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Some properties of Red deer (*Cervus elaphus*) at exceptionally high population-density in Scotland

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This paper records some features of Red deer (*Cervus elaphus* L.) at very high population density on a Scottish island. About half the total population was shot-out in autumn 1974, and half the remainder in autumn 1975, with special searches for deer which had died of natural causes during the intervening year. In all, the animals examined amounted to 80% of the original population, and from the data gathered it was possible to (i) assess the structure and reproductive features of the original population; (ii) examine the level of animal performance at this exceptionally high population-density; and (iii) check for any changes in performance arising from the initial reduction in density.

The sex-ratio of adults in the original population showed a small excess of hinds, stags being apparently subject to a higher mortality rate than hinds after about six years of age. In performance, these deer were much the same as those living elsewhere on Scottish hill-land at relatively high population-density, i.e. with delayed puberty and poor breeding rates in hinds, and with much smaller adults than in woodland habitats. But, contrary to expectation, the general level of performance was not unusually low for Red deer on Scottish hill-land, and there was no evidence of transmissible diseases or excessive parasitism. It was also surprising that the animals showed no improvements in performance following their first reduction; if anything, they were slightly poorer after one year at reduced density. This may have been a temporary consequence of the severe disruption of existing behaviour patterns brought about by the sudden loss of many groups of deer.

Contents

Introduction

In this paper, some properties of Red deer (*Cervus elaphus* L.) at exceptionally high population-density on the island of Scarba (S.W. Argyllshire, Scotland) are considered, using data collected during a partial shoot-out of the population. Before the control

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operation, the deer had been almost unexploited by man for at least 10 years, and presumably had the composition and structure of a "natural" population unaffected by predation. A deer-count done on Scarba in spring 1974 had shown one of the highest population-densities of Red deer recorded on hill-land in Scotland, and for purposes of land-use it was decided to reduce the deer population to 15–25% of its density by non-selective shooting. About half the population was accounted for in autumn 1974, and half the rest in autumn 1975.

The main interest was in the properties of the deer population immediately before the control operation, i.e. in early autumn 1974. But it was also of interest to find if the performance of the deer improved after their preliminary reduction in density, i.e. by comparing the body size, condition and fertility of deer shot in the two years. For both purposes, it was a considerable advantage that the deer were shot non-selectively.

It is well known that Red deer living in exposed upland habitats in Scotland show much poorer growth and lower rates of reproductive output than those in woodland habitats in Britain, and it is reasonable to believe that much of this between-habitat variability is phenotypic. Even on Scottish hill-land, there is also evidence that performance varies with population-density (Mitchell, 1973; Mitchell, Staines & Welch, 1977; Staines, 1978), the Scarba data providing some interesting questions on this.

The island and its deer population

Scarba (latitude 56°10′N, area 1530 ha, and maximum altitude 448 m) lies about 5 km off the S.W. Argyllshire coast, amongst several other islands of which some are permanently or temporarily occupied by Red deer, with much of the neighbouring mainland ground also well populated with deer. Most of Scarba consists of quartzite, with peaty soils and rather poor forage (predominantly *Calluna* and *Molinia*). The eastern third of the island includes some black schist, with mineral soils and better grazings (herb-rich grassland), and a narrow coastal strip of woodland. It is here that domestic cattle are confined by a stock-fence, although this is no barrier to the Red deer. Superficially at least, Scarba does not seem unusually favourable as hill-land habitat for Red deer, and the only large mammalian herbivores besides Red deer and domestic cattle (*c.* 200 in 1974–5) are Fallow deer (*c.* 20 in 1974–5).

Although Whitehead (1960) concluded that Red deer are indigenous on Scarba having found no records of deliberate introductions, it is unlikely that this deer population is completely isolated and self-contained. However, movements of deer amongst the islands in this group must be quite rare and mostly involuntary, e.g. through disturbance. Local observers confirmed that live deer had appeared sporadically on some islands, presumably after swimming or drifting distances up to 1–1·5 km.

Until the early 1960s, Scarba was used for grazing sheep, and the deer were then exploited heavily for sport (deer-stalking). But since then, the island was leased for grazing cattle, and the deer population was almost ignored. A few stags and hinds were shot officially by sportsmen, and there was known to be some unauthorized killing ("poaching"), but with little effect on the population; difficulties of extracting carcases from the rough terrain may have deterred both sportsmen and poachers. The steady increase in Red deer led to concern about grazing competition, possibly to the detriment of the cattle. Therefore, following a deer-count in spring 1974 (described below), it was decided to reduce the deer population by about 75–85%.

