THE INFLUENCE OF REINDEER ON THE VEGETATION OF SOUTH GEORGIA: I. LONG-TERM EFFECTS OF UNRESTRICTED GRAZING AND THE ESTABLISHMENT OF EXCLOSURE EXPERIMENTS IN VARIOUS PLANT COMMUNITIES

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ABSTRACT. A summary is given of the history of reindeer on South Georgia and the rapid increase in population numbers has been traced from the few published reports on the animals. The influence of the deer on individual plant species and on the predominant ecosystems in the three areas of the island occupied by reindeer is discussed. In order to monitor the degree and rate of degradation or change in the principal plant communities which are being grazed and trampled, a number of exclusion sites were established in 1973–74 at five widely separated localities. Large fenced exclosures and small cages were erected on communities being modified by the deer. Each exclusion site had an unfenced control site nearby which is accessible to the animals. Permanent quadrats in each site were analysed quantitatively for species composition and percentage cover afforded by each, photographs were taken of each quadrat, and soils from each site have been chemically analysed. Examples are given of rapid regeneration by certain species during the first 4 months of the programme.

HISTORY OF THE REINDEER ON SOUTH GEORGIA

Reindeer were introduced to South Georgia over 60 years ago to provide a source of fresh meat for the whaling communities, the first of which (Grytviken) was established in November 1904 (Bannister, 1964). The first importation was made in 1911 when three bulls and seven cows were brought from Numedal in central Norway (Allen, 1920; Rankin, 1951). However, there appears to be a difference of opinion in that Olstad (1930) recorded that the original introduction, by C. A. Larsen and L. Larsen, consisted of 11 deer (two bulls and nine cows) and that the animals were released at Ocean Harbour, Barff Peninsula (Fig. 1) in 1909. It appears that in the only comprehensive account on the South Georgian reindeer Bonner (1958) quoted Olstad's data. A second importation of animals was made at Leith Harbour in Stromness Bay (Fig. 2) which, according to Allen (1920), comprised two bulls and five cows liberated in March 1912, but Olstad (1930) reported that a total of five deer was introduced at Leith Harbour "about 1911".

It is evident that the more isolated Barff Peninsula herd had increased rapidly, unlike the Stromness Bay herd which was easily accessible for hunting. By August 1917 the Leith population had risen to 17 animals (Allen, 1920), although Olstad (1930) stated that "after having increased to a number of about 20, they all perished in a snowslide". Three further bulls and four cows were introduced at Husvik, also in Stromness Bay, in 1925 and these had produced several calves 2 years later (Olstad, 1930). Between 1955 and 1957 Bonner recorded between 100 and 200 animals in the Husvik area, and by 1974 the population had risen to *c.* 800 according to an air survey by H.M.S. *Endurance* (personal communication from N. Leader-Williams).

According to Allen (1920), the Barff Peninsula population had increased by 1917 to "forty-five animals in one herd, and it is believed that there are other small herds". By 1921–22, the *Quest* expedition reported that "the number of reindeer that were introduced in 1911 . . . have now increased in numbers to nearly 300" (Wilkins, 1925). By 1928 the Norwegian Antarctic Expeditions recorded between 400 and 500 deer, while 150–200 had been killed up to that time (Olstad, 1930). Although Bonner (1958) recorded *c.* 4,000 individuals in the Barff Peninsula–northern St. Andrews Bay area between 1955 and 1957, this figure is now considered to be an overestimate (personal communication from W. N. Bonner). Payne (1972) indicated that the number of deer in this area was *c.* 1,300 in 1972.

In recent years the Barff Peninsula population has spread southward, across Heaney and Cook Glaciers or possibly along the narrow beach beneath their snouts, to the peninsular area on the north side of Royal Bay (Fig. 1) (Burley, 1966). They have also crossed the high ridge above Pirner Point to reach the small valley inland from Little Moltke Harbour. The entire area

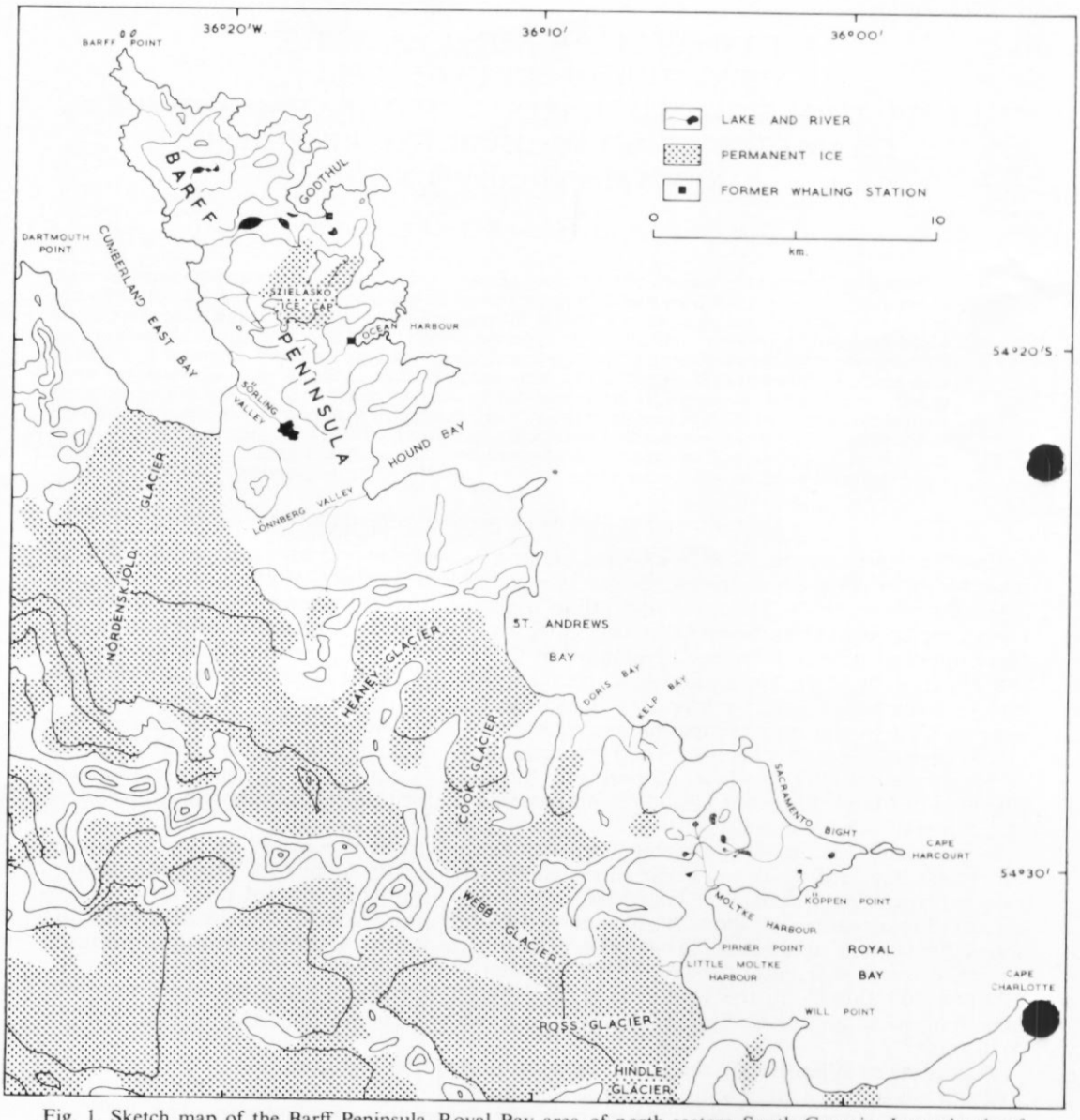

Fig. 1. Sketch map of the Barff Peninsula–Royal Bay area of north-eastern South Georgia. Large herds of reindeer roam Barff Peninsula, particularly the southern part, and a smaller number of deer has recently spread into the area on the north side of Royal Bay. The contours are at 1,000 ft. intervals.

is enclosed by Cook, Webb and Ross Glaciers. Lindsay (1973) has outlined the history of this population, noting that reindeer were first observed in February 1965 in the valley inland from Doris and Kelp Bays, south-east of St. Andrews Bay on the north side of the peninsula, although none was seen in the Moltke Harbour area (Burley, 1965). No deer were seen in February 1961 when S. W. Greene visited the area. However, on 8 October 1959 W. N. Bonner (personal communication) found one dead reindeer at "Sondags Beach" between Cook Glacier and Doris Bay, while Captain Bogen of one of the sealing vessels saw several live deer

