Some Effects of Fire on Vertebrate Herbivores in the Scottish Highlands

G. R. MILLER AND ADAM WATSON

Institute of Terrestrial Ecology, Banchory, Scotland

LARGE blocks of the Scottish Highlands are used as free-range grazing for domesticated ruminants and game animals. This is a long-established land use that can be traced back for nearly 3 centuries and has arisen because the cool oceanic climate and the predominance of infertile soils make the area generally unsuitable for intensive agriculture. Today the most important herbivores are domestic sheep (chiefly the Blackface and Cheviot breeds), red deer (*Cervus elaphus*), red grouse (*Lagopus lagopus scoticus*) and, to a lesser extent, mountain hares (*Lepus timidus*). Cattle are also important locally on low ground.

The management of these animals involves manipulation of their food supply by burning or fertilizing the vegetation, by providing supplements such as hay, and by controlling the numbers of animals. Of these practices, periodic burning is the most common and widespread. The effects of fire on British range vegetation have been the subject of much research. Particular attention has been given to heathland ecosystems (cf. Gimingham 1971), and the influence of fire in maintaining the characteristics of the vegetation is well-understood. In recent years, several studies (e.g. Allen, Evans & Grimshaw 1969) have concentrated on the possible effects of burning on the circulation and fate of the nutrients in vegetation and soil.

By contrast, the effects of fire on animals have been largely neglected. Virtually nothing is known about invertebrates, and information on vertebrates is fragmentary and often anecdotal. This is particularly surprising in view of the fact that range vegetation is burnt supposedly for the benefit of animals. The aim of this paper is to summarise present knowledge and to highlight what additional research is needed. The few data available refer mainly to heathlands in north-east Scotland, and almost entirely to vertebrate herbivores.

WHY BURNING IS DONE

Two hundred years ago there was a flourishing cattle industry in the Highlands based on numerous smallholdings farmed at a subsistence level. At that time, sheep were kept almost entirely for home use and were not much more numerous than cattle. The cattle herds were carefully managed, being driven on to high ground for summer pasturage and taken back down to the valley bottoms in winter. Those seasonal movements would have ensured efficient use of the grazings, with all parts having a period of rest each year. Moreover, the unselective feeding habits of the cattle would have kept a check on the coarser vegetation. By all accounts, burning was less frequent then than it is now.

In the late-eighteenth century, however, Highland landowners discovered that upland grazings could be more profitably exploited by deploying large flocks of sheep. There followed a rapid development of sheep-ranching on a large scale and, in consequence, many small farmers in the North and West Highlands were evicted. In the east, emigration was voluntary but the end result was the same. Sheep became the predominant herbivores and have remained so till the present day.

The coming of sheep and the depopulation of people and cattle had important consequences. No longer are domestic herbivores so carefully herded. On most hill ground, sheep are allowed to range freely throughout the year and they graze selectively on the most palatable plants, so allowing the coarser ones to increase. The grazings are set-stocked at a level which allows the animals to survive an average winter without excessive mortality or loss of condition. But this means that grazing pressure is inadequate to control the growth of the vegetation in summer: in other words, most Scottish hill pastures are under-grazed.

Take, for example, the heathlands of north-east Scotland that are dominated by *Calluna vulgaris* and used mainly for sheep farming and grouse-shooting. The annual production of green shoots and flowers by *Calluna* growing in more or less pure stands varies from 1800 to 4000 kg/ha (Table 1). This is only the potentially edible fraction of the production, but Forrest's (1971) data suggest that about 23 percent, i.e. 400–900 kg/ha, should be added to allow for wood increments, so giving a total annual production averaging about 3500 kg/ha. The estimates of the annual consumption of herb-

TABLE 1. ESTIMATES OF THE ANNUAL PRODUCTION OF GREEN SHOOTS AND FLOWERS FROM MORE OR LESS PURE STANDS OF *Calluna vulgaris* ON HEATHLAND IN NORTH-EAST SCOTLAND.

Altitude (m)	Mean production (kg/ha/year)	Source
107	4030	Barclay-Estrup (1970)
120–220	2460	Miller & Watson (in press)
215	1780	Grant (1971)
300–500	1940	Moss (1969)

age by the main herbivores (Table 2) are crude, but the total of 315 kg/ha, i.e. some 10 percent of the production, probably errs on the generous side. However the accuracy of this figure is relatively unimportant: it remains generally true that production by the vegetation vastly exceeds consumption by herbivores. The result is that a large biomass of uneaten plant material accumulates as wood or falls to the ground as litter. As decomposition is slow in the cool wet climate and predominantly acid soils of the Highlands, a deep layer of plant litter and raw humus forms at the soil surface. Only locally, such as immediately around hill farms, does consumption equal or exceed production. The same is true of the wetter blanket bog areas of western Scotland.

TABLE 2. ESTIMATES OF CONSUMPTION OF HERBAGE BY THE MAIN HERBIVORES PRESENT ON HEATHLAND IN NORTH-EAST SCOTLAND.

	Average body-weight (kg)	Annual intake of dry matter (kg)	Average stock density no./ha)	Herbage consumption (kg/ha/year)	Source of data on intake of dry matter
Sheep	50	500	0.30	150	Eadie (1970)
Red deer	80	1,200	0.089	110	P. MacDonald (personal communication)
Mountain hare	2.8	200	0.16	30	Myrcha (1968)
Red grouse	0.7	40	0.65	25	Moss & Parkinson (1972)

Note. With the exception of sheep, all data on food consumption were obtained from captive animals under experimental conditions. Energy requirements are probably greater in the wild than in captivity and so the original data on intake of food were increased by 50 percent. Thus these figures for herbage consumption are unlikely to be under-estimates.

Faced with this rapid accumulation of dead and woody plant material, and with the increasing spread of coarse, unpalatable graminoids such as *Nardus stricta* and *Trichophorum cespitosum*, sheep farmers and gamekeepers have resorted to fire as a cheap and apparently effective means of management. Burning is therefore a crude method of pruning the vegetation—old and dead growth is removed and those plants not killed by the fire produce new sprouts. Together with grazing, it maintains the vegetation at an early stage of plant succession and prevents the growth of scrub and woodland. In Scotland, fire thus maintains the heathland habitat and ensures a continuing supply of food for the herbivores exploited by man.

EFFECTS OF BURNING ON VEGETATION

The distribution of animals in space and time is often related to the quantity and quality of food available to them. Therefore, to understand the effects of burning on herbivores, we must first consider its effects on vegetation.