The control operation

A deer-count done by the Red Deer Commission's field staff in spring 1974 (method described by Stewart, 1976) gave a total of 527 Red deer (165 stags, 260 hinds and 102 calves). The population-density of 344 deer/1000 ha was one of the highest yet recorded on hill-land in Scotland (average = *c.* 100 deer/1000 ha, from survey data in R.D.C. Annual Reports, 1961 onwards). By autumn 1974, the population would have increased to about 649 deer, including about 122 new calves born that summer.

In late November 1974, towards the end of the rutting season, 318 deer (105 stags, 163 hinds and 50 calves) were shot. The shooting was done over the whole island, and the animals were selected group by group until about half the total population had been shot out. Another cull of 183 deer (81 stags, 78 hinds and 24 calves) was taken in autumn 1975, accounting for about half the remaining population. In this case, groups of adult stags were taken in late August to late September (just before the rutting season), and groups of hinds with their followers (calves and young stags) in late October and November (towards the end of rutting).

Searches covering most of the island were also done in spring and summer 1975 for the remains of any deer which had died of natural causes during that year, i.e. for the carcases of animals which had been alive in autumn 1974. In all, 46 carcases were found which seemed to be from the live-population that autumn, and further searching would have shown at least a few others.

Therefore, from the total of 547 deer (199 stags, 258 hinds and 90 calves) examined, 523 of them (as 191 stags, 239 hinds and 93 calves) had been alive in autumn 1974, i.e. representing a sample of 80% from that population.

A check count done from a helicopter immediately after the shooting in autumn 1975 showed at least 86 Red deer, but the remaining population was probably a little higher than this, i.e. a little over 100.

Treatment and assessment of animals

Using much the same methods as Mitchell, McCowan & Nicholson (1976), age, jaw-bone length (as an index of skeletal size), carcase weight (apparatus shown in Plate 4, Mitchell, Parish & Crisp, 1978), condition (as a kidney-fat-index, and by % extractable fat in long-bone marrow), reproductive status (whether lactating and whether pregnant in hinds, and whether spermatogenesis occurring in stags), and weight of paired antlers in stags, in all the shot deer was assessed. For the deer found dead, it was usually only possible to assess sex, age, approximate month of death, and probable condition at the time of death. In other studies (unpublished), it was found that long-bones gave reliable indications as to whether an animal had died in good condition (e.g. by accident or shooting) or in poor condition (e.g. of exposure or under-nutrition). Long-bones from animals which died in good condition usually retained rods of fat, whereas those from animals which died in poor condition were empty or fluid-filled, and these differences persisted beyond the late stages of carcase decomposition.

Carcases and body constituents (except alimentary tracts) of all shot deer were transported to a temporary game-larder for marketing treatments and scientific work. Current venison-export regulations meant that individually-labelled offal (heart, lungs, liver, spleen and kidneys) had to be submitted with each carcase for veterinary inspection at the venison dealer's store within 24 hours of killing, and this necessitated rapid work on each animal. The only items retained for later study were jaw-bones (for age estimation), reproductive organs, mammary glands, antlers (cut off just above the skull) and metatarsals (for marrow fat measurements).

The carcase weight given in this paper is that of the fully dressed but unskinned carcase, i.e. live animal less blood, alimentary tract, head (cut off at the skull-atlas articulation), spleen, heart, liver, lungs, mammary glands, genitals, kidneys, perinephric fat and feet (from the metacarpal and metatarsal joints). By long tradition in Scotland, Red deer are also weighed as "larder carcases", i.e. complete animal less blood and alimentary tract; Table I gives conversion factors between live weight, larder carcase weight and dressed carcase with skin weight (from data in Mitchell, McCowan & Nicholson, 1976).