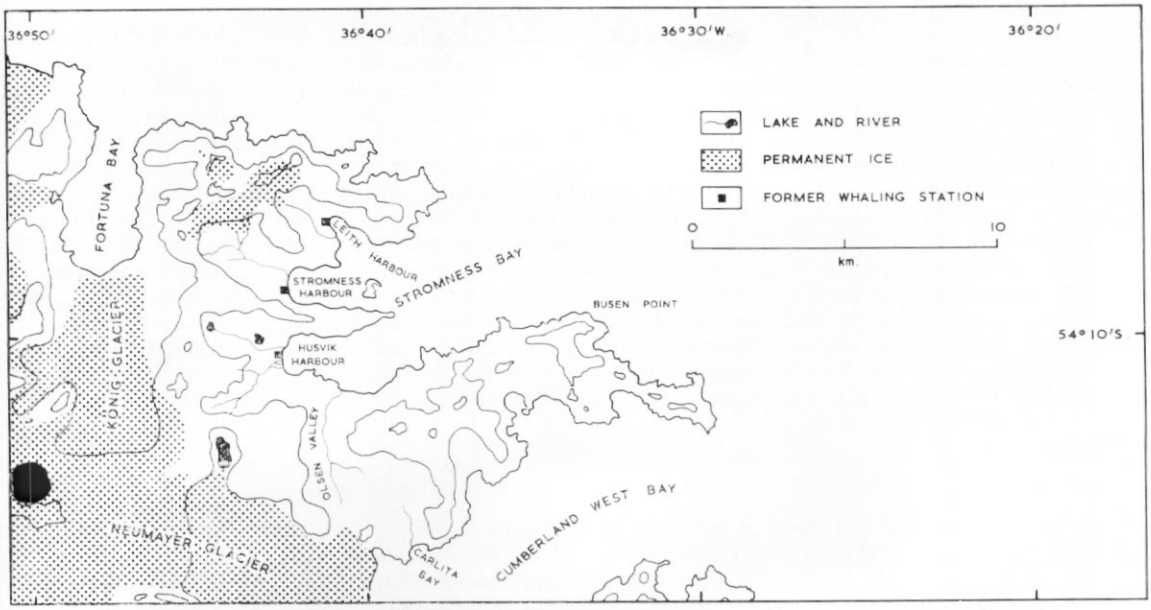

Fig. 2. Sketch map of the Stromness Bay area of north-eastern South Georgia. The area around the former whaling stations and the peninsula between Stromness Bay and Cumberland West Bay is occupied by reindeer but they have not yet penetrated the Fortuna Bay area. The contours are at 1,000 ft. intervals.

at Doris Bay. This is probably the first sighting of reindeer in this area, although Lindsay (1973) considered that they did not reach Moltke Harbour until after February 1965. It is of interest to note that sealers reported that the deer were "said to range . . . to the Ross Glacier in the South", suggesting that they may have been in the Royal Bay area as early as 1928 (Olstad, 1930), although there were no subsequent reports until Bonner's observation in 1959. The number of deer counted in 1972 was 788 (Payne, 1972), but it is possible that this population fluctuates in numbers since it is suspected that a proportion of the reindeer migrate at specific times of the year to and from Barff Peninsula across Heaney and Cook Glaciers or along the beach beneath their snouts. Observations on the ground during January and February 1974 suggested that present numbers in the Royal Bay area were less than 500.

Effect of Reindeer Grazing on Vegetation

During the 1973–74 summer all three areas with reindeer populations were visited (by S.P.J.K.) and the nature and extent of grazing effects were surveyed. One of the authors (R.I.L.S.) also carried out a brief survey of vegetational changes caused by grazing on Barff Peninsula in March 1971.

Although many features of grazing were common to the three areas, the impact of the deer and the degradation of the vegetation differed in some respects between each area. The development and floristic diversity of the vegetation in each of the areas is very similar to adjacent ones which are inaccessible to the deer and with which direct comparisons may be made. However, it is often difficult to interpret the degree of damage or change in the vegetation caused by the deer, due to natural community dynamics and succession resulting from such abiotic factors as erosion, cryoturbation phenomena and possibly even short-term climatic fluctuations. Although the influence of grazing or trampling is immediately visible in some plant communities (e.g. *Poa flabellata* grassland, *Aceana magellanica* swards and *Polytrichum alpestre* banks), the effect on others is not so obvious. It is only after careful inspection that the selective grazing by the deer becomes apparent (e.g. the absence or scarcity of terricolous fruticose and foliose lichens in *Festuca contracta* grassland and of *Acaena* spp. from various

communities). A comparison of floristically similar communities in grazed and ungrazed areas by Lindsay (1973) revealed a considerable reduction in cover afforded by macrolichens. However, it is assumed that the species which are now absent or rare were present before the introduction of the deer, in similar abundance to that in corresponding communities in nearby ungrazed areas. In some communities it was difficult to distinguish between vegetation undergoing natural succession and that modified by grazing. Furthermore, several alien vascular species, especially grasses, have become naturalized and are common around the former whaling stations (Walton and Smith, 1973) and *Poa annua* is important as reindeer food.

As indicated by Bonner (1958), the main routes of the deer are marked by well-defined narrow tracks, and the short grassland and fellfield communities, in particular, are criss-crossed with such paths. When grazing, the deer are well spread out but when they travel from one area to another they follow these tracks in single file. Even in dense vegetation these well-worn paths are barren and there is little opportunity for regeneration or re-colonization of plants. Many tracks converge on passes through the mountains but elsewhere they frequently lead to small ponds. The bryophyte-dominated vegetation around some ponds and the semi-aquatic bryophyte–alga communities around their margins are sometimes badly broken up by the hooves of the deer.

Poa flabellata

Most of the few accounts of the reindeer of South Georgia have commented on the fact that they feed largely on the native tussock grass, *Poa flabellata* (Olstad, 1930; Matthews, 1931; Bonner, 1958; Lindsay, 1973). T. C. Gunn (personal communication) has obtained an exceptionally high total carbohydrate level of 73 per cent dry weight for tussock shoots, emphasizing the importance of the grass to the deer.

Tussock-dominated communities are widespread in all the reindeer areas and in each intensive grazing pressure has caused severe degradation of the grass and its stools. On sheltered gentle slopes and raised beach areas near the shore, formerly dense stands of *Poa flabellata* have commonly been reduced to scattered live tussocks interspersed among dead plants and eroding stools. In the Stromness Bay and Barff Peninsula areas, most tussock stands are damaged to a greater or lesser extent, but in the Royal Bay area there remain extensive, virtually ungrazed stands on easily accessible terrain particularly on the peninsular area extending towards Cape Harcourt. If these stands become important feeding grounds for the deer, the tussock grass covering the small island lying off the cape will provide an excellent ungrazed control area. The dense stands towards the beach in lower Whale Valley are still well preserved, while the more open stands farther inland are badly damaged. The presence of wallowing seals near the beach may deter the deer from grazing this vegetation. In each area, dense tussock locally dominates steep coastal slopes which often end abruptly above a low cliff which renders the grass inaccessible to the deer. Elsewhere, steep tussock-covered slopes which can be reached by the deer are relatively or completely ungrazed (e.g. the more easterly and southerly areas of Busen Peninsula, parts of north-eastern Barff Peninsula, the coastal slopes between St. Andrews Bay and Sacramento Bight, and the higher slopes on the south-west side of Whale Valley), possibly because of the excessive gradient (up to 75°) or because there are still sufficient food resources in more accessible places to support the present numbers of deer.