Structure

The most obvious consequence of burning is an immediate and total loss of plant cover. There follows a period of regeneration and recovery when the cover, height and density of the vegetation gradually increase (Fig. 1). Such changes can drastically affect the microenvironment, depending on the complexity of the structure of the original vegetation (see Delany 1953). New gradients in illumination, temperature, humidity and air movement are created instantly by fire, and these are further modified as plants gradually grow up. These changes in micro-environment can influence plant growth. For example, Grant & Hunter (1968) found that *Calluna* grew faster and earlier in the season on burnt than on unburnt ground, and attributed this to differences in temperature gradients near the ground.

Productivity

Burning sometimes boosts primary production but can also result

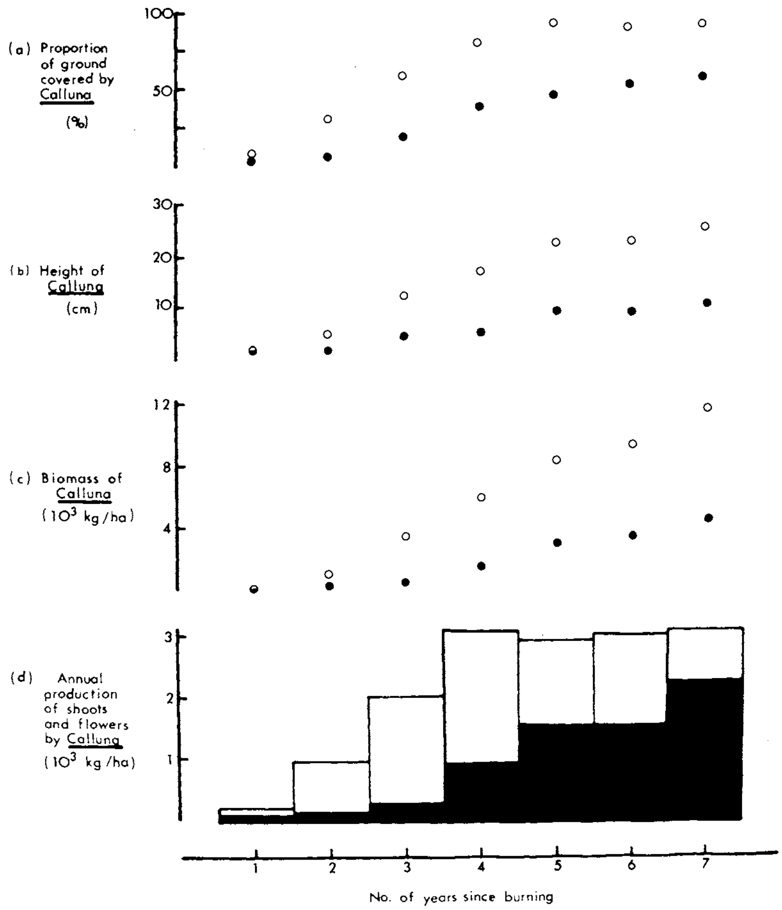

FIG. 1. Changes in (a) cover, (b) height, (c) biomass, and (d) productivity of *Calluna* at heathland sites where regeneration after burning was slow (solid circles and histogram) and fast (open circles and histogram).

in no change or a decrease. Daubenmire (1968) considers that grassland fires in arid climates are most likely to cause losses of production. Despite the humid climate, fire does not usually increase the productivity of Scottish range vegetation. Grant, Hunter & Cross (1963) obtained smaller yields from burnt *Molinia* grassland than from unburnt ground. Similarly, we have found that the yield from newly burnt *Calluna* heathland is much less than from the original vegetation. Indeed, the annual production of shoots and flowers attains the average of about 3000 kg/ha only when the ground cover of *Calluna* has been wholly restored (Fig. 1). This may take several years.

Rates of regeneration after heath fires are very variable. Figure 1 traces the recovery of *Calluna* for 7 successive years at two sites where ground cover was about 90 percent prior to the fire. At one site regeneration was rapid: after 4 years *Calluna* covered 80 percent of the ground, was 17 centimetres tall, and was producing 3000 kg/ha of shoots and flowers annually. Recovery was more or less complete. But regeneration was much slower at the other site. There, ground cover was a mere 40 percent at 4 years, with height about 5 centimetres and annual production less than 1000 kg/ha. Even after 7 years, ground cover was only about 60 percent and productivity was correspondingly low.

Such differences in the speed of recovery are potentially important for any animals dependent on the vegetation for food or cover. Indeed, the rate of regeneration is one of the main criteria for assessing the success of a heath fire in Scotland. The most important variables influencing regeneration are well-known and have been discussed at length by Miller (1964) and Gimingham (1972) amongst others. They include the age of the *Calluna* at the time of burning, the temperature and duration of the fire, the nature of the soil, and the severity of grazing on young plants after the fire.

Botanical Composition

The speed of regeneration can also be of indirect importance to animals because of its influence on the botanical composition of the vegetation. In the eastern Highlands, where the annual potential water deficit generally exceeds 15 millimeters, careful burning on podzolic soils can promote fast regeneration and ensure the monoculture of *Calluna*, a species that is highly valued for its winter green-ness. The more humid environment and peaty soils of the western Highlands are much less favourable for *Calluna*. There its regeneration is often slow, or fails altogether, and repeated burning has resulted in the dominance of the tussocky plants *Molinia caerulea* and *Trichophorum cespitosum* over vast areas of wet heath (McVean & Ratcliffe 1962). The mechanism whereby *Calluna* is eliminated and replaced by *Molinia* has been described by Grant *et al.* (1963). This species, and *Trichophorum*, are of no value to herbivores in winter because neither remains green.

Frequent burning can also eliminate *Calluna* on more fertile soils, especially if there is heavy grazing by sheep. Well-drained sites with brown earths tend to develop a cover of grasses, *Festuca ovina* and *Agrostis* spp., or may be invaded and totally occupied by the bracken fern (*Pteridium aquilinum*). Poorer gleyed soils favour the mat grass (*Nardus stricta*). Both *Pteridium* and *Nardus* are unpalatable to herbivores but *Agrostis* and *Festuca* are highly valued.

All these changes in botanical composition, whether on poor or good soils, are to some extent reversible. Stopping all burning can result in *Calluna* recovering, but this may not be complete.

Chemical Composition

The availability of mineral nutrients in soil is usually enhanced by forest fires (Ahlgren & Ahlgren 1960), but this effect is less apparent after grassland fires (Daubenmire 1968). Allen *et al.* (1969) found that potassium salts were readily dissolved from the ash formed by burning *Calluna*, but that calcium and magnesium were less soluble; phosphorus was deposited in a relatively insoluble form. Most of the organic nitrogen is volatilized and lost in the smoke (Evans & Allen 1971). Clearly, a large proportion of the mineral nutrients contained in the heathland ecosystem is either lost or is unavailable to plants regenerating after a fire and the fertilizing effect of the ash may not be great.