TABLE I

Carcase conversion factors (%) for Red deer in autumn

		Carcase type	
Class of deer	Live animal (%)	Larder carcase (live animal less blood and alimentary tract) (%)	Dressed carcase with skin (larder carcase less head, feet, heart, liver, lungs, kidneys and fat, udder and genitals) (%)
Stags (full grown)	100	73	56
Hinds (adult yeld)	100	66	52
Hinds (milk)	100	60	45
Calves	100	67	53

The two measurements of condition (kidney-fat-index = weight of perinephric fat plus kidneys/ weight of kidneys, and % fat in marrow from metatarsals by extraction with petroleum ether) were taken as a means of detecting variability in different parts of the total range of condition; KFI values are most sensitive in the upper and middle parts, and marrow fat in the lower part, of this scale. Condition measurements were not done on stags shot in 1975.

The times of shooting were particularly convenient with hinds, being late enough for most current ovulations to have occurred, but still well within the period of active lactation, and when they were at their maxima in body weight and condition. Hence it was possible to identify those hinds which had given birth the previous calving season (June) and were still lactating ("milk hinds"), and those without calves ("yeld hinds"); most yeld hinds were either sexually immature or adults which had failed to breed the previous season, but a few were thought to have been milk hinds which had lost their calves soon after calving. The presence of large corpora lutea, or early signs of pregnancy, were interpreted as potential births the following summer. Immature hinds, first breeders and fully mature hinds were easily separated on ovarian, uterine and mammary gland features, and the size of the uterine artery gave additional guidance on whether a hind had bred previously. The times of shooting were less useful with stags, being post-rut in 1974 and pre-rut in 1975, thus giving some problems of data interpretation (discussed further under Results).

Age, in this paper, is given to the nearest completed year (omitting the extra few months); animals less than one year old are called calves, and those in their second autumn of life are yearlings.

Results

Natural mortality

Over 60 carcases were detected during spring and summer 1975, but there must have been at least a few others which were less accessible. Most were in the late stages of decomposition, or as skeletal remains, the presence of jaw-bones often being the best indication of an individual. Of those found, only 46 (13 stags, 17 hinds and 16 calves) seemed to have died since autumn 1974, and the others consisted of older skeletal material which had been well-chewed and scattered by the deer; the chewing of bones and cast antlers by Red deer is well known on Scottish hill-land (Mitchell, McCowan & Parish, 1973).

Most of the adult stags and hinds found dead had flattened or well-worn cheek teeth, indicating their age, and from dental cement sections they were 8–15 years old. The calves and yearlings seemed to be stunted individuals, being significantly shorter in jaw-bone length than those shot in 1974 and 1975. Two yearling stags found dead had only barely-detectable antler buds (1–2 cm long) compared to the knobs and spikes (3–18 cm) in shot yearlings. In almost all the deer found dead, the lack of fat in their long-bones suggested that most had died in poor condition, being therefore typical of natural "winter deaths" examined elsewhere in Scotland (Mitchell & Staines, 1976). In any case, from their decompositional state, a large proportion of these animals were thought to have died in late winter or early spring. Because of advanced decomposition, it was not possible to examine any of these deer internally for information on parasites, diseases, pregnancies or lactation. However, examining carcases and organs (except, in most cases, alimentary tracts) of all the shot deer gave no indications of transmissible diseases or exceptional parasite infestations. Lymph nodes, livers, spleens, lungs and kidneys appeared "normal" in most individuals, though liver abscesses were found in a few, and the veterinary inspectors apparently found no causes for concern. The larger, and more obvious, parasites (i.e. ticks, *Ixodes ricinus*, deer keds, *Lipoptena cervi*, nostril maggots, *Cephenomyia auribarbis*, warble maggots, *Hypoderma diana*, and liver flukes, *Fasciola hepatica*) were present, and in much the same levels of infestation as found previously on the island of Rhum and in mainland study areas (Mitchell, McCowan *et al.*, 1973, and unpublished observations). Therefore, no indications were found that diseases or parasites were important as factors affecting the well-being of the population.

With such a small number of animals found dead, the age-frequency patterns (not given separately here) were rather irregular, simply showing that most natural mortality occurred in the younger (calves and yearlings) and older (above 8 years) age classes, with comparatively little in early adult life. The apparent patterns of natural mortality with sex and age are considered further below.