The sequence of degradation of tussock communities commences with the grazing of the long (up to 1 m.) broad leaves (Fig. 3). However, *P. flabellata* does not appear to be an important forage plant in the summer diet of the deer and only occasionally were animals seen cropping the foliage (Fig. 4). Damage to the grass is undoubtedly greatest during winter. In early and late winter, tussock foliage protrudes well above the level of snow, although on sheltered north-facing tussock-covered slopes there may be little snow cover. At these times the foliage is heavily grazed. During periods of deep snow-cover (particularly between May and September), tussock is the only food widely and abundantly available to the deer except where wind prevents drifting over other vegetation types. The deer scrape away the snow (see Olstad, 1930) to reach the overwintering green leaves and they frequently select the succulent basal portions of the tillers and developing shoots ensheathed in the lower parts of

Fig. 3. Healthy tussock grass, *Poa flabellata*, with foliage *c.* 1 m. high and numerous inflorescences showing no indication of being grazed. Husvik whaling station, Stromness Bay. March 1974.

Fig. 4. Cropped tussock grass, *Poa flabellata*, and an extensive closely cropped "lawn" of the naturalized alien grass, *Poa annua*, on a sandy raised beach. The latter grass has probably formed a "replacement sward" following the eradication by the deer of other species, such as *Acaena magellanica*, as is common elsewhere on Barff Peninsula. Ocean Harbour, Barff Peninsula. March 1971.

the leaves. This prevents much of the following season's growth taking place and also exposes the young growing shoots to frost and desiccation, thereby killing the new tillers. An important cause of damage to the grass in late summer is by reindeer rubbing the velvet from their antlers. Tussocks which have been subjected to such grazing and antler rubbing usually have a high proportion of torn and dead foliage, and are also surrounded by dead leaves detached by the deer's hooves (Fig. 5). As erosion by trampling and weathering proceeds and the decreasing

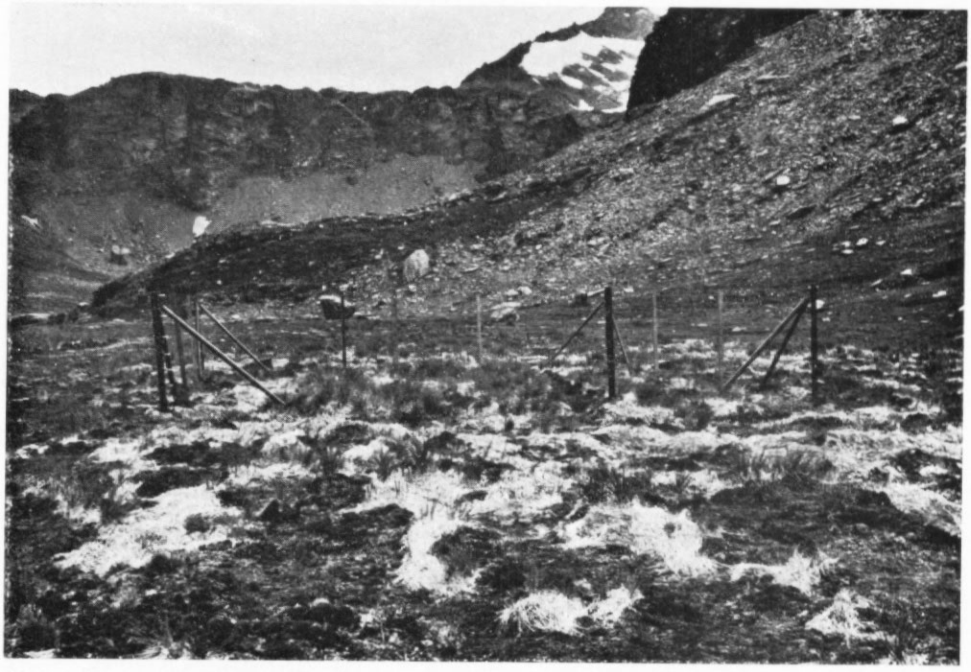

Fig. 5. Heavily grazed tussock grass, *Poa flabellata*, with few living shoots. Individual tussocks have been destroyed by trampling and remain as scattered dead foliage while the intervening moss banks of *Polytrichum alpestre* and *Chorisodontium aciphyllum* are largely dead and broken up. Lower Whale Valley, Moltke Harbour. January 1974.

number of living tillers is continually being grazed, the tussocks ultimately die completely and become compact mounds of organic debris (see Fig. 11). Eventually they may become colonized by mosses (e.g. *Ceratodon* cf. *purpureus*, *Pohlia nutans*, *Polytrichum alpestre* and *P. alpinum*), occasional sterile crustose lichens and the squamulose bases of *Cladonia* spp., and vascular plants (*Deschampsia antarctica*, *Juncus scheuchzerioides*, *Poa annua*, *Ranunculus biternatus* or regenerating *Poa flabellata*). Locally, on dry level ground, erosion caused by excessive trampling and subsequent wind and frost action may completely remove the remnants of the former tussock vegetation, revealing a stony substratum which becomes sparsely colonized by *Rostkovia magellanica* and short cushion-forming mosses (e.g. at the periphery of the tussock stands in lower Whale Valley).

Acaena magellanica

The most selectively grazed vascular plant in summer appears to be the greater burnet, *Acaena magellanica*. On sheltered well-drained slopes in ungrazed parts of the island, this dwarf shrub develops extensive closed swards in which there is a very dense canopy of foliage attaining a height of up to 30 cm. above ground level. Such communities often have a closed understorey of *Tortula robusta*. *Acaena* is also an associate of varying importance in many other community types, particularly *Festuca* grassland, *Tortula–Juncus–Rostkovia* bog,

bryophyte-dominated late snow beds and flushes, and tussock–moss bank stands. However, in many grazed areas this species has been almost eradicated in all situations except on inaccessible ledges. On Barff Peninsula only two ungrazed stands of *A. magellanica* are known, both on scree slopes adjacent to the north-east margin of Nordenskjöld Glacier (personal communication from M. R. Payne). Elsewhere, the species occurs only very sporadically as short creeping rhizomes with few small leaves, particularly in *Festuca* grassland and wet *Rostkovia* bogs. The *Acaena* shoots rarely exceed 5 cm. in length and seldom afford more than *c.* 10 per cent cover. In tussock and *Festuca* communities the shoots and leaves tend to be even shorter and more isolated. These observations apply in general to the two other reindeer areas.

Dense luxuriant swards of *Acaena* with abundant inflorescences are still common on the slopes around Leith Harbour (Fig. 6). Although easily accessible to reindeer, these stands are

Fig. 6. Healthy, ungrazed greater burnet, *Acaena magellanica*, with a dense canopy of large leaves and many inflorescences. The stand is easily accessible to reindeer. Leith Harbour, Stromness Bay. February 1973. (Photograph by C. J. Barrow.)

ungrazed. During the 1973–74 survey no fresh droppings or recently cast antlers were seen in or near the whaling station and it appears that the deer seldom, if ever, frequent this area, at least during summer. This suggests that the Stromness Bay area is still well below its holding capacity and the deer are only exploiting restricted areas for food. As this herd appears to be expanding rapidly, the deer may have to utilize the considerable resources around Leith Harbour during the next few years. There are no indications that this population has penetrated the well-vegetated eastern side of Fortuna Bay which is accessible to the deer by way of mountain passes at *c.* 300–380 m. a.s.l. (personal communication from D. W. H. Walton). However, in 1916 Worsley ([1933]) reported seeing reindeer tracks near the beach in Fortuna Bay.

The floor of lower Whale Valley comprises a large expanse of flat well-drained river terraces and fluvio-glacial debris. Tussock in various stages of degeneration occupies the seaward third of the valley, river banks and steep sides of the valley, the remainder being vegetated largely by a closed *Acaena* community with occasional plants of *Festuca*, grading into a

Festuca-dominated community and an open community dominated by *Rostkovia* and cushion-forming mosses on the drier, more wind-swept stony ground. However, as reported by Lindsay (1973), the *Acaena* stands owe their high cover to the multitude of dead ramifying rhizomes, while the cover afforded by living foliage and shoots is low (Fig. 7). 40–60 per cent of the cover consists of a litter of fragmented woody shoots and rhizomes and moribund *Tortula robusta*. A similar community exists behind the Husvik whaling station but with a higher *Festuca* component. At both sites the *Festuca* was not grazed and it appeared that the grass was increasing in abundance as competition from *Acaena* was removed. During the summer, reindeer herds were seen to concentrate on these degraded stands. Some growth parameters for *A. magellanica* in grazed and ungrazed sites are compared in Table I.