Yet, the replacement of senescent plants by young, rapidly growing plants with a larger proportion of meristematic tissue can change the chemical content of the vegetation on offer to animals. Early analyses by Thomas (1934) established that foliage stripped from young *Calluna* contained a greater concentration of some nutrients than similar material taken from old plants. Our studies have confirmed this and revealed the detailed pattern of change that takes place as a result of burning. Analyses of the terminal unlignified shoots of the current year, about 1 centimetre in length, show that the major changes occur during the first 4 years after a fire (Fig. 2). The contents of potassium, magnesium (not shown), phosphorus, nitrogen and soluble carbohydrate all decrease rapidly and then level out from the fourth year onwards; calcium at first increases but then decreases in concentration, and there is a fairly steady increase in crude fat. Nitrogen and phosphorus are particularly significant, not only because they are essential for the nutrition of animals, but also because they are in short supply in heathland ecosystems. These analyses, and others, indicate that the post-burning flush of growth rich in nitrogen and phosphorus is short-lived and that 4-year-old *Calluna* is no better in this respect than plants aged 25 or more years.

Thomas & Trinder (1947) documented the mineral composition of several common range plants, including *Molinia* and *Trichophorum*, making comparisons between species and seasons. Few other data have been published. Grant *et al.* (1963) found that *Molinia* leaves from a recently burnt area contained more potassium than foliage from unburnt vegetation; but there were only small differences in calcium and phosphorus contents. In limestone grassland, Lloyd (1971) also found small and short-lived differences between burnt and unburnt grassy vegetation. These results suggest that any changes in the chemical status of grassland associated with burning are less marked and last an even shorter time than those in *Calluna* heath.

To sum up, burning immediately changes the physical structure of an animal's habitat by removing all existing vegetation and accumulated litter. Habitat structure then undergoes further, more gradual, modification as plants recolonise after the fire. Also, the sudden loss of plant cover followed by its progressive renewal entails a period of reduced primary production. How long it takes before full production is restored varies with the speed of regeneration. Repeated burning can, in certain circumstances, eliminate *Calluna* which is then replaced by less desirable graminoids that die back in

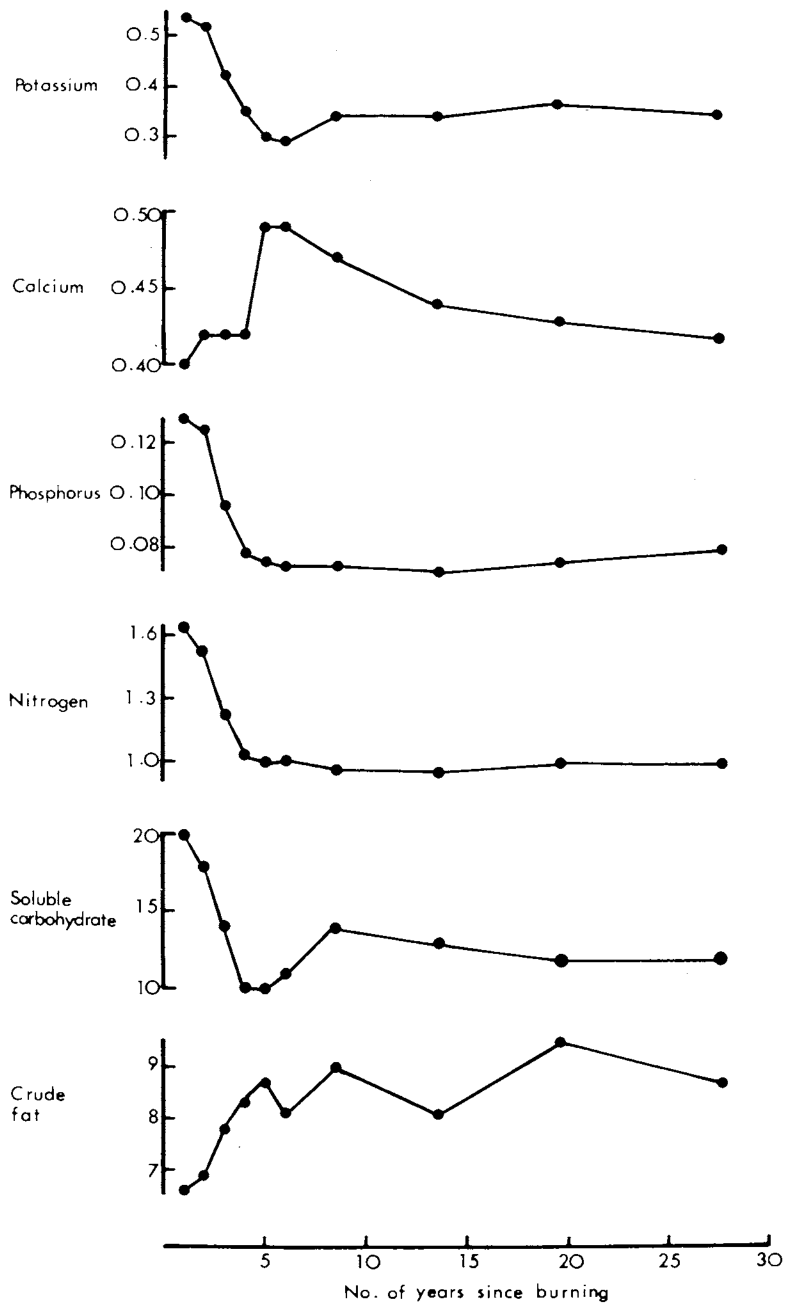

FIG. 2. Changes after burning in the nutrient content (% dry matter) of shoot tips of *Calluna* sampled in December.

winter. Finally, with *Calluna,* the loss of production during the period of recovery after a fire may be at least partly offset by the improved quality of the new growth.

ANIMAL BEHAVIOUR IN RELATION TO BURNING

Selectivity

Herbivores select their diet at four levels—plant community, plant species, individual plant, and plant part. Hill sheep will graze on a wide variety of communities (Hunter 1954, 1962) and in so doing eat many different plants (Martin 1964). However they are well-known as selective grazers (e.g. Nicholson, Paterson & Currie 1970), and Arnold (1964) considers that they select particularly for high nitrogen and phosphorus but against high fibre. It is not surprising, therefore, that sheep are attracted to patches of young vegetation regenerating after fires (Hunter 1954; Grant & Hunter 1968).