Composition of the original population

Table II gives a breakdown by sex, age and reproductive state of all animals obtained from the population present in autumn 1974. The number in each age class is the sum of: (i) individuals of that age shot in autumn 1974, (ii) those found dead the following year, and (iii) those of the next higher age class shot in autumn 1975. Although at least a few other natural deaths were presumably not detected, these would have comparatively little effect on the relative frequencies of the age classes. Therefore, this large sample of animals must be reasonably representative of the sex-ratio and age-composition of the original population (in autumn 1974).

Mammalian life-tables tend to have much the same general form (Caughley, 1977), being also similar to those of man-made machines (Buckland, 1964), i.e. with an initial stage of high mortality ("early failures"), relatively low mortality in middle life ("random

TABLE II

Composition of the population in autumn 1974, based on sample of 523 deer from that population

			C	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Totals
Stags	Total		48	33	26	27	33	15	16	7	13	7	3	7	3	1	0	0	0	Adults
	Immature		48	5	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	191 stags
Hinds	Total		45	38	33	37	27	25	14	20	20	6	5	5	4	3	0	2	0	239 hinds
	Lactation	Yeld	45	38	33	26	12	12	4	6	8	1	2	0	4	0	0	0	0	Milk hinds
		Milk	—	—	—	11	15	13	10	14	12	5	3	5	0	3	0	2	0	93
	Fertility	Infertile	45	38	20	13	14	8	4	7	7	3	2	5	3	3	0	2	0	Potential births
		Fertile	0	0	13*	24†	13	17	10	13	13	3	3	0	1	0	0	0	0	110

Age classes: C–16.

Notes: Milk = lactating; Fertile = with current corpora lutea or early signs of pregnancy.
*First pregnancies; †mainly first pregnancies.

losses"), and increasing mortality thereafter ("fatigue" or "wearing out"). Whilst the unknown growth-rate of the Scarba population precludes life-table calculations, the age-frequencies in Table II strongly suggest a typically mammalian pattern of survival with age. The sex-ratio in calves was almost exactly 1 : 1 (48 males: 45 females), but amongst yearlings and above the ratio was 1 stag: 1·25 hinds (191 stags: 239 hinds), with indications that stags had a higher mortality rate than hinds beyond 6 years of age, i.e. during the age-range when stags would be rutting most actively.

In the most favourable habitats, Red deer hinds can become sexually mature as yearlings, calving every year thereafter (Mitchell, Staines & Welch, 1977). Therefore, since multiple births are very rare (Mitchell, 1973), the maximum attainable birth-rate is a little over 70 calves/100 hinds (yearlings and above). On Scarba, the potential birth-rate of 46 calves/100 hinds was related to the relatively late attainment of puberty in hinds, and to the high frequency of yeld adults; only 55% of the adult (≥ 3 years) hinds were supporting calves, the other 45% being yeld. Furthermore, the low proportion of milk hinds was not apparently due to early calf-mortality, but mainly to the low pregnancy rate (58%) in adult hinds; so many hinds must have tended to breed only in alternate years, or to have been less likely to ovulate and conceive when they were already supporting calves (discussed further below). The data in Table II also give useful indications of the mortality rate from conception to the second autumn of life, i.e. by comparing the expected number of births with the numbers of calves and yearlings actually present in the autumn population. Here the expected birth-rate of 46 calves/100 hinds became reduced to 39/100 by mid autumn, and to the equivalent of 30 surviving calves/100 hinds by the following autumn. These represent losses of 15% from conception (or, more likely, from calving) to about five months, 23% from then until the second autumn of life (probably mainly over the winter), and a total of 35% from, say, calving until the end of the first winter of life.

Animal performance

Between year comparisons

Shooting out half the population in autumn 1974 meant that the remaining deer had almost a full year at reduced population-density before the final stage of the control operation. Consequently, some change in animal performance was anticipated, all other things being equal. Although detailed observations on the vegetation were impractical, the wintering conditions for cattle and sheep on neighbouring ground were said to be "about average" throughout the study period. Amongst the features assessed in each age class of stags and hinds, some could be expected to be more sensitive than others to short-term environmental changes. Jaw-bone length, for instance, would be the least sensitive indicator of change, except in the youngest (growing) deer. Similarly, the proportions of yeld and milk hinds in each age class of hinds would be of little value, being dependent on effects spread over more than a year. However, condition, antlers weight in stags, carcase weight (especially in young deer), and fertility in hinds would be more responsive to within-year effects. Finally, because of seasonal changes in some of the latter features, the time of sampling is important in making between-year comparisons. The fact that hinds were shot at much the same time in both years was an advantage, but since stags were shot later in 1974 than in 1975 more caution was required in interpreting these data; stags lose considerably in body weight and condition during the rut (Mitchell, McCowan & Nicholson, 1976).