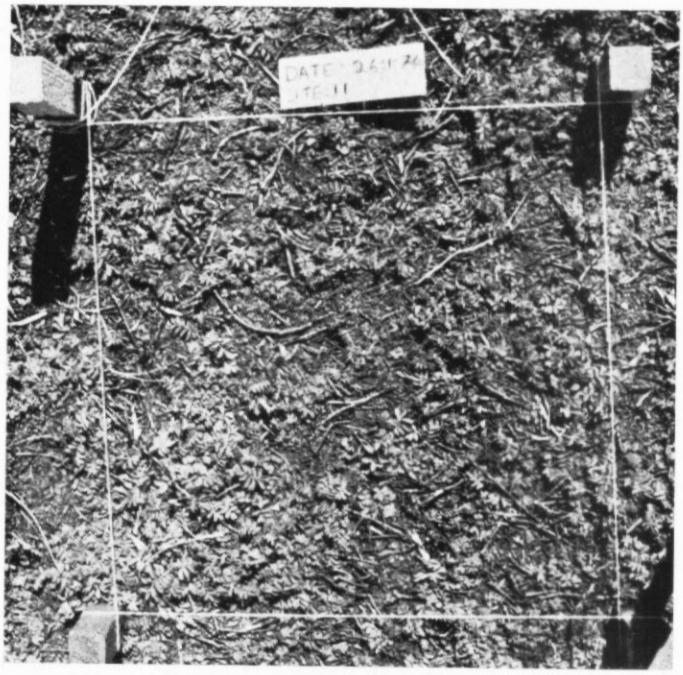

Fig. 7. Closely cropped greater burnet, *Acaena magellanica*, with only a small proportion of leaves all of which are small. The ground is littered with dead broken sections of woody rhizome. Lower Whale Valley, Moltke Harbour. January 1974.

In ungrazed localities, *Acaena tenera* is generally a sparse associate in the more open *Festuca*, *Rostkovia* and fellfield communities. It is frequently present in such vegetation in grazed areas, although usually reduced to very small non-flowering plants. Because of the diminutive size of grazed *A. magellanica*, it is extremely difficult to distinguish from grazed *A. magellanica* × *tenera* as most of the larger morphological characters used to differentiate this taxon are lacking. Consequently, a proportion of the dwarf shrub recorded as *A. magellanica* is likely to be the hybrid. Olstad (1930) identified *A. adscendens* (= *A. magellanica*) in the three rumen samples he collected from the Barff Peninsula population. The rumen contents of seven deer from Barff Peninsula all contained *Acaena tenera*, *Rostkovia magellanica* and unspecified mosses, while some also contained *Deschampsia antarctica*, *Poa annua*, *P. flabellata* and *Phleum alpinum* (Bonner, 1958). In view of the scarcity of *Acaena tenera* on Barff Peninsula and the fact that the small amount of *A. magellanica* there is invariably short, procumbent and with atypically small leaves due to continual grazing, it is probable that Bonner's *A. tenera* was, in part at least, *A. magellanica*.

TABLE I. MEAN PRODUCTION DATA FOR CURRENT YEAR'S GROWTH IN *Acaena magellanica* IN GRAZED AND UNGRAZED SITES

Sites	*Dry weight of shoot (rhizome + leaves)* (g.)	*Length of rhizome* (cm.)	*Length of largest leaf* (cm.)	*Number of leaves/ rhizome*
Grazed *Acaena* sward on level ground, lower Whale Valley, Royal Bay				
a. Exclosure site	0·08	2·5	*c.* 1·7	7·7
b. Control site near exclosure	0·06	2·5	*c.* 1·5	7·3
Ungrazed *Acaena* sward on north-facing slope on south side of King Edward Cove, Cumberland East Bay	0·08	5·3	*c.* 12	14·0
Ungrazed *Acaena* pioneer plants colonizing stony level ground behind Grytviken whaling station, King Edward Cove, Cumberland East Bay	1·92	21·6	*c.* 10	16·0

Royal Bay data are means of 50 samples collected in mid-February 1974. King Edward Cove data are means of 25 samples collected in early March 1974 and provided by D. W. H. Walton (personal communication).

Poa annua

This is the most successful naturalized alien plant on South Georgia (Walton and Smith, 1973) and in many localities it forms extensive swards near the shore, especially on raised beaches and on gravelly stream margins. It is probably the second most important summer food plant of the deer. This short, often abundantly flowering grass is tolerant of continual cropping and trampling, and the largest known swards on the island all occur in reindeer areas. Although *Poa annua* occurs in varying abundance in heavily grazed communities dominated by *Callitriche antarctica*, *Colobanthus quitensis*, *Deschampsia antarctica*, *Poa flabellata* and various mesophytic bryophytes, it readily invades degenerate communities where the principal native species have largely disappeared. The most extensive closed swards, where the grass affords 50–90 per cent cover, occur on the better-drained soils and where it is kept cropped to about 1·5 cm. above ground level, and in such areas few inflorescences survive. The maximum development of *Poa annua*-dominated communities is on the sandy and stony raised beach in and near the remains of the whaling station at Ocean Harbour (Fig. 4). In the southern part of Barff Peninsula, the grass has commonly developed "replacement swards" on coastal flats and moist gravelly depressions up to *c.* 200 m. It appears that the native species, probably mainly *P. flabellata* at the lower altitudes and *Acaena magellanica* higher up, had been so intensively grazed that they were eventually eradicated. Because of its prolific flowering behaviour (in less heavily grazed stands) throughout the entire summer and its high seed viability, *P. annua* has become widespread. Heavily grazed habitats become enriched with deer excrement which may contain *P. annua* seeds and the grass rapidly colonizes such biotically disturbed areas.

Other vascular species

The remaining vascular species do not appear to be intensively grazed. Although some of the graminoids form extensive stands, e.g. *Deschampsia antarctica*, *Festuca contracta* and *Rostkovia magellanica*, selective cropping is seldom serious and most damage to the communities generally results from trampling.

Many dry undulating hillsides are covered by *Festuca* grassland which is frequented by reindeer but it is the associated species, particularly *Acaena magellanica* and macrolichens, which are being sought. The short tussocky nature of *F. contracta* and the very high proportion of loosely attached standing dead foliage in such stands (Smith and Stephenson, 1975) renders the plants vulnerable to disturbance and detachment from the substratum. Although the

authors did not witness the grazing of *Festuca*, J. R. B. Tallowin (personal communication) observed deer on Barff Peninsula during winter scraping at tussocks of the grass beneath the snow and eating the more succulent bases of the shoots and culms. Lindsay (1973) noted that *Festuca* in the Moltke Harbour area appeared not to be grazed but was locally damaged by trampling when the deer forage for lichens, and may have increased in cover where other species had been eradicated by grazing, thereby removing the element of competition. Bonner (1958) stated that besides tussock grass, the main feeding ground was the "*Festuca–Phleum* association" but, although grazing was unselective, a smaller proportion of *Festuca* appeared to be eaten. Olstad (1930) commented that *Festuca* was represented by some fragments of leaves in the three rumen samples he examined.

Swards of *Deschampsia antarctica* frequently occur on wet or moist ground near colonies of gentoo penguins or relatively undisturbed areas close to elephant-seal wallows, usually in "clearings" in stands of *Poa flabellata*. The grass seems unaffected by the casual grazing and the often severe trampling by deer, seals and penguins. Lindsay (1973) reported that some *Deschampsia* swards in the lower part of Whale Valley were intensively grazed and in such situations *Rostkovia magellanica* appeared to have increased considerably in abundance, while some stands of the grass had disappeared during the past decade. However, those around several gentoo penguin colonies showed little sign of being grazed. *Phleum alpinum* rarely forms dense stands of more than 1 m.^{2} but commonly occurs as a scattered associate in *Festuca* grassland, drier *Rostkovia* bogs and exposed fellfield communities. While most *Phleum* plants were ungrazed, entire freshly uprooted plants were often seen lying amongst the bog vegetation, apparently pulled up and rejected by the deer. *Alopecurus magellanicus* is a frequent associate in some areas of *Festuca* grassland and certain wetter communities in Husvik and Olsen Valleys where this relatively rare grass is more widespread than elsewhere on the island. There is no evidence of it being selectively grazed but its widespread distribution in this area may be attributed to dissemination of seed by deer casually eating *Alopecurus* inflorescences or by seed adhering to their coats or hooves.