Less information is available on the feeding behaviour of Scottish red deer. However studies in Europe (Dzieciolowski 1970a, b; Jensen 1968) and experience with North American deer (Klein 1970) suggest that red deer are similar to sheep in preferring the most nutritious foods within a wide range of palatable plants. Moreover, Miles (1971) has shown that *Molinia* on newly burnt grassland is more attractive to deer than plants on unburnt ground for up to 3 years after the fire.

The smaller herbivores, mountain hares and red grouse, are much less catholic in their choice of plant species. Both animals are largely restricted to *Calluna* during winter, and even in summer it comprises about one-half of their diets (Hewson 1962; Jenkins, Watson & Miller 1963). Despite this, hares and grouse are highly selective and experiments with fertilizers have shown that they can readily detect chemical and/or small morphological differences between adjacent patches of *Calluna* (Miller 1968). Grouse appeared to select for nitrogen in winter but not in summer, and showed no preference at all for *Calluna* shoots with a large phosphorus content; hares selected for both nitrogen and phosphorus in winter, and nitrogen alone in summer.

Hares and grouse might be expected to feed selectively on recently burnt *Calluna* as it contains abnormally large amounts of nitrogen and phosphorus during the first 3 years after a burn. There is no quantitative evidence for hares, but we have studied grouse more intensively. Observations of birds feeding in the wild (Table 3) reveal a strong preference for the youngest 'pioneer' *Calluna*, much of which was aged about 2 years. Laboratory studies have to some extent confirmed this pattern, though less clearly. In a series of 13 palatability trials in which grouse were offered 10–12 alternatives (Moss, Miller & Allen 1972), heather aged 2–3 years was preferred most often: it was first choice in six trials, and second choice in a further two. A notable feature of these results was that 1–2 year-old heather, which has the highest content of nitrogen and several other nutrients (Fig. 2), was consistently and inexplicably preferred least.

TABLE 3. FEEDING BEHAVIOUR OF RED GROUSE IN RELATION TO THE AGE OF *Calluna* ON A 56 HA STUDY AREA IN NORTH-EAST SCOTLAND.

Type of *Calluna*	Approximate age (years)	Proportion (%) of 56-ha study area occupied	Proportion (%) of 23572 observations of grouse feeding
Pioneer	1– 5	30.7	64.9
Early building	6–10	11.6	19.7
Late building	11–15	19.7	15.2
Mature	16–25	25.4	0.3
Degenerate	25 +	2.6	0.0
Calluna absent	—	10.0	0.0

Notes 1. Descriptions of the different types of *Calluna* are given by Gimingham (1972).
2. The 56-ha study area is described and the types of *Calluna* mapped by Watson & Miller (1971).
3. Observations were made every 30 seconds during periods of behaviour study.

Selection of feeding areas can be influenced by factors other than the chemical characteristics of the food. Fire can modify the physical structure of vegetation and so affect feeding behaviour. For example, one of the main reasons for burning *Molinia* and other grasses is to incinerate the litter and so make the new spring growth more accessible to sheep and deer. The dwarf shrub *Calluna* can grow to 50 centimetres high, occasionally more, and a mature stand may contain several hundred stems per square metre. Such dense vegetation can obstruct the movements of hares and grouse and restrict those of even the larger herbivores. Fire can therefore be beneficial by exposing preferred food items and by creating open areas for free movement.

The burning of *Calluna* can improve the accessibility of food in yet another way. Red grouse are about 25 centimetres in height and feed mostly on the tips of the terminal shoots of *Calluna* whilst standing on the ground. The rate at which the plant grows in height varies with factors such as wind exposure and grazing. We have measured the height of *Calluna* in lightly-grazed stands at an elevation of about 200 metres (Fig. 3). Net growth is relatively fast in such circumstances, and by the 10th year after burning the vegetation equals the average height of a grouse; after the 15th year, the most favoured shoot tips are well beyond easy reach. Indeed,

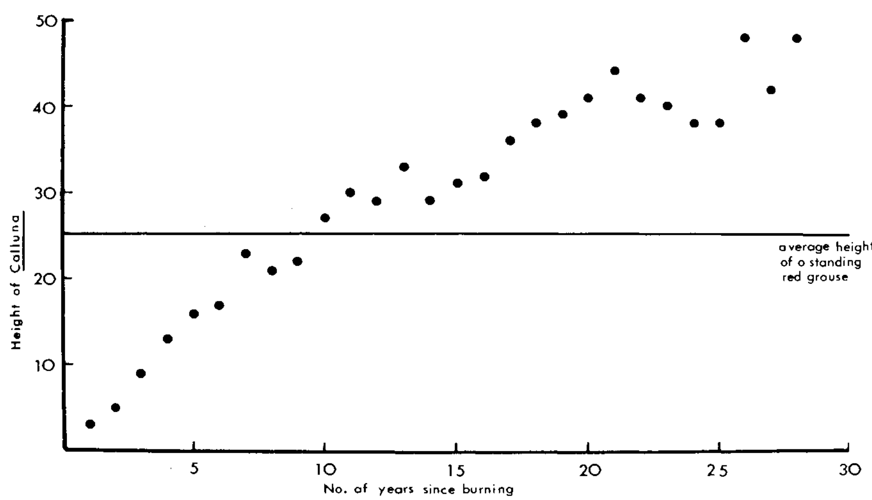

FIG. 3. Increase in the height of *Calluna* after burning in relation to the average height of a standing red grouse.

experiments with captive grouse have shown that they prefer to feed from plants 20–30 centimetres high rather than from taller or shorter plants (Moss *et al.* 1972). Thus the evident distaste for mature *Calluna* (Table 3) may be as much due to the impenetrability of the stand and to the inaccessibility of the shoots as to chemical factors.

Ranging behaviour

Although hill sheep in Scotland are apparently free to roam at will over the extensive and unfenced grazings, they do not do so. Hunter (1964) has shown that individual sheep confine themselves to particular sections of pasture within which they search for food. The home range of an individual may be up to about 50 hectares but it is not exclusive and is not defended against other sheep; up to 50 sheep can share the same range. Most of these are in family groups, as the offspring tend to use the same grazing area as their dams (Hunter & Milner 1963).

Similarly, red deer have common grazings and live in parties of up to 40 or more animals. An individual remains on the same home range throughout the year but this overlaps with that of others. On Rhum, an island of 10,680 hectares off the west coast of Scotland, Lowe (1966) found average home ranges of about 400 hectares for hinds and 500 hectares for stags. On the more extensive deer forests of the Scottish mainland, home ranges are probably much larger and Staines (1969) has reported areas of more than 5000 hectares for hinds.

Mountain hares are also non-territorial and have undefended home ranges that overlap. Flux (1970) found that the average range of adult males was 16 hectares, and adult females 10 hectares, by day. However hares are chiefly nocturnal and may travel 2 or more kilometres to their communal feeding ground. The area of their night range is not known accurately but, by tracking animals, Flux estimated that an individual might cover over 50 hectares when searching for food during heavy snow.

