

Part I

Reindeer in the Arctic and Antarctic

This section is an introductory preamble. It aims to set the scene for readers not familiar with reindeer, South Georgia or the consequences of introducing mammals to new environments. Reindeer and caribou are a species of northern herbivore uniquely adapted to Arctic life. They fill the lichen-based food niche and are predated upon by wolves. Man now has a pervasive effect on the fate of most reindeer and caribou populations (Chapter 1). Included amongst man's activities is the introduction of mammals to novel environments. This may result in dramatic irruptions, and introductions of reindeer made to islands are of considerable comparative interest (Chapter 2). Amongst recent introductions has been the establishment of northern herbivores on southern islands. South Georgia lies in the subantarctic and lacks indigenous terrestrial mammals. The island's fauna is dominated by marine species and its terrestrial ecosystems are simple. Reindeer were introduced early this century and have had a considerable impact on plant communities, which led to the initiation of this study (Chapter 3).

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Excerpt

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Figure 1.1 Reindeer and caribou are unusual amongst cervids in that both males and females possess antlers. Antlers are used as a taxonomic feature for the genus *Rangifer*.

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Reindeer and caribou: taxonomy, habitats and ecology

Tarandus. Horns branched, round, recurvate; summits palmate. *Rein Deer* Inhabits the Alpine mountains of *America*, *Europe* and *Asia*, southern parts of *Russia* and *Sardinia*; descends in winter into the plains, and is driven back into the mountains in summer by the persecution of marsh insects: feeds on the rein-deer lichen, which in winter it digs out of the snow with its feet; the male casts his horns at the end of November, the female not till she fawns, about the middle of May; gravid 33 weeks, brings often twins; lives about 16 years; when castrated loses the horns, not till the 9th year: is trained in Lapland to draw sledges, and supplies the inhabitants with milk, flesh and clothing; when domesticated 3 feet high, wild 4.

Body brown above, growing gradually whiter with age, beneath and *mouth* white; *tail* white; *hair* thick, under *neck* long; teats 6, the 2 hinder spurious. Carl Linnaeus (1735)

1.1 Taxonomy and relationships with other deer

Linnaeus made an early scientific description of reindeer whilst journeying in his native Sweden. Though incorrect in the odd detail, he provided a good portrait of the species upon which this monograph is based. Present-day taxonomists consider that both Eurasian reindeer and North American caribou together form a monotypic genus with an holarctic distribution, its single representative being *Rangifer tarandus* (Linnaeus, 1758). The genus *Rangifer* belongs to the family Cervidae, the sub-order Ruminantia and the order Artiodactyla, which is one of the two groups of large herbivorous animals known as ungulates. Perissodactyls, the other group of ungulates, have one or an odd number of functional toes and simple stomachs, and include in their number equids, rhinos and tapirs. Artiodactyls, by contrast, have an even number of functional toes and ruminants, as one of the main sub-orders, have three- or four-chambered stomachs and chew the cud to complete their digestive processes. Cervids are distinguished from other ruminants such

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as bovids, ovids and giraffes, because most male cervids possess bony antlers which are grown and shed annually.

A major taxonomic feature of the genus *Rangifer* is that both sexes normally possess antlers (Figure 1.1). Antler shape has been used to divide the genus into two groups which transgress the continental division between reindeer and caribou (Jacobi, 1931). The group *Cylindricornis* have round antler beams in cross-section and occur in forest or woodland habitats, and the group *Compressicornis* have flattened antler beams and occur in tundra and mountain habitats. Whilst there have been other taxonomic schema for the genus (Herre, 1955; Sokolov, 1959; Flerov, 1960), Jacobi's two groups were maintained in the most recent and now accepted revision of the genus (Banfield, 1961), which lists nine extant sub-species (Table 1.1). Two of these sub-species appeared to be evolutionarily senile and became extinct early this century without the intervention of man. The present distribution of the remaining sub-species is shown in Figure 1.2, emphasising the extreme northerly latitudes that the genus occupies. In addition to the already accepted taxonomic separation between forest and tundra groups, the latter might be subdivided in future into continental and High Arctic groups. Recent taxonomic and electrophoretic evidence suggests that Peary caribou and Spitzbergen reindeer are more closely related to each other, with the likelihood of a recent common origin, than to barren-ground caribou and tundra reindeer (Røed, 1985).