The locally extensive *Rostkovia magellanica*–bryophyte bogs (see Fig. 9), in which *Juncus scheuchzerioides* is often present, show no widespread degradation, although deer were often observed in these communities and the vegetation is frequently pitted with hoof marks filled with standing water. Grazing of *Rostkovia* or *Juncus* was not seen. It is likely that the main attraction of such communities is the occurrence of *Acaena magellanica* which is often common as scattered, small few-leaved plants. Small dense stands of *Juncus* are sometimes found on *Polytrichum alpestre* banks, re-colonized *Poa flabellata* stools and around pool margins. These are occasionally closely cropped and *Juncus* (together with *Deschampsia antarctica*, *Phleum alpinum*, *Poa annua*, *P. flabellata* and *Acaena magellanica*) has been identified by R.I.L.S. in the rumen content of several deer from Barff Peninsula.

In lower Husvik and Olsen Valleys some stands of *Acaena magellanica* have been virtually eradicated by grazing and re-colonized by *Blechnum penna-marina*. This fern has the most restricted distribution of all the native South Georgian vascular plants (Greene, 1964), being confined to this small area of the island. It is generally a sparse associate in *Festuca* grassland but it appears to have invaded several degraded *Acaena* communities and developed small dense stands (personal communication from B. G. Bell). In the Falkland Islands, *Blechnum* commonly dominates areas of heathland where the surface vegetation has been removed at sites of peat cutting.

Other herbs and pteridophytes are generally widely scattered amongst various communities but they have not been noticeably grazed. However, the relative scarcity of several species in the reindeer area suggests that some casual grazing may occur. Several naturalized alien vascular species grow in and near the derelict whaling stations (Walton and Smith, 1973). Of the grasses, besides *Poa annua*, only *P. pratensis* and *Deschampsia caespitosa* appear to be selectively grazed, but the tall inflorescences of the latter tend to be deliberately avoided. The more abundant *Agrostis capillaris* and the isolated stands of *Carex aquatilis* and *C. nigra* show no sign of being eaten. As a result of grazing, *Taraxacum officinalis* and *Ranunculus repens* at Ocean Harbour are prostrate, small and few-leaved, whereas the same species at the Stromness Bay whaling stations are relatively unaffected, with leaves of the former species reaching 30 cm. in length.

Lichens

Macrolichens are the group of plants which have been most affected by grazing, and in none of the areas occupied by reindeer do they grow as luxuriantly or abundantly as in adjacent non-grazed localities. In *Festuca* grassland and mixed stands of tussock grass and bryophyte banks, scattered squamulose bases of fruticose lichens, particularly species of *Cladonia* (*C. rangiferina*, *C. furcata*, *C. gracilis* and *C. balfourii*), are often frequent but bear few podetia which rarely exceed 1 cm. in height. In corresponding stands in non-grazed areas, dense colonies of podetia 5–10 cm. tall often provide high cover which, in some moderately exposed grasslands, may be as high as 75 per cent of the total vegetation cover. Other terricolous and muscicolous species (e.g. *Cetraria islandica*, *Hypogymnia lugubris*, *Leptogium* spp., *Peltigera* spp., *Pseudocyphellaria* spp., *Stereocaulon* spp. and *Sphaerophorus globosus*), which are common and often locally abundant in *Festuca* grassland, *Acaena magellanica* swards, relatively dry *Rostkovia magellanica* bogs, on *Polytrichum alpestre* banks, moss-covered ledges and fellfield communities in non-grazed areas, are either very scarce or totally absent in grazed areas. In the Moltke Harbour area, Lindsay (1973) commented on the loss of *Cladonia rangiferina*, *Pseudocyphellaria* spp. and *Stereocaulon glabrum*, which Will (1890) had reported as abundant there. Similarly, saxicolous macrolichens (e.g. *Usnea* spp.) are generally lacking from the rocky plateaux, screes and cliffs accessible to the deer, although there are some extensive *Usnea*-dominated stands near Moltke Harbour (Lindsay, 1973).

Bonner (1958) considered that the South Georgian deer are probably unique in their feeding habit, being the only stock of feral reindeer whose staple diet is not lichens, adding that none of the numerous species of lichens occurs in sufficient quantity to be of any importance to the deer.

Macrolichens are highly susceptible to damage by reindeer grazing and trampling (see Pegau, 1970*a*), and, because of their relatively slow rates of growth and regeneration (see Pegau, 1968), there is little chance of recovery of the "reindeer lichens" where damage has been severe and grazing persists. Lindsay (1975) has demonstrated that the annual linear growth of *Cladonia rangiferina* podetia on South Georgia can be as high as 5·3 mm. and that the regenerative capacity of this species is fairly rapid but he commented that the present density of reindeer, at least in the Royal Bay area, is seriously inhibiting any regeneration of macrolichens.

Bryophytes

The authors found no evidence of bryophytes being selectively grazed by deer, although Bonner (1958) reported considerable quantities of mosses in two rumen contents, eaten as a result of "indiscriminate cropping of the *Rostkovia* association". Olstad (1930) found a few fragments of mosses and lichens in rumen samples but he commented that they had undoubtedly been eaten accidentally. The authors believe that bryophytes may be taken unintentionally when the deer are foraging for selected plants. The greatest damage to stands dominated by bryophytes is by trampling. Bryophyte-dominated flushes and bogs are often pitted with hoof marks and turves of *Drepanocladus uncinatus*, *Calliergon sarmentosum*, *Brachythecium* spp. and other hydrophytic mosses are sometimes torn from the substratum by foraging or running deer, particularly around drinking pools. Banks of *Polytrichum alpestre* (see Fig. 9) and *Chorisodontium aciphyllum* on the drier tussock-covered slopes are susceptible to considerable damage by trampling, as Lindsay (1973) noted in the Moltke Harbour area. During wet weather the deer can sink up to 20 cm. into the peat, resulting in holes and fissures which remain indefinitely due to the relatively slow growth rate of the component mosses. The long-term effect of trampling leads to erosion of the banks as is seen on the south-east slopes of lower Whale Valley (Royal Bay) (see Fig. 5) and the west side of Barff Peninsula. The areas where the living moss is removed may provide sites for the establishment of *Rostkovia*, *Juncus* or occasionally other phanerogams. This is best illustrated by the banks behind the Husvik whaling station (see Fig. 9).

Marine algae

J. R. B. Tallowin (personal communication) has observed deer in winter eating kelp (*Macrocystis pyrifera*) which had been washed up on a storm beach near Sörling Valley, and

he has also noted the frequent occurrence of seaweed in rumens. Reindeer on Iles Kerguelen have been observed wading in the sea close to beds of *M. pyrifera* near the shore (Lésel, 1967), but the authors have not seen this on South Georgia.

Reindeer Exclusion Programme

A long-term experimental programme was established to monitor and survey the vegetational changes caused by the reindeer in a number of ecologically important plant communities. Several sites were selected at each of the three reindeer areas where vegetation was being subjected to grazing and trampling. At each site a number of permanent quadrats were staked, one set of which was contained within a deer-proof fence and a second set in a similar but unfenced control site nearby. The vegetation within each quadrat was quantitatively assessed and photographed so that comparisons could be made in future years. It is expected that the vegetation in the enclosed sites will undergo progressive recovery by regeneration of existing plants and establishment of new seedlings or other propagules and possibly revert to a community type closely resembling that which was present before the introduction of the deer. The vegetation in the unfenced control sites is expected to show continued degradation as grazing and trampling persist, assuming that the proximity of the fenced site and the short stakes of the control site do not deter the deer from approaching the area.

Two types of construction were used to prevent deer from entering the sites, the larger (10 m. by 10 m.) being referred to as *exclosures* and the smaller (2·5 m. by 2·5 m.) being referred to as *cages*.

Site selection

The choice of study area and plant communities for analysis and monitoring was predetermined and based on a knowledge of which species were preferred by reindeer and which communities were being most severely affected. Another consideration was that the exclosures should be erected in communities in which the dominant species were major food plants of the deer. Cages were to be sited in communities of lesser importance to the deer and those of particularly homogeneous composition and small-scale growth habit.