Of the four main vertebrate herbivores feeding on Scottish range vegetation, only the red grouse are territorial. Territories are taken by males in autumn and defended more or less vigorously throughout the year. During summer and early winter, territories are occupied and defended for only part of the day—usually early in the morning or late at night. But the birds are confined to their own ground throughout the day in late winter and spring when food supplies are at lowest ebb. The size of individual territories can vary from 0.2 to 13.2 hectares (Watson & Miller 1971); but on most good grouse moors, the average fluctuates between 2 and 5 hectares depending on whether stocks are large or small.

Sheep, deer, hares and grouse clearly have different requirements for space in which to live and feed (Table 4). Because of these differing needs, the animals cannot be expected to react in the same way to a particular pattern of burnt patches. The needs of sheep and deer are most easily met by burning a few wide expanses each

TABLE 4. FEEDING HABITS AND SIZE OF HOME RANGE OF SHEEP, RED DEER, MOUNTAIN HARES AND RED GROUSE.

	Use of late winter feeding area	Area of home range (ha)	Source
Sheep	communal	30–40	Hunter (1964)
Red deer	communal	500–5000	Lowe (1966); Staines (1969)
Mountain hare	communal	10–16*	Flux (1970)
Red grouse	exclusive	2–5	Watson & Miller (1971)

* Day range only: hares feed nocturnally and their night range is not known accurately.

year. The animals can move some distance to graze communally on the new growth and, if the burnt areas are big enough, the plants will not be damaged severely by heavy grazing. On the other hand, the territorial habits of grouse indicate that burning should take the form of an extensive mosaic of many small patches to ensure an equitable distribution of young growth. Although not territorial, hares do not range so widely as sheep and deer and so their requirements may be nearer to those of grouse.

Besides areas of short *Calluna* for feeding, grouse require patches of tall vegetation for shelter and cover. The birds usually nest amongst mature *Calluna* (Jenkins *et al.* 1963) and a large tract of short vegetation is unsuitable habitat for them. Indeed, we know of a case where grouse took 5 years to recolonize 200 hectares burnt by an accidental fire despite the fact that *Calluna* had regenerated to cover over half the ground in only 2 years.

The needs of the larger herbivores are not entirely incompatible with those of grouse: burning that is suitable for sheep can be totally unsuited to grouse, but the converse is not necessarily true. In fact the deliberate burning of moorland as rough grazing for sheep preceded that for grouse. In the early nineteenth century shepherds used to burn large areas at one time; and this is still the practice on present-day deer forests and West Highland sheepwalks where fires of over 100 hectares are by no means rare. When grouse-shooting became fashionable and, indeed, profitable to the landowner, the management of the moorland vegetation changed. The chief difficulty in burning for grouse is that a large labour force is needed: many more men are required to burn 100 patches of 0.5 hectares each in the same time that it takes to burn one 50-hectare patch. The result is that the pattern of burning is often sub-optimal and not suited to the needs of any species.

The frequency and size of fires are the chief distinctions between the management of grouse moor and deer forest. In the eastern Highlands grouse moors are usually on the lower slopes of hills where the annual rainfall is less than about 1250 millimetres and *Calluna* is predominant in the vegetation. Here it is advantageous to deploy enough labour to burn the many small patches that are desirable for grouse. Above about 550 metres in the east, and on lower ground in the west, the climate is wetter, soils are generally less fertile, and the environment is sub-optimal for *Calluna* and for grouse. Moreover, it is less easy to manage high or remote ground intensively because of its inaccessibility and because burning is sometimes prevented by wet weather or late snow-lie in spring. Therefore fires are large and infrequent, and the land is used as deer forest.

In summary, fire can strongly influence the behaviour, movements and dispersion of herbivores. However its effectiveness is not due simply to creating a larger supply of young nutritious food plants. It also alters the structure of the habitat and, in so doing, can facilitate movements and improve access to food. Finally, the size of burnt patches and the way in which they are distributed are important in catering for the needs of animals with restricted home ranges or with exclusive territories.

ANIMAL PERFORMANCE IN RELATION TO BURNING

The aim of burning is to improve the performance of herbivores and to maximise production. This can be achieved by enhanced growth rates, increased breeding or better survival amongst animals on the managed area, or by net immigration on to it from other areas.

Sheep

The husbandry of hill sheep has been much studied over the past 50 years or so. Most of this work has been concerned with pasture utilization and with the performance of individual animals in relation to their plane of nutrition. It is now well-established that nutrition limits production from hill sheep and that the animals are performing well below their potential (Eadie 1970). There have been no studies of the influence of fire as such on the performance of sheep. However, sheep confined in metabolism crates have been used to measure the digestibility of *Calluna* at various times after burning. Smith & Thomas (1956) found that although the digestibility of organic matter declined only slightly with age, crude protein became much less digestible after 7 years. Burning *Calluna* thus provides a more digestible diet for sheep as well as one that is enriched with mineral nutrients. Even small and temporary improvements must be of considerable benefit to animals subsisting on a nutritionally marginal diet.

Red Deer

All available information relating burning to the performance of Scottish red deer is based on description, association of events, and speculation; no experiments have been done.

The earliest observations are those of Evans (1890) on the island of Jura over a period of 12 years. During the first 6 years, 1878–83, little or no burning was done and deer numbers remained more or less constant; regular burning started in 1884 and thereafter numbers increased (Fig. 4). The hind population in particular rose by more than 50 percent in 6 years. Evans inferred that burning had increased birth rates and decreased mortality. Indeed, there was a notable reduction in the numbers of carcasses found during the latter 6 years of the study (Table 5). Nonetheless the fact that there was no unburnt control area makes these findings difficult to interpret. For example, changes in weather, which are known to be related to deer performance (Watson 1971), might equally have caused the observed improvement.