Table 1.1. *Taxonomic division of the genus Rangifer (after Banfield, 1961)*

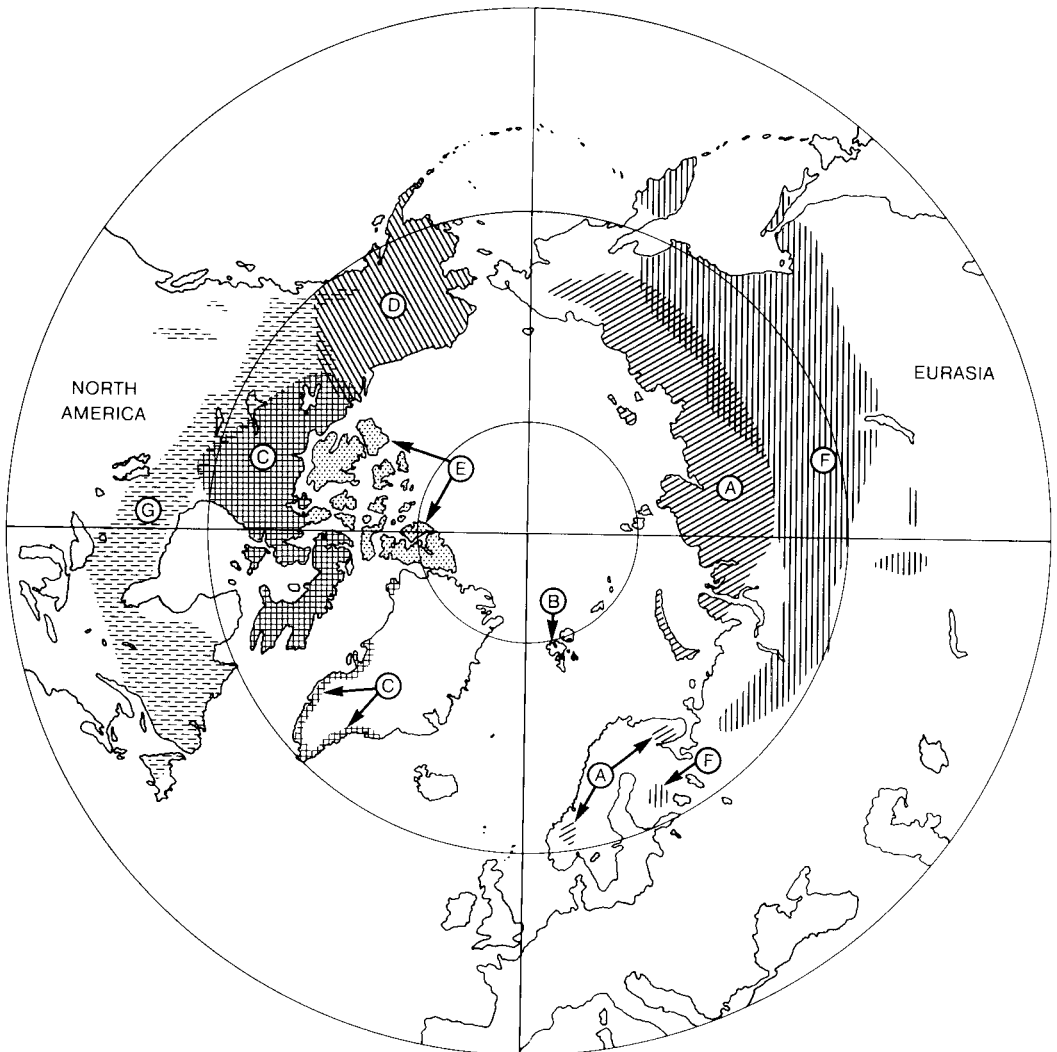
Latin name	Common name
Type Species: <i>Rangifer tarandus</i>	Reindeer, caribou
Group <i>Cylindricornis</i> :	
<i>R. t. tarandus</i>	Mountain or tundra reindeer
<i>R. t. platyrhynchus</i>	Spitzbergen reindeer
<i>R. t. groenlandicus</i>	Barren-ground caribou
<i>R. t. granti</i>	Alaskan caribou
<i>R. t. pearyi</i>	Peary caribou
<i>R. t. eogroenlandicus</i> (Extinct since c. 1900)	East Greenland caribou
Group <i>Compressicornis</i> :	
<i>R. t. fennicus</i>	Forest reindeer
<i>R. t. caribou</i>	Woodland caribou
<i>R. t. dawsoni</i> (Extinct since c. 1935)	Queen Charlotte Island caribou