The location of each site was decided after a cursory inspection of the areas, the principal criteria for selection being (a) the community should have undergone some degree of degradation or change due to the influence of the deer; (b) the community should be ecologically important in the overall pattern of the vegetation in the area; (c) the community should be relatively uniform in cover abundance and homogeneous in species distribution throughout the stand; (d) the community should be of sufficient area to accommodate an exclosure or cage and a control site of equal dimensions nearby without occupying too much of the stand; (e) the sites should not be in areas susceptible to snow drifting in winter or late lying snow patches in summer which would cause variation in the effects of grazing and the rates of plant growth across the site; (f) the avoidance of areas prone to devastation and wallowing by elephant seals.

A description of the sites where exclosures, cages and their controls were established is given in Table II, while the localities described are shown in Figs. 1 and 2.

Exclosures

These were constructed using plastic coated steel-reinforced concrete corner posts, each supported by two struts of the same material, with two creosoted wooden posts along each side (Fig. 8). The former posts were embedded in concrete, while the latter were driven or dug into the ground or embedded in concrete where the ground was soft, to a depth of at least 0·6 m. The 1·8 m. high fence with 10 m. long sides was completed using seven strands of 3·15 mm. diameter plastic coated wire positioned at 0·23–0·30 m. intervals with the wider spacing commencing *c.* 1 m. above the ground. Several strands of wire were chosen in preference to chain-link fencing as the latter was considered likely to aid snow accumulation during winter which could result in late snow banks persisting over the vegetation or permit access by the deer to the exclosure.

TABLE II. LOCATION OF EXCLOSURES AND CAGES, AND DISTRIBUTION OF PLANT COMMUNITIES BEING MONITORED

Site and date of construction	*Exclosures*	*Cages*
Cumberland East Bay Lower Sörling Valley (December 1973)	*Poa flabellata* tussock grassland (completely killed and eroded) on dry raised beach at 1·5 m. a.s.l.	*Festuca contracta* grassland (cage encloses section of deer path) on dry, level stony ground at 50 m. a.s.l.
	Rostkovia magellanica–Tortula robusta bog on wet raised beach at 6 m. a.s.l.	*Polytrichum alpestre* bank (amongst *Poa flabellata*) on dry gentle slope at 10 m. a.s.l.
	Festuca contracta grassland (with occasional *P. flabellata*) on dry slope at 10 m. a.s.l.	
Ocean Harbour (December 1973)	*Rostkovia magellanica–Tortula robusta* bog on wet glacial outwash debris at 3 m. a.s.l.	*Poa annua* sward on moist, level gravelly ground at 10 m. a.s.l.
Hound Bay Lower Lönnberg Valley (December 1973)		Open *Festuca contracta* grassland (with *Deschampsia antarctica* and *Acaena magellanica* locally dominant) on dry, stony, glacial outwash debris at 2 m. a.s.l.
		Polytrichum alpestre bank on dry crest of moraine at 6 m. a.s.l.
Moltke Harbour (Royal Bay) Lower Whale Valley (January–February 1974)	*Poa flabellata* tussock grassland (moderately grazed) on dry raised beach at 8 m. a.s.l.	*Deschampsia antarctica* sward on moist gravelly ground near gentoo penguin rookery at 9 m. a.s.l.
	Acaena magellanica sward (intensely grazed; with scattered *Festuca contracta*) on dry raised beach at 6 m. a.s.l.	
Upper Whale Valley (January–February 1974)		*Rostkovia magellanica–Calliergon sarmentosum–Drepanocladus uncinatus* bog (with scattered *Acaena magellanica*) on wet, stony valley floor at 65 m. a.s.l.
		Calliergon sarmentosum–Deschampsia antarctica bog (with scattered *Acaena magellanica* and *Juncus scheuchzerioides*) on wet, stony valley floor at 65 m. a.s.l.
Husvik Harbour (Stromness Bay) Lower "Husvik Valley" (March 1974)	*Poa flabellata* tussock grassland (slightly grazed) on dry knoll crest at 16 m. a.s.l.	*Poa annua* sward on moist, gravelly gentle slope at 50 m. a.s.l.
	Festuca contracta grassland (with *Acaena magellanica* frequently co-dominant) on dry, level stony ground at 6 m. a.s.l.	*Rostkovia magellanica–Polytrichum alpestre* bog on dry level ground at 6 m. a.s.l.
		Polytrichum alpestre bank on dry level ground at 6 m. a.s.l.

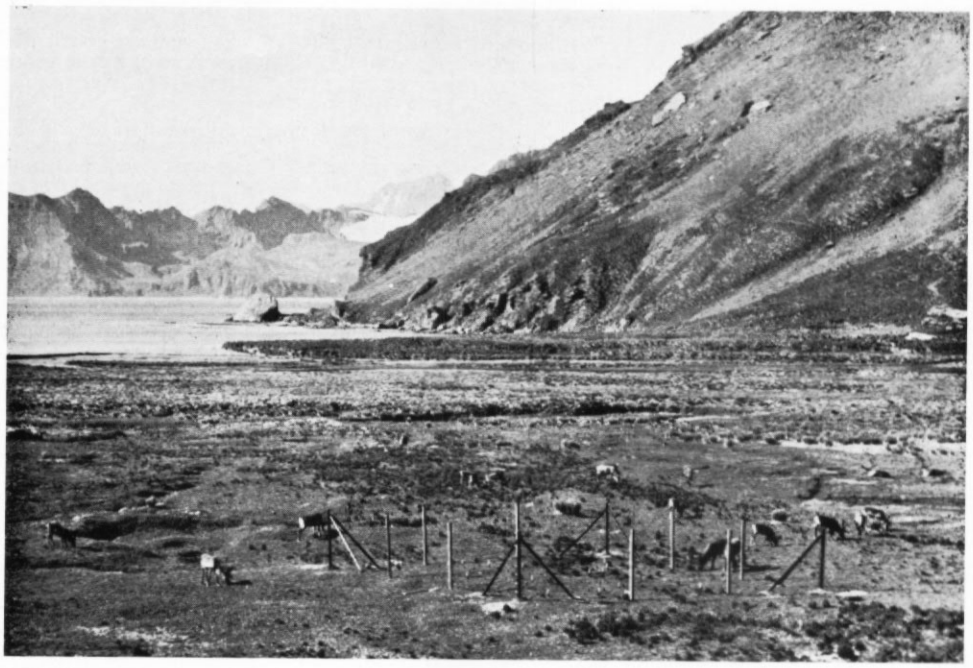

Fig. 8. Exclosure on a heavily grazed stand of *Acaena magellanica* with scattered *Festuca contracta* (short dark tussocks). The larger light-coloured tussocks of *Poa flabellata* (middle ground) are grazed and consist largely of dead foliage, while the dark tussocks of *P. flabellata* beyond these and on the slopes are healthy and not seriously grazed. The posts of the exclosure are 1·8 m. high. Lower Whale Valley, Moltke Harbour. February 1974.

Within the exclosure a 1 m. wide border was left unsampled to allow for possible grazing by reindeer through the fence. Ten 1 m.^{2} quadrats (in tussock- and *Festuca*-dominated sites) or 15 0·25 m.^{2} quadrats (in all other types of vegetation) were marked with short pegs, the positions of each quadrat being determined by the intersection of two random coordinates. Close to each exclosure, in the same community type, an unfenced control site was established and the corners marked with short wooden pegs. The same number of quadrats as was chosen for the corresponding exclosure was also pegged out. The control site was therefore freely accessible to the deer. The same random distribution of quadrats was used for both quadrat sizes throughout the 16 exclosures and control sites. A metal label, die-stamped with the site and quadrat number, was affixed to one stake in each quadrat.

