13	50·0
4	17	15	53·1
5–7	49	40	55·1
8–10	35	29	54·7
11+	24	19	55·8
Reproductive status of mother			
First breeders	21	18	55·3
Yeld	34	28	54·8
Milk	78	63	53·8
Dam's home range area			
Upper Glen	19	18	51·4
Kilmory	47	42	52·8
Intermediate	36	24	60·0
Shamhnan Insir	26	27	49·1
Year			
1971	15	10	60·0
1972	24	15	61·5
1973*	13	17	43·3
1974	27	25	51·9
1975	26	23	53·1
1976	30	26	53·6

* These figures may be biased because some calves were sexed at the age of 11 months.

There was no significant difference in birth weight between the offspring of milk and yeld hinds in the overall sample ($t = 0{\cdot}443$; d.f. = 137; $P > 0{\cdot}5$), or from the median birth weights in each year (Kilmogorov–Smirnov 2-sample test, $D = 0{\cdot}13$; $n_1 = 79$; $n_2 = 33$; $P > 0{\cdot}1$). The importance of this result is that it indicates that any differences in calf mortality between the offspring of milk and yeld hinds (Guiness *et al.*, 1978b) are unlikely to be a product of differences in calf weight.

Birth weight differed significantly between hinds using different parts of the study area

Table 6. Birth weight in calves born to hinds of different ages

	Age (years)					
	3–4	5–6	7–8	9–10	11–12	13+
No. of hinds	42	35	37	25	19	14
Birth weight (tg)						
Mean	6·35	6·72	7·04	7·32	6·33	6·08
Range	3·04–8·89	2·68–9·16	4·72–10·16	2·54–11·16	4·08–8·57	4·08–7·71

($F = 5{\cdot}04$; d.f. = 3,168; $P < 0{\cdot}005$): in Upper and Lower Kilmory the calves weighed $7{\cdot}47 \pm 1{\cdot}32$ kg ($N = 16$) and $7{\cdot}01 \pm 1{\cdot}65$ kg ($N = 72$) respectively and in Shamhnan Insir and the Intermediate area they were $6{\cdot}48 \pm 1{\cdot}02$ kg ($N = 38$), and $6{\cdot}28 \pm 1{\cdot}39$ kg ($N = 45$), respectively.

Birth weight showed no significant relationship with date of birth. Calculation of the medians and interquartile ranges of birth dates for each year showed that birth weight did not differ significantly between quartiles either in the whole sample or in any particular year ($F = 1{\cdot}247$; d.f. = 3,165, $P > 0{\cdot}25$), although there was a tendency for calves born in the first and last quartiles to be heaviest. Birth weight (mean ± s.d.) apparently differed between years, being $6{\cdot}67 \pm 1{\cdot}27$ kg ($N = 15$) in 1971, $6{\cdot}73 \pm 1{\cdot}36$ kg ($N = 20$) in 1972, $7{\cdot}16 \pm 1{\cdot}68$ kg ($N = 36$) in 1974, $6{\cdot}39 \pm 1{\cdot}36$ kg ($N = 40$) in 1975, and $6{\cdot}70 \pm 1{\cdot}45$ kg ($N = 52$) in 1976, the sample size was too small to show overall significant differences ($F = 1{\cdot}253$; d.f. = 5,158; $P > 0{\cdot}25$). There was no evidence that population density interacted with mother's age, reproductive status, home range area or birth dates to affect birth weight.