More recently, Lowe (1969, 1971) reported a halving of the fecundity of 2-year-old hinds immediately after regular burning ceased on Rhum National Nature Reserve; he presumed that this was cause and effect, particularly since there was a recovery of

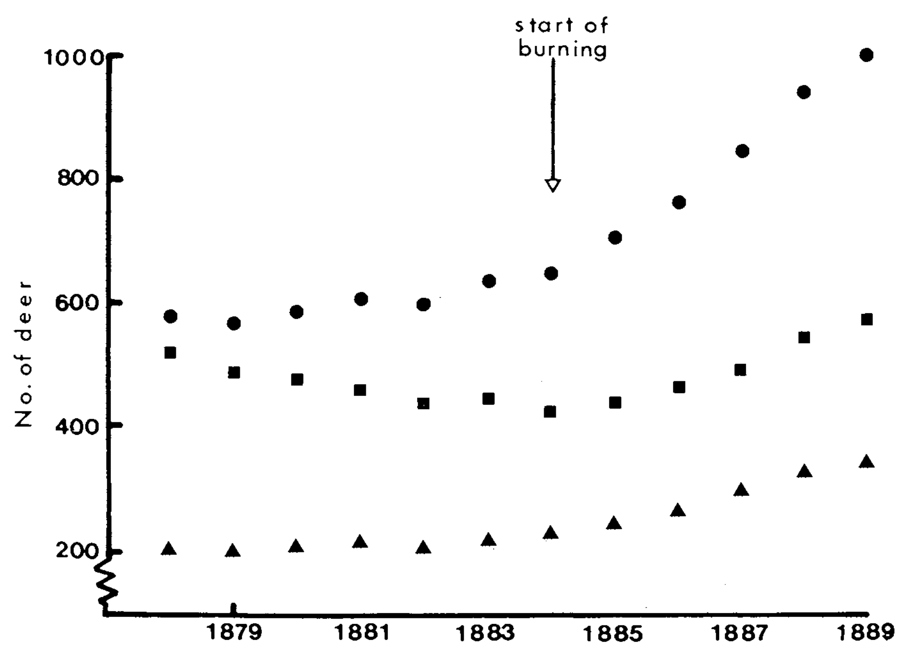

FIG. 4. Estimates of the numbers of red deer stags (squares), hinds (circles) and calves (triangles) on Jura before and after the start of regular burning in 1884.

TABLE 5. AVERAGE PROPORTION (%) OF RED DEER STOCK ON JURA FOUND DEAD BEFORE AND AFTER THE START OF REGULAR BURNING (EVANS 1890).

	Stags	Hinds	Calves
1878–83 before burning	6.7	7.0	26
1884–89 after burning	2.6	2.5	11

fecundity amongst a few young hinds with access to fire-breaks burnt at a later date. Further, Lowe attributed an apparent slight decline in the average body weight of adult deer over 8 years to the same cause. However, the lack of a control again makes it difficult to sustain this interpretation.

North American literature is rich in examples of how growth, body size, mortality and breeding amongst different species of deer are related to the quality of their diet (Klein 1970). Some of these studies have associated improvements in performance with burning (e.g. Taber & Murphy 1971). However, the lack of experiments and ignorance of the nutritional requirements of deer, both in Europe and America, makes interpretation difficult. For example, it remains uncertain whether the animals respond to the improved quality of their food after burning, to its increased availability, or to the interaction of the two. Therefore the implications of burning for the management of red deer are understood only at the crudest level.

MOUNTAIN HARES

Information on the response of mountain hares to fire is even more scanty, presumably because they are of little economic importance. However their heavy dependence on *Calluna* for food suggests that hares might be sensitive to the burning of heathlands for the benefit of red grouse.

In Table 6, counts of hares done during population studies of grouse are compared with estimates of the cover and age of *Calluna* on the study areas. When similar comparisons were made with breeding stocks of grouse (Miller, Jenkins & Watson 1966), the partial correlation coefficients were + 0.669 for cover and — 0.611 for age, both being statistically significant. This was regarded as evidence

TABLE 6. AVERAGE DENSITIES OF MOUNTAIN HARES IN SPRING IN RELATION TO THE AGE AND COVER OF *Calluna* ON STUDY AREAS IN NORTH-EAST SCOTLAND.

Study area	Average density of hares in spring (no./km²)*	Average age index of *Calluna* +	Average cover of *Calluna* (%)
Glen Esk Low AB	3	3.9	60
C	3	3.4	39
D	4	4.1	59
E	4	3.9	56
Glen Esk High A	30	4.2	56
B	28	4.3	65
C	28	4.2	55
Intermediate	8	5.4	63
Boundary	4	7.1	75
Punchbowl	38	3.8	53
Glen Isla	3	4.3	46
Glen Tarken	1	5.9	43
Forvie	0	6.3	42
Lochnagar	4	4.9	44
Kerloch I-II	9	4.2	51

* Many of these data are taken from Watson, Hewson, Jenkins & Parr (1973).
+ *Calluna* was scored according to its age on a scale ranging from 1 for plants aged 1–5 years up to 12 for plants aged over 25 years (Miller, Jenkins) & Watson, 1966).

that grouse stocks are influenced by the amount of *Calluna* on a moor and by the way that it was managed by burning. For mountain hares the coefficients are much smaller, + 0.363 (not significant) for the cover, and − 0.441 ($P < 0.10$) for the age, of *Calluna.* Although the partial correlation between density of hares and age of *Calluna* is suggestive, these results indicate that hares are much less sensitive than red grouse to the gross availability and management of their main food plant. Possibly this is because hares range much more widely than grouse and have communal, not exclusive, feeding grounds (Table 3).

RED GROUSE

The first documentary evidence that fire might be used to increase stocks of red grouse was given over 60 years ago. When grouse shooting became fashionable in the mid-nineteenth century, gamekeepers took over the responsibility of burning from the sheep-farmers. Instead of burning large tracts each year, it became standard practice to burn only a few small patches because it was considered desirable to encourage rank growth as cover for the grouse. There followed a general decline in grouse bags culminating in the disasters of 1872–73 when no shooting was done on many moors. Lovat (1911) advocated a return to the old system of burning on a 10-year rotation, and supported his arguments by documenting the spectacular increase in bags on a few grouse moors where such management was practised.

The more recent survey of Miller *et al.* (1966) on study areas of 120 hectares in north-east Scotland, showed that grouse were more numerous where there was a high proportion of young heather; old heather was also present on every area. Later, Picozzi (1968) compared grouse bags with the amount and pattern of burning on grouse moors. He found that most grouse were shot where there were many small burnt patches, and least where fires were few and/or large.

All these studies were descriptive and the conclusions were based on correlations. However, experimental evidence that grouse numbers could be increased by burning was obtained by Miller, Watson & Jenkins (1970). About 30 percent of a 49-hectare area was burnt in small patches averaging 0.28 hectares over a period of 4 consecutive years from 1962–65. Three years after burning began, the stock of grouse on the burnt area suddenly increased by more than 50 percent; it remained at this level for a further 3 years, and then in 1968 declined just as suddenly to the original density (Fig. 5). Meanwhile, no change in numbers was recorded on a nearby unburnt control area. This experiment demonstrates the effectiveness of burning as a means of boosting grouse stocks, but the exact mechanism of the response is still uncertain. The increase that was observed cannot be accounted for by better breeding or by better survival of the resident grouse. It seems probable that it was caused by a higher proportion of the young birds being able to take a territory and/or by immigration from outside.