Cages

These were constructed with eight creosoted wooden posts embedded in concrete where the substratum was loose to provide a small exclosure 1 m. in height with 2·5 m. long sides (Fig. 9). This frame supported a removable lid made of similar wood covered with 2 mm. diameter galvanized chain-link fencing with a 5 cm. mesh. Around the sides of each cage three strands of 3·15 mm. diameter galvanized wire were secured at 25 cm. intervals. As with the exclosures, it was considered that wire mesh on the vertical sides would cause snow accumulation, thereby providing atypical shelter and prolonged snow-cover on the vegetation. An identical site nearby was selected as a control and marked with short wooden stakes, as described for the exclosure control sites. Within each cage and control site two 0·25 m.^{2} quadrats were marked with wooden pegs in the same manner as for the exclosure sites, allowing a 0·75 m. border around the internal perimeter in case of grazing through the wire. It is considered that, in the event of a deer penetrating snow covering a cage during winter,

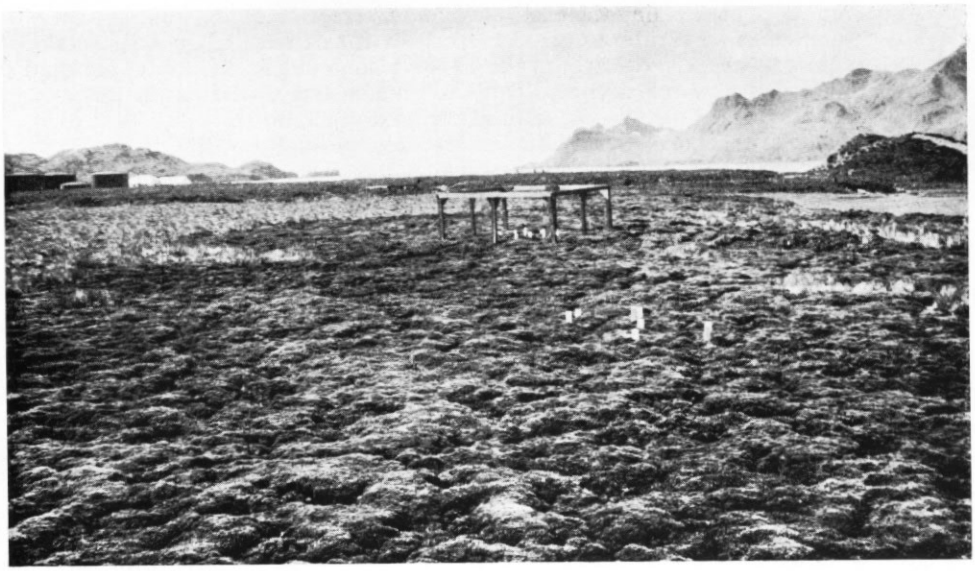

Fig. 9. Cage and control quadrats on a deep stand of almost pure *Polytrichum alpestre*. A second cage lies behind and slightly to the left in a stand of lighter-coloured *Rostkovia magellanica* growing through the *Polytrichum*. The posts of the cage are *c.* 1 m. high. Near Husvik whaling station, Stromness Bay. March 1974.

the lid should be strong enough and the wire mesh small enough to support the animal and prevent its hoof from penetrating the cage.

Site analysis

All phanerogamic and cryptogamic species occurring in each quadrat were listed and a visual estimate of the percentage cover afforded by each was determined to the nearest 5 per cent. The mean percentage cover and percentage frequency of occurrence was determined for each species at each site, thereby providing an approximate floristic analysis of each community studied. Changes in the species composition and of the cover of individual plants within each quadrat will be followed over a number of years.

Vertical photographs were taken on panchromatic film of all 0·25 m.^{2} quadrats and oblique photographs taken of the 1 m.^{2} quadrats. Selected quadrats were also photographed using colour film.

In each exclosure and its corresponsing control site one to three soil samples were collected for chemical analysis from a depth of 5–10 cm., the sampling positions being permanently marked with a wooden stake. Within the cages and their control sites a single soil sample was similarly collected. Further samples will be collected for the same analyses over the following few years to assess the importance of deer excrement and urine as a source of nutrients to the ecosystem.

Comments on the first season's work

Several complications arose after the exclosures and cages had been erected. At all sites the reindeer showed no wariness of these constructions and within a few days of completing one of the Royal Bay exclosures a young calf succeeded in penetrating the lower strands of wire to which no great tension could be applied. Consequently, additional strands were used to reduce the spaces from 23 cm. to 11 cm. Later in the summer deer frequently rubbed their antlers on the fences to strip their velvet. Animals occasionally became entangled in the wire and one exclosure was extensively damaged as a result of this. It is now considered that such damage is unavoidable and it will be necessary to attach "spreaders" joining successive strands

of wire to prevent deer penetrating the exclosures and to erect an outer "rubbing fence". The sites will be re-visited as frequently as possible to check for damage to the constructions and to carry out repairs as necessary. Early in the 1974–75 summer, R. M. Pratt (personal communication) noted that an adult deer and calf had entered one of the Royal Bay exclosures and caused some damage to the fencing and the enclosed vegetation.

Although several of the exclosures and cages are sited within a few hundred metres of the shore on low-lying level ground, it was believed that they were beyond the area frequented by elephant seals. However, N. Leader-Williams (personal communication) has reported that the exclosure situated on the destroyed tussock community on the raised beach in lower Sörling Valley was demolished beyond repair by elephant seals during the 1974 winter (Figs. 10 and 11). Since it is now obvious that this area is within the range of seals, this exclosure has had to be abandoned.

The results of the soil analyses revealed little difference between the chemical composition of soils developed under specific types of vegetation in areas occupied by deer and corresponding soils in areas where there are no deer, e.g. the area between Cumberland East and West Bays where an extensive survey of the vegetation and soils has been carried out (unpublished work of R. I. L. Smith). The more organic soils of bogs, bryophyte banks and tussock grassland invariably have higher levels of nutrient elements, while the more mineral soils of open grassland and fellfield communities generally have low concentrations. Several of the wetter sites where deer were commonly seen to congregate or to graze had high levels of total nitrogen (e.g. 3·0–5·9 per cent dry weight); these were considerably greater than the levels in similar peats sampled in non-reindeer areas, even those associated with elephant-seal wallows or penguin rookeries. These soils had a high concentration of extractable ammonium nitrogen (e.g. 20–50 mg./100 g. dry weight) but low extractable nitrate nitrogen (e.g. 0·01–0·15 mg./100 g. dry weight), whereas more mineral soils tended to have comparatively high values (0·1–1·0 mg./100 g.) and low ammonium nitrogen values (1–10 mg./100 g.). The wetter organic soils also tended to have relatively high extractable P levels (5–20 mg./100 g.). Na, K, Ca and Mg are largely derived from abiotic sources and their levels in the soils, although fluctuating somewhat between sites, did not differ significantly from the levels obtained in similar soils in areas not inhabited by reindeer. It is possible that during the next few years some differences in the concentrations of certain elements may be detected between the exclusion sites and their corresponding control sites where nutrients may be expected to be added to the soil in the form of excrement and urine. However, this assumes that there will be negligible enrichment of the exclusion site soils by down-hill leaching of nutrients.

By late March, at the Barff Peninsula sites (lower Sörling Valley, Ocean Harbour and lower Lönnberg Valley), significant growth of some species was recorded in several quadrats in exclosures and cages in comparison with the corresponding control sites. During the 16 weeks since the construction of the exclosures and cages, *Acaena magellanica* had produced new above-ground rhizomes 15–20 cm. in length and numerous large leaves. No comparable growth had occurred in the control sites. Fig. 12 illustrates the growth of *A. magellanica*, *Phleum alpinum* and *Deschampsia antarctica* in a cage quadrat at Hound Bay during this period. Negligible change had occurred in the two control quadrats a few metres away where grazing had obviously continued. In the exclosure on the devastated tussock community in lower Sörling Valley, the protected *Poa annua* was more robust and bore many more inflorescences than the plants growing in the unfenced control site nearby. Also, at this site the few surviving small *P. flabellata* plants within the exclosure had produced relatively long entire leaves, whereas those in the control site were frayed and short due to grazing or possibly antler rubbing.

From these short-term (4 month) comparisons, it may be anticipated that during the following few years considerable changes are likely to occur in the phanerogamic vegetation protected from the deer, particularly with regard to phytomass and percentage cover of certain species. Changes in the cryptogamic vegetation are likely to proceed at a slower rate but may be significant after several years. It is expected that the net annual production and standing crop of several species, particularly *Acaena magellanica*, *Deschampsia antarctica*, *Poa annua*, *P. flabellata* and *Phleum alpinum*, will increase greatly. *A. magellanica* is an important colonist of open habitats and it is likely that in the more open exclusion sites where the dwarf shrub

Fig. 10. Exclosure in winter with over 1 m. of snow. The track in the foreground is that of the elephant seal at the extreme left middle ground, *c.* 0·5 km. from the shore. Lower Sörling Valley, Barff Peninsula. September 1974. (Photograph by N. Leader-Williams.)