With these considerations in mind, the two years' data were compared (using "t tests"), separately for each aspect of performance in each age class of stags and hinds. In brief, the main results were as follows. With jaw-bone length, the only class showing a significant difference was stag calves ($t=2{\cdot}38$, °F$=27$, $P=0{\cdot}05$–$0{\cdot}02$), jaw-bone length being smaller in 1975 than 1974. There was no such difference in hind calves. With carcase weight also, stag calves were significantly lower in 1975 than 1974 ($t=2{\cdot}28$, °F$=27$, $P= <0{\cdot}01$), with similar differences in fully-grown hinds ($t=2{\cdot}81$, °F$=92$, $P= <0{\cdot}001$); the other age classes of hinds also showed differences in the same direction, but these were not significant. Over most age classes, the carcase weights of stags were much more similar between the two years. Hinds were apparently in poorer condition (KFI) throughout the age classes in 1975 than 1974, the differences being significant in yearlings, 2-year-olds, 3-year-olds, and in the pooled fully-grown adults (t values$=3{\cdot}17$, $2{\cdot}34$, $2{\cdot}84$ and $2{\cdot}38$, °F$=28$, 28, 25 and 79, $P= <0{\cdot}01$, $<0{\cdot}05$, $<0{\cdot}01$ and $<0{\cdot}05$, respectively). Hinds apparently differed little in fertility between the two years, i.e. 59% (1974) and 55% (1975) of hinds ≥ 3 years with current ovulations; in fact, the slightly lower value in 1975 may have been due to the slightly earlier time of shooting (i.e. possibly missing some of the late ovulations). Weights of antlers were a little higher in 1975 than 1974, although the differences were only significant in 2 and 3-year-olds (t values, $3{\cdot}68$ and $2{\cdot}24$, °F$=20$ and 19, $P< =0{\cdot}01$ and $<0{\cdot}02$).

On balance, and against expectation, the evidence did not suggest any improvement in the deer after almost a year at reduced density. Indeed, the hinds seemed generally a little poorer in 1975 than 1974, but much larger samples would have been necessary to confirm this. This may also have been true of the stags, despite minor differences the other way in antlers. With no real change in performance, stags shot before the rut (as in 1975) should have been around 20% heavier in carcase weight than ones shot after the rut (as in 1974) (see Mitchell, McCowan & Nicholson, 1976). But there were no such differences, so the stags must have been poorer in 1975 than 1974. In fact, these findings agreed well with comments made by the stalkers at the time in handling the carcases. The deer were of much better quality than the stalkers had expected in 1974 at such a high population density, and they were thought to be lighter and leaner in 1975.

In view of the comparatively small differences between years, the performance data summarized in Tables III and IV are pooled.

Developmental and reproductive features

Red deer are at their best in body weight and condition (fatness) in autumn, adult stags being at their peak in late September (at the start of the rut), and hinds and young deer of both sexes a month or two later (during or just after the rut). All classes of Red deer are at their poorest in late winter and early spring (February to April) (Mitchell, McCowan *et al.*, 1976), and this is when most of the natural mortality occurs (Lowe, 1969; Mitchell, McCowan & Parish, 1973). Therefore, the data summarized in Tables III and IV reflect some features of the Scarba Red deer by sex, age, and reproductive status, during autumn, i.e. when most classes of deer would have been close to their best in body weight and condition. With each item measured, the age-specific means and standard deviations were linearly related, so average coefficients of variability are given in these Tables for brevity. The fact that sample size (item 1 in each Table) declines with age means that the patterns and differences are clearer amongst the young than the old deer.