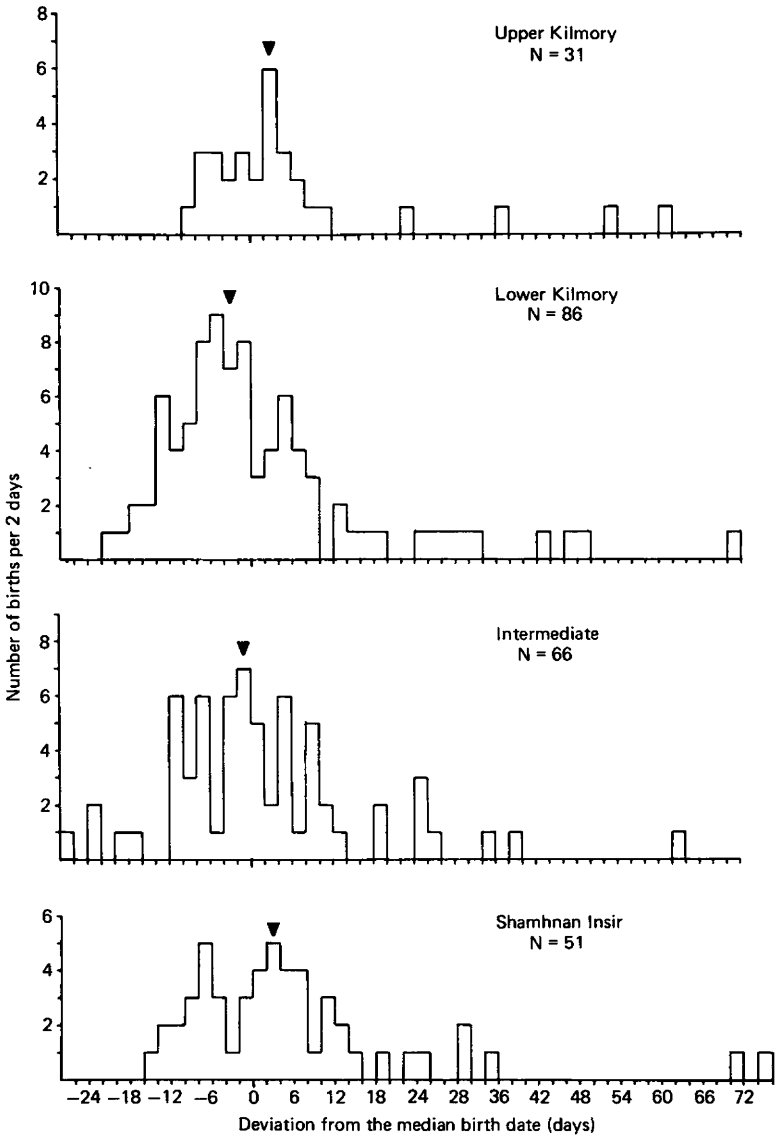
Date of birth

Date of birth was not significantly related to the sex of the calf or to the mother's age, although there was a tendency for old hinds (≥11 years) to calve later than prime animals (5–10 years) ($G = 4{\cdot}18$; d.f. = 1; $P < 0{\cdot}05$). Hinds using different parts of the study area varied significantly in their dates of calving ($G = 8{\cdot}86$; d.f. = 3; $P < 0{\cdot}05$: see Text-fig. 2), those using Lower Kilmory Glen calving earliest.

Discussion

Perhaps the most important outcome of the study was the demonstration that, within a population, the dam's home range area had an important effect on most aspects of reproductive performance, being related to fertility (especially among young animals), birth weight (especially in the offspring of yeld hinds), birth date and calf mortality (see Guinness *et al.*, 1978b). As expected, Lower Kilmory hinds, with a relative abundance of good grazing, showed high fertility, high birth weights and early birth dates. In contrast, Shamhnan Insir animals showed comparatively low fertility, late calving and low birth weights. Hinds using the Intermediate area resembled those using Lower Kilmory in birth date and those using Shamhnan Insir in birth weight. If variation in reproductive success exists within red deer populations because of differences in resource access, it is likely that increasing population density will affect the various categories of individuals differentially and have important consequences for the process of population regulation (Lomnicki, 1978).

Although most of our results were similar to those of previous studies of the Rhum population (Lowe, 1969; Mitchell, 1971, 1973; Mitchell & Lincoln, 1973; Mitchell *et al.*, 1976), some differences were obtained. For example, our estimates of the number of milk hinds calving were considerably higher than those found by Lowe (1969) and Mitchell (1973), although data from several other Highland deer forests (Mitchell, 1973) give figures as high as ours. Also, the fertility of the older milk hinds was higher in the present study than in that of Lowe (1969): in milk hinds ≥11 years of age 51 out of 56 (91·1%) calved in the present study compared with 5 out of 12 (42·5%) ($G = 7{\cdot}42$; d.f. = 1; $P < 0{\cdot}01$).



Text-fig. 2. Distribution of birth dates for red deer hinds in the four parts of the study area. The data are those for 1971–1976 and are expressed as deviations from the median birth date for each year. The overall median is indicated by the arrow.

It seems unlikely that fertility differences could be due to bias in the measurement of fertility, and the present results suggest that fertility varies according to the areas sampled. Both Lowe (1969) and Mitchell (1971, 1973) collected their samples from the whole island while ours were collected from a limited area only. Comparison of calf/hind ratios between different parts of the island for the periods 1957–1970 and 1970–1976 showed a tendency for calf/hind ratios to be higher in the northern block than elsewhere, perhaps because the area is comparatively sheltered and low-lying and the abundance of grassland is relatively high (Nature Conservancy Council, unpublished data).

Birth weights and birth dates were similar to those obtained in previous studies (Mitchell, 1971; Mitchell & Lincoln, 1973; Blaxter *et al.*, 1974), but we found no significant association between birth

date and mother's age, and birth date was not related to birth weight as at the Glen Saugh deer farm (Blaxter *et al.*, 1974). Our data, like those of Mitchell (1971), showed no significant relationship between calf sex ratio and the mother's age or reproductive success (see Caughley, 1971).

As found in previous studies (Mitchell, 1971; Mitchell & Lincoln, 1973), reproductive performance also differed widely between years although our sample size was generally too small to produce significant results. In particular, fertility and birth weight were high in 1974 and low in 1975 while birth date was significantly later in 1976, showing some recovery in 1977. These results suggest that some ecological factor (perhaps weather) affected reproductive performance in 1975. An analysis of inter-year differences in mortality on Rhum (Anderson, 1972) suggests that temperature in November –December may be important. None of the three variables we investigated was obviously related to density changes despite the rise in the number of hinds using the study area between 1971 and 1976.

The present analyses raise a number of questions which we are, as yet, unable to answer. Why does the sex of the calf influence the mother's chances of being fertile in the succeeding year? Why did the mother's reproductive status affect fertility and date of birth but not birth weight? It is hoped that an increased sample size will eventually provide the answers.

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