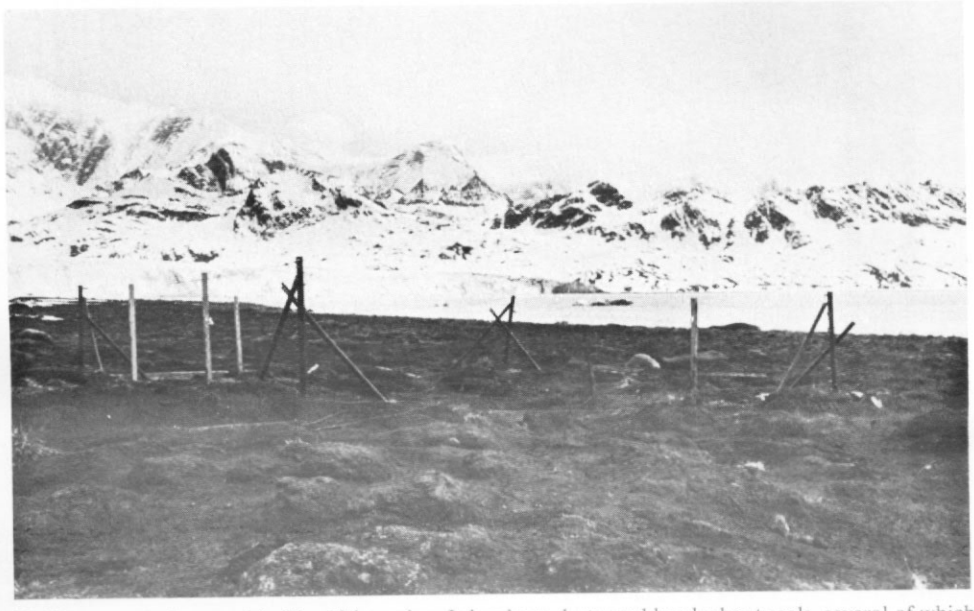

Fig. 11. The same exclosure as in Fig. 10 in spring. It has been destroyed by elephant seals, several of which can be seen lying beyond the exclosure. The hummocky topography is all that remains of an extensive stand of tussock grass, *Poa flabellata*, which, following intensive grazing and ultimate destruction by reindeer, was later completely killed and eroded by wallowing seals. Lower Sörling Valley, Barff Peninsula. November 1974. (Photograph by N. Leader-Williams.)

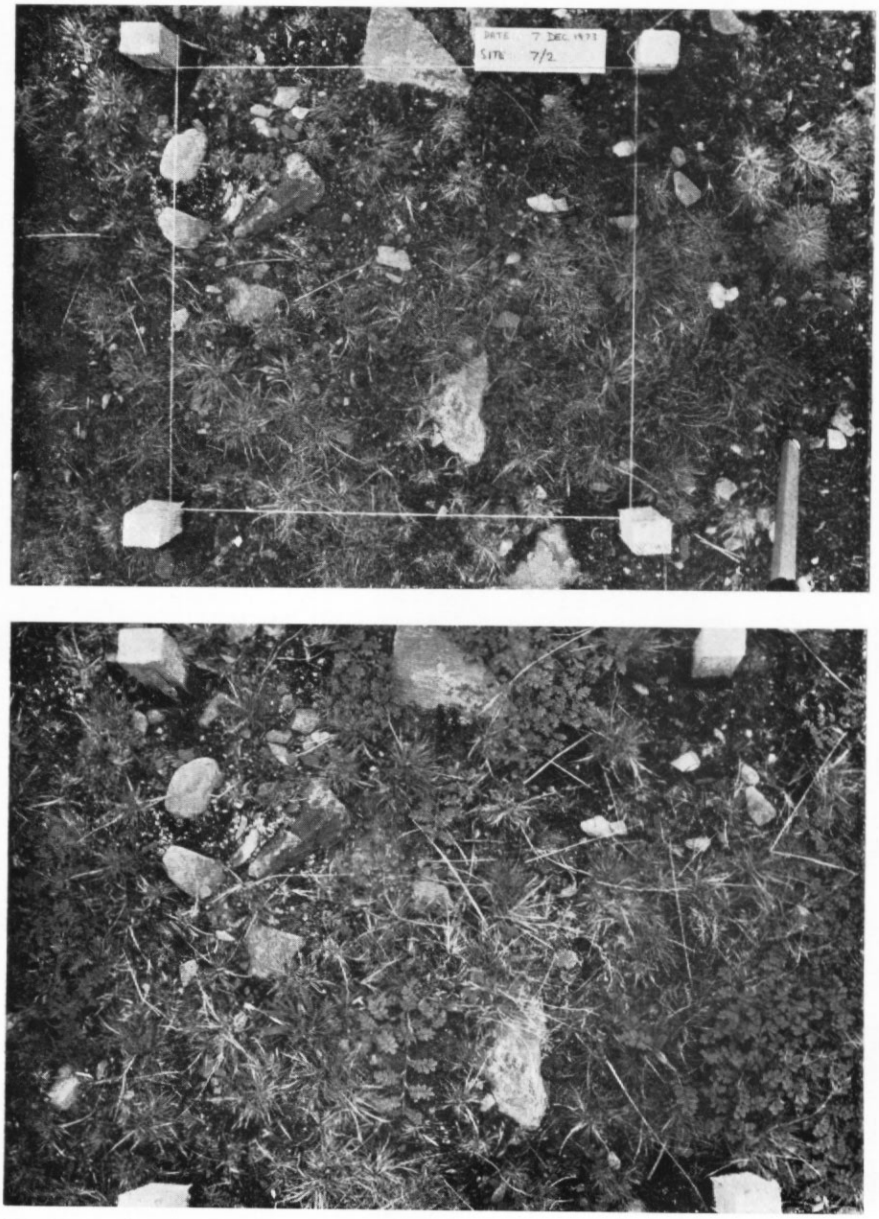

Fig. 12. 50 cm. by 50 cm. quadrat in grazed fellfield community before (upper) and 16 weeks after (below) being enclosed in a cage. The three principal vascular species, *Deschampsia antarctica* (fine-leaved grass), *Phleum alpinum* (broad-leaved grass towards lower left) and *Acaena magellanica* (pinnate-leaved dwarf shrub) have all grown considerably as a result of the grazing factor being removed. A new rhizome of *Acaena*, *c.* 15 cm. long, can be seen below the centre of the lower photograph. Hound Bay, Barff Peninsula. Upper photograph, 7 December 1973; lower photograph, 25 March 1974.

is present it will rapidly spread at the expense of other species. In the absence of *A. magellanica* in similar habitats, *Poa annua* may colonize the open spaces and eroded tussock stools in communities where this alien grass is already present. Eroding tussock stools and moss banks may successfully regenerate or become sites for propagules of various species to become established. Some degree of re-colonization by bryophytes may be expected wherever there is open ground. Although they are slow growing, macrolichens should exhibit increased growth, particularly on *Polytrichum alpestre* banks and in *Festuca contracta* grassland.

Experiments involving exclosures and permanent quadrats were successfully used by Palmer and Rouse (1945) to investigate succession and grazing effects in tundra vegetation in Alaska. In some instances, changes in the vegetation were monitored over a period of 14 years. In vegetation types comparable with those on South Georgia they found, for example, that over-grazing opens up a stand and renders it susceptible to invasion by mosses, reduces the quantity of forage species, and exposes the soil to erosion by wind, frost and rain. They suggested that heavily grazed lichen stands would require between 20 and 40 years for complete recovery to normal cover and height of the lichen species once the grazing impact is removed. Pegau (1970*b*) re-examined the same exclosures in 1965 and found that, although all were in an advanced state of disrepair, two were still of value since the reindeer had apparently not been able to penetrate them for over 20 years, i.e. since the time when they had been last maintained. He noted that lichen recovery was still only *c.* 60 per cent of the original cover afforded and that the vascular plant component of the community had changed considerably.

It may be anticipated that recovery of the vegetation from heavy grazing and excessive trampling may be quite rapid since the impoverished vascular flora and relatively slow growth rates of many of the species will permit the faster-growing species, particularly *Acaena magellanica*, to regenerate or become established without much serious competition. However, the succession which may be expected to occur within each deer-proof site may result in the development of a totally different community from that in which the site occurs and which will always be accessible to the reindeer.

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