TABLE III

Stags: numbers shot (total=224) and performance features

Items	Age classes C	1	2	3	4	5	6	7	8	9	10	11	12	13	Mean 5–10 years	Mean ≥11 years	Mean C.V.
Numbers shot	38	33	26	22	29	20	16	10	11	7	4	3	4	1	—	—	—
Jaw length (mm)	172	210	227	238	249	255	259	262	263	266	262	260	257	266	260	260	0·03
Carcase weight (kg)	21·5	35·1	42·9	49·1	57·7	63·6	68·1	68·8	78·4	71·6	77·4	78·4	71·4	66·2	70·1	75·4	0·15
Condition (KFI)	1·43	1·54	1·92	1·98	1·56	1·53	1·57	1·34	1·24	1·31	—	1·25	1·38	—	1·43	1·29	0·21
Antlers weight (kg)	0	0·05	0·24	0·31	0·61	0·76	1·02	1·18	1·48	1·20	1·50	1·20	1·61	1·34	1·12	1·33	0·40
Fertility (%)	0	86	94	100	100	100	100	100	100	100	100	100	100	100	100	100	—

Notes: Mean C.V. = age-class average coefficient of variability (C.V. = $\frac{\text{S.D.}}{\text{mean}}$)

KFI results from 1974, other items are means of both years.

TABLE IV

Hinds: numbers shot (total=278) and performance features

Item	Class	Age classes C	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Mean 5–10 years	Mean ≥11 years	Mean C.V.
Numbers shot	All	36	40	37	29	32	26	17	17	18	9	8	3	3	1	0	1	—	—	—
	Yeld	36	40	37	20	14	13	5	5	7	2	4	0	3	0	0	0	—	—	—
	Milk	—	—	—	9	18	13	12	12	11	7	4	3	0	1	0	1	—	—	—
Jaw length (mm)	All	169	203	221	231	237	240	242	241	241	241	240	240	234	240	—	236	241	238	0·03
	Yeld	169	203	221	230	238	243	244	241	241	238	242	—	235	—	—	—	242	235	0·03
	Milk	—	—	—	234	236	236	241	241	241	242	239	240	—	240	—	236	240	239	0·03
Carcase weight (kg)	Yeld	21·1	29·3	38·1	44·3	48·5	49·3	47·5	49·8	48·3	47·2	46·2	—	49·8	—	—	—	48·7	49·8	0·13
	Milk	—	—	—	39·3	41·3	42·5	44·9	43·5	44·5	44·1	43·7	—	—	35·4	—	31·0	43·8	33·6	0·11
Condition (KFI)	Yeld	1·40	1·57	2·35	3·40	4·21	4·19	3·75	3·37	3·24	3·38	2·67	—	2·92	—	—	—	3·64	2·92	0·36
	Milk	—	—	—	1·31	1·46	1·81	1·51	1·69	1·50	1·20	1·19	—	—	1·09	—	1·14	1·58	1·11	0·33
Udder weight (g)	Yeld	44	57	80	120	128	109	143	135	116	157	—	120	—	—	—	—	132	120	0·26
	Milk	—	—	—	368	378	353	408	389	459	571	461	261	—	435	—	323	419	325	0·25
Fertility (%)	All	0	0	39	64	47	65	71	63	65	56	60	0	25	0	—	0	70	25	—
	Yeld	0	0	39	70	86	83	80	100	88	100	100	—	25	—	—	—	93	25	—
	Milk	—	—	—	50	17	38	67	45	50	43	33	0	—	0	—	0	56	0	—

The broad patterns of change with age in stags and hinds shown by our data are much the same as those found in other Red deer populations in Scotland (Lowe, 1969, 1971; Mitchell, 1973; Mitchell, Staines *et al.*, 1977; and Staines, 1978) and in Europe (e.g. in Germany by Raesfeld & Vorreyer, 1964; and in Poland by Dzięçiołwski, 1970). In essence, the life of a Red deer consists of three distinct stages: (i) growth and development (up to about 5 years); (ii) a period of maximum body weight, condition and reproductive efficiency (5–10 years); and a period of progressive decline (above 10 years). Only some of the features of the Scarba deer require extra comment here, and the differences between populations in Scotland are considered below.