Also, it is not known which of the several changes in environment that resulted from the burning was responsible for the increase in grouse numbers. Feeding trials (Moss *et al.* 1972) suggest that grouse prefer to eat *Calluna* aged 2–3 years and avoid 1-year old plants.

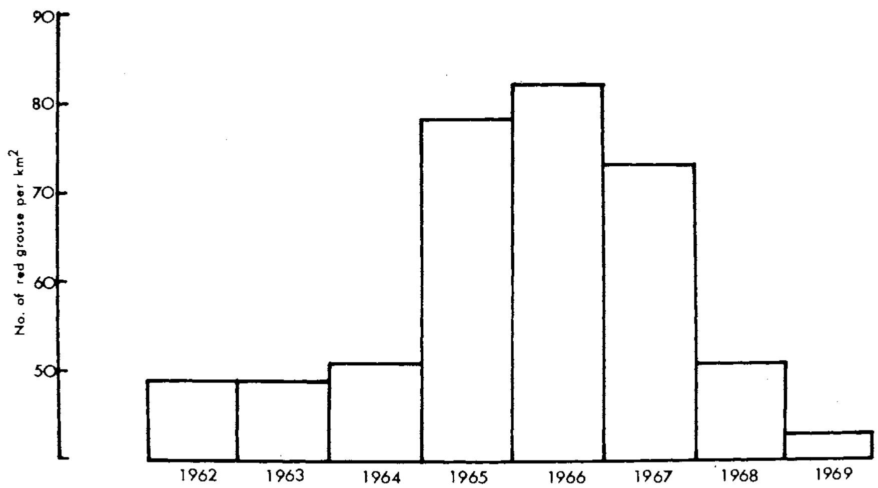

FIG. 5. Changes in the breeding stock of red grouse after experimental burning of heathland dominated by *Calluna*.

Thus the delayed increase in grouse numbers could be explained by the fact that small patches of *Calluna* aged 2–3 years were not numerous until 1965, 3 years after burning began (Fig. 5); but it does not satisfactorily explain the population decrease in 1968 when, although there were fewer than in the previous 3 years, some patches of this age still remained on the study area. This is a matter for further research.

CONCLUSIONS

In Scotland, fire has long been used as a crude instrument for manipulating vegetation. It may have contributed to the extinction of some animals, for example elk (*Alces alces*) and reindeer (*Rangifer tarandus*), by destroying their habitats. Other species have thrived. The most notable amongst these is the red grouse, but probably sheep, red deer and mountain hares also benefit from the after-effects of burning. Fire is used in the management of these herbivores, yet there is no clear understanding of what their needs are and how these are related to the effects of burning.

There is almost total ignorance about the effects of fire on most other rangeland vertebrates. Fire is sometimes regarded as incompatible with wildlife conservation, and there is certainly circumstantial evidence that frequent burning reduces plant and animal diversity. Many ecologists believe that repeated burning has caused a serious loss of *Calluna* cover in the western Highlands and that this has led to a widespread decrease in stocks of red grouse during this century. Since grouse are a favoured prey of the peregrine falcon (*Falco peregrinus*), Ratcliffe (1963) has argued that indiscriminate burning is ultimately responsible for the decline of this species too. In fact there is no reason why judicious burning should not be a valuable aid to wildlife management; for example, the range and density of the greenshank (*Tringa nebularia*) might be increased in Scotland by appropriate burning to create suitable habitats for it (Nethersole-Thompson & Watson 1974). However, much more needs to be known about the habitat requirements of even common moorland birds such as golden plover (*Pluvialis apricaria*) and black grouse (*Lyrurus tetrix*) before fire can be used intelligently to manage wildlife.

Concern about the possible deleterious effects of burning stimulated much recent research into its effects on the distribution and movements of mineral nutrients within the ecosystem. A similar effort aimed at evaluating fire as a creator and destroyer of animal habitats would enable us to make a balanced judgement of its role in the environmental conservation of the Highlands.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge the generous invitation from Tall Timbers Research Inc. that made it possible for me (G.R.M.) to attend this conference. I should also particularly thank Dr. and Mrs. E. V. and Mr. R. Komarek for their many kindnesses during my visit to the United States.

LITERATURE CITED

Ahlgren, I. F. & Ahlgren, C. E. 1960. Ecological effects of forest fires. Bot. Rev. 26:483–533.

Allen, S. E., Evans, C. C. & Grimshaw, H. M. 1969. The distribution of mineral nutrients in soil after heather burning. Oikos 20:16–25.

Arnold, G. W. 1964. Factors within plant associations affecting the behaviour and performance of grazing animals. Pp. 133–154 in Grazing in terrestrial and marine environments (Ed. by D. J. Crisp). Oxford.

Barclay-Estrup, P. 1970. The description and interpretation of cyclical processes in a heath community. II. Changes in biomass and shoot production during the *Calluna* cycle. J. Ecol. 58:243–249.

Daubenmire, R. 1968. Ecology of fire in grasslands. Adv. ecol. Res. 5:209–266.

Delany, M. J. 1953. Studies on the microclimate of *Calluna* heathland. J. Anim. Ecol. 22:227–239.

Dzieciolowski, R. 1970a. Foods of the red deer as determined by rumen content analyses. Acta theriol. 15:89–110.

Dzieciolowski, R. 1970b. Variation in red deer (*Cervus elaphus* L.) food selection in relation to environment. Ekol. pol. 18:635–645.

Eadie, J. 1970. Sheep production and pastoral resources. Pp. 7–24 in Animal populations in relation to their food resources (Ed. by A. Watson). Oxford & Edinburgh.

Evans, C. C. & Allen, S. E. 1971. Nutrient losses in smoke produced during heather burning. Oikos 22:149–154.

Evans, H. 1890. Some account of Jura red deer. Printed for private circulation. Derby.

Flux, J. E. C. 1970. Life history of the mountain hare (*Lepus timidus scoticus*) in north-east Scotland. J. Zool., Lond. 161:75–123.

Forrest, G. I. 1971. Structure and production of North Pennine blanket bog vegetation. J. Ecol. 59:453–479.

Gimingham, C. H. 1971. British heathland ecosystems: the outcome of many years of management by fire. Proc. Ann. Tall Timbers Fire Ecol. Conf. 10:293–321.

Gimingham, C. H. 1972. Ecology of heathlands. London.

Grant, S. A. 1971. Interactions of grazing and burning on heather moors. 2. Effects on primary production and level of utilization. J. Br. Grassld Soc. 26:173–181.

Grant, S. A. & Hunter, R. F. 1968. Interactions of grazing and burning on heather moors and their implication in heather management. J. Br. Grassld Soc. 23:285–293.