As elsewhere, the stags and hinds on Scarba clearly differed in their growth rates, in their maximum body sizes, and in the ages at which they were at their best in body weight, condition and reproductive efficiency. Differences in body size (jaw-bone length and carcase weight) were smallest in the early years of life and greatest amongst adults, fully-grown stags being 1·5 times as heavy as fully-grown hinds. Stags were at their best in body weight (7 to 9 years), and presumably also in condition (see below), a little later in life than hinds (5 to 7 years), but seemingly with some asynchrony amongst various aspects of performance; in stags, for example, maximum antlers weight occurred later in life than maximum body weight. Kidney-fat indices in stags were measured only in those shot in 1974 (post-rut), thus giving only poor indications of the real changes in condition with age; adult stags would have shown much higher KFI values before the rut, as found on Rhum (Table 1 in Mitchell, McCowan *et al.*, 1976) and at Glen Feshie (Table 8 in Mitchell, Staines *et al.*, 1977; and Mitchell & Parish, in preparation). Even so, there were significant correlations within each age class of both stags and hinds between KFI and carcase weight (see also Mitchell, 1973), and, between age classes of hinds, KFI clearly changed in parallel with carcase weight. The marrow-fat results (not given here) showed no distinct patterns with sex and age, few individuals (i.e. a few very poor calves and two-well-rutted stags) having fat concentrations of less than 85%. In fact, these measurements were taken on the expectation of extremely low performance and condition in the Scarba deer, which, as discussed further below was not the case.

Once again, much as found in other Scottish populations (Mitchell, 1973; and Mitchell & Brown, 1974), there were clear relationships between reproductive features and body weight (or weight and condition together). With stags, puberty occurred mainly in yearlings, but there were small numbers of sexually-immature two and three-year-olds. Stags were mostly sexually immature and had small skin-covered antler-buds below a dressed carcase weight of 35 kg (approximate live-weight = 73 kg), but mature with hard antlers above this weight. Puberty occurred later, and was spread over several age classes, in hinds. There were no sexually mature yearling hinds, and only 39% of the two-year-olds were mature. Whilst a few hinds apparently reached puberty as four-and five-year-olds, the majority became sexually mature as three-year-olds, the critical dressed carcase-weight being about 40 kg (approximate live wt = 85 kg). Adult hinds differed in carcase weight, condition and fertility according to whether they were "milk" (supporting a current calf) or "yeld" (with no calf), the latter being higher in weight condition and fertility than the former. It seemed that the ability to ovulate and conceive depended on carcase weight and condition, and, again, the critical values for breeding were about 40 kg in dressed carcase-weight (approximate live wt = 85 kg) and about 1·8 in KFI. These findings were based on data inspection; much larger samples (especially of non-fertile adults) would have been required for the kind of multivariate analysis done by Mitchell & Brown (1974), but the patterns were clear enough anyway. Clearly, therefore, on Scarba as on other areas of hill-land in Scotland, a fairly large proportion of the hinds must have tended to breed successfully in alternate years, or to have bred for a year or two and lost sufficient condition to make breeding in the next year much less likely. Presumably, this was a consequence of a nutritionally poor environment.

Comparative aspects of performance

Up to now, aspects of performance have been assessed in nine different populations of Red deer on Scottish hill-land, i.e. on the isle of Rhum by Lowe (1969, 1971) and Mitchell, McCowan *et al.* (1976), at Invermark, Glen Fiddich, Ross of Mull, Fiunary, Glen Prosen and Glen Feshie by Mitchell (1973), Mitchell, Staines *et al.* (1977) and Mitchell & Parish (in preparation), at Glen Dye by Staines (1978), and on Scarba by ourselves. These studies were made over different spans of years, and they varied considerably in measurements taken and in sampling intensity, thus making detailed comparisons both complex and tedious. However, some comparisons (mainly on hinds) were done by Mitchell (1973) and Mitchell, Staines *et al.* (1977), and others (on both sexes) by Staines (1978). These results suggested firstly that different aspects of performance were correlated, and secondly that differences in performance between populations were associated with differences in population density. For example, early sexual maturation was associated with good growth, especially in young deer, and those populations with pregnancies in yearling hinds also showed high pregnancy rates in milk hinds. Weights of calves soon after birth also seemed to depend on the growth rates of hinds (Mitchell, 1971). High performance was associated with low population density, the lowest density population (at Glen Dye) having the highest pregnancy rate in yearling hinds and the highest carcase weights in young hinds generally (Staines, 1978).