Grant, S. A., Hunter, R. F. & Cross, C. 1963. The effects of muirburning *Molinia*-dominant communities. J. Br. Grassld Soc. 18:249–257.

Hewson, R. 1962. Food and feeding habits of the mountain hare *Lepus timidus scoticus*, Hilzheimer. Proc. zool. Soc. Lond. 139:515–526.

Hunter, R. F. 1954. The grazing of hill pasture sward types. J. Br. Grassld Soc. 9:195–208.

Hunter, R. F. 1962. Hill sheep and their pasture: a study of sheep-grazing in south-east Scotland. J. Ecol. 50:651–680.

Hunter, R. F. 1964. Home range behaviour in hill sheep. Pp. 155–171 in Grazing in terrestrial and marine environments (Ed. by D. J. Crisp). Oxford.

Hunter, R. F. & Milner, C. 1963. The behaviour of individual, related and groups of South Country Cheviot sheep. Anim. Behav. 11:507–513.

Jenkins, D., Watson, A. & Miller, G. R. 1963. Population studies on red grouse, *Lagopus lagopus scoticus* (Lath.) in north-east Scotland. J. Anim. Ecol. 32:317–376.

Jensen, P. V. 1968. Food selection of the Danish red deer (*Cervus elaphus* L.) as determined by examination of the rumen content. Dan. Rev. Game Biol. 5:1–44.

Klein, D. R. 1970. Food selection by North American deer and their response to over-utilization of preferred plant species. Pp. 25–46 in Animal populations in relation to their food resources (Ed. by A. Watson). Oxford & Edinburgh.

Lloyd, P. S. 1971. Effects of fire on the chemical status of herbaceous communities of the Derbyshire Dales. J. Ecol. 59:261–273.

Lovat, Lord. 1911. Moor management. Pp. 372–391 in The grouse in health and in disease (Ed. by A. S. Leslie). London.

Lowe, V. P. W. 1966. Observations on the dispersal of red deer on Rhum. Symp. zool. Soc. Lond. 18:211–228.

Lowe, V. P. W. 1969. Population dynamics of the red deer (*Cervus elaphus* L.) on Rhum. J. Anim. Ecol. 38:425–457.

Lowe, V. P. W. 1971. Some effects of a change in estate management on a deer population. Pp. 437–456 in The scientific management of animal and plant communities for conservation (Ed. by E. Duffey & A. S. Watt). Oxford, London & Edinburgh.

McVean, D. N. & Ratcliffe, D. A. 1962. Plant communities of the Scottish Highlands. London.

Martin, D. J. 1964. Analysis of sheep diet utilizing plant epidermal fragments in faeces samples. Pp. 173–188 in Grazing in terrestrial and marine environments (Ed. by D. J. Crisp). Oxford.

Miles, J. 1971. Burning *Molinia*-dominant vegetation for grazing by red deer. J. Br. Grassld Soc. 26:247–250.

Miller, G. R. 1964. Land use in the Scottish Highlands. VII. The management of heather moors. Advmt. Sci., Lond. 21:163–169.

Miller, G. R. 1968. Evidence for selective feeding on fertilized plots by red grouse, hares and rabbits. J. Wildl. Mgmt. 32:849–853.

Miller, G. R., Jenkins, D. & Watson, A. 1966. Heather performance and red grouse populations. I. Visual estimates of heather performance. J. appl. Ecol. 3:313–326.

Miller, G. R. & Watson. Heather productivity and its relevance to the regulation of red grouse populations. *In* The ecology of some British moors and montane grasslands. (Ed. by O. W. Heal and D. F. Perkins) Berlin, Heidelberg & New York. In press.

Miller, G. R., Watson, A. & Jenkins, D. 1970. Responses of red grouse populations to experimental improvement of their food. Pp. 323–335 in Animal populations in relation to their food resources (Ed. by A. Watson). Oxford & Edinburgh.

Moss, R. 1969. A comparison of red grouse (*Lagopus l. scoticus*) stocks with the production and nutritive value of heather (*Calluna vulgaris*). J. Anim. Ecol. 38:103–112.

Moss, R. & Parkinson, J. A. 1972. The digestion of heather (*Calluna vulgaris*) by red grouse (*Lagopus lagopus scoticus*). Br. J. Nutr. 27:285–298.

Moss, R., Miller, G. R. & Allen, S. E. 1972. Selection of heather by captive red grouse in relation to the age of the plant. J. appl. Ecol. 9:771–781.

Myrcha, A. 1968. Winter food intake in European hare (*Lepus europaeus* Pallas 1778) in experimental conditions. Acta theriol. 13:453–459.

Nethersole-Thompson, D. & Watson, A. 1974. The Cairngorms. London.

Nicholson, I. A., Paterson, I. S. & Currie, A. 1970. A study of vegetational dynamics: selection by sheep and cattle in *Nardus* pasture. Pp. 129–143 in Animal populations in relation to their food resources (Ed. by A. Watson). Oxford & Edinburgh.

Picozzi, N. 1968. Grouse bags in relation to the management and geology of heather moors. J. appl. Ecol. 5:483–488.

Ratcliffe, D. A. 1963. The status of the peregrine in Great Britain. Bird Study 10:56–90.

Smith, A. N. & Thomas, B. 1956. The nutritive value of *Calluna vulgaris*. IV. Digestibility at three, seven and fourteen years after burning. J. agric. Sci., Camb. 47:468–475.

Staines, B. W. 1969. Our knowledge of deer behaviour and its possible effects on deer husbandry. Pp. 29–31 in The husbanding of red deer (Ed. by M. M. Bannerman & K. L. Blaxter). Rowett Research Institute, Aberdeen.

Taber, R. D. & Murphy, J. L. 1971. Controlled fire in the management of North American deer. Pp. 425–435 in The scientific management of animal and plant communities for conservation (Ed. by E. Duffey & A. S. Watt). Oxford, London & Edinburgh.

Thomas, B. 1934. The composition of common heather. J. agric. Sci., Camb. 24:151–155.

Thomas, B. & Trinder, N. 1947. The ash components of some moorland plants. Emp. J. exp. Agric. 15:237–248.

Watson, A. 1971. Climate and the antler-shedding and performance of red deer in north-east Scotland. J. appl. Ecol. 8:53–67.

Watson, A. & Miller, G. R. 1971. Territory size and aggression in a fluctuating red grouse population. J. Anim. Ecol. 40:367–383.

Watson, A., Hewson, R., Jenkins, D. & Parr, R. A. 1973. Population densities of mountain hares compared with red grouse on Scottish heather moors. Oikos 24:225–230.