With the Scarba data, therefore, interest was concentrated on finding if these deer showed unusually low performance associated with their exceptionally high population density. For this purpose, the populations were simply ranked according to their relative values (in each sex and age class) in jaw-bone length, carcase weight (using conversion factors where necessary), antlers weight in stags (where available), and various measures of reproduction in hinds (e.g. pregnancy rates in yearling hinds and milk hinds). With carcase weights of yearling hinds, for example, Glen Dye came out at the top of the list, and Glen Feshie at the bottom, and much the same patterns were found in most other items of comparison. The detailed results are unnecessary here, and our main finding was that the three highest density populations (Rhum and Glen Feshie, both *c.* 130 deer/1000 ha, and Scarba, 344 deer/1000 ha) were at the bottom of the performance scale, and Glen Dye (mean density = 16 deer/1000 ha) at the top (see also Figs 2 and 3 in Staines, 1978). The three highest density populations were characterized by their lack of pregnancies in yearling hinds, by their relatively low pregnancy-rates in milk hinds (*c.* 50%), and by their lower jaw-bone lengths and carcase weights in most age classes of stags and hinds (especially amongst the youngest age classes). Comparing these three high-density populations, however. showed Glen Feshie as the lowest in performance, Rhum next, and Scarba as the highest. Glen Feshie and Rhum were closest in most aspects of performance, with average differences in carcase weight of 5–7%. In carcase features, the Scarba deer were appreciably better than the Rhum deer, with average differences in carcase weight of almost 9%. Clearly, therefore, the Scarba Red deer were not the poorest in performance of the Scottish populations studied up to now.

For technical reasons, few estimates of birth-rates exist for Red deer on Scottish hill-land, and these may not all be strictly comparable because of differences in methodology. However, those that have been published are all of the same order. Lowe (1971), using a population reconstruction, estimated the birth-rate on Rhum at 37·6–42·5 calves/100 hinds, and, by the same method, Mitchell & Parish (in preparation) found 43 calves/100 hinds at Glen Feshie. Partial shoot-outs of Red deer during autumn at Fiunary and Ross of Mull both gave about 46–47 calves/100 hinds. The Scarba value (*c.* 46 potential births/100 hinds) falls into this range. In view of the earlier puberty and higher pregnancy rate of milk hinds in the lowest density populations on Scottish hill-land, some values of 50–60 calves/100 hinds could be expected, although this has to be confirmed.

Final comments

It seemed quite reasonable to expect that the exceptionally high population-density of Red deer on Scarba would have led to a much poorer-than-average level of animal performance (and perhaps to an unusually high incidence of transmissible disease or parasitism) for deer in this kind of habitat, and the impressions of the island itself merely reinforced this expectation; Scarba seemed fairly typical of the poor-quality hill-land on which most of Scotland's Red deer live. But, in neither performance nor health were the Scarba deer markedly atypical, being a little better in performance than the deer in two other areas of only moderately high population density, and with no signs of disease or excessive parasitism. There are two possible explanations. Animal performance must depend on the combined effects of several environmental factors, e.g. habitat quality and population density. Habitat quality is difficult to measure objectively, and the authors' subjective impressions on Scarba could have been misleading, although this is doubtful. Alternatively, it may be that there is little further change in animal performance above a certain density level on this kind of ground, or, possibly, that such responses depend on time; the Scarba population had been increasing steadily over the previous 10 years or more.

The authors were also surprised at the apparent lack of improvement in the deer following their first reduction in population-density; the remaining deer had almost a full year at half their earlier density, presumably with less competition for the best forage. If anything, the deer were slightly poorer in autumn 1975 than autumn 1974, and with no evidence of changes in either wintering conditions or shooting practice to explain this. In one minor respect, however, the shooting could have affected the apparent performance in yearling deer. Any calves orphaned by the shooting in autumn 1974 would have become rather poor yearlings in autumn 1975, but there could have been only a few of these. The most likely explanation is in the effects of the sudden loss of so many groups of deer on the behaviour of the survivors. Learned traditions seem important in the home-range behaviour and dispersion patterns of Red deer, as indicated by their slow adaptation to new features of their environment, e.g. man-made fences crossing pathways or cutting off areas of wintering ground used by particular groups of deer; this fact is well known amongst Scottish deer-stalkers and foresters. In this case, the sudden and severe reduction in the population must have seriously disrupted the established patterns of distribution, range-use and social grouping. In the development of new behaviour patterns, the animals may have been temporarily less efficient in foraging behaviour, and hence in maintaining their level of performance.

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