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Rangifer is a recent genus amongst the deer family. It originated in the early Pleistocene, centering probably in the Nearctic or in northeastern Asia, even though the earliest identifiable remains of *Rangifer* so far recovered date to 440 000 years ago and were found in Western Europe (Banfield, 1961). The genus was a prominent member of the late Pleistocene fauna which included the woolly mammoth, hairy rhinoceros, muskox, cave bear and mastodon (Zeuner, 1959). *Rangifer* survived the extinction of many of its associates and occurred either in High

Figure 1.2. Present distribution of the sub-species of *Rangifer tarandus* (after Banfield, 1961). A – *tarandus*; B – *platyrhynchus*; C – *groenlandicus*; D – *granti*; E – *pearyi*; F – *fennicus*; G – *caribou*.

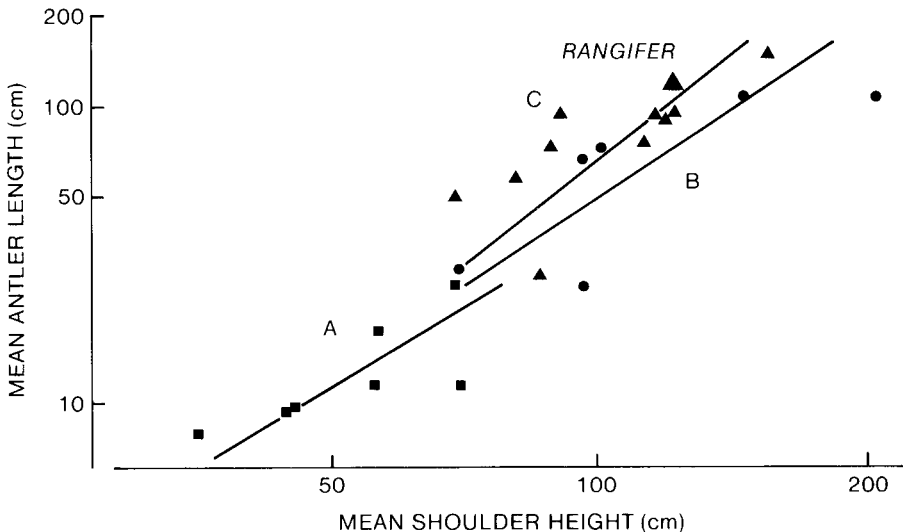


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Arctic glacial refugia or at far more southerly latitudes during the Wisconsin glaciation (Macpherson, 1965). When this glaciation began to recede from its southerly limit of 40°N some 12 000 years ago, *Rangifer* surviving in more southerly ranges moved north to become important members of the present-day continental Arctic fauna. By contrast, *Rangifer* surviving in glacial refugia probably gave rise to present-day High Arctic forms, which have since colonised new areas by crossing sea-ice in winter (Banfield, 1961; Hakala, Staaland, Pulliainen & Røed, 1985).

Muskox are amongst the contemporary species of ungulate which survived the Pleistocene extinction and with which *Rangifer* overlap in their present-day range. Muskox prefer the oasis areas within the High Arctic desert and now only occur naturally in North America and Greenland (Tener, 1965), having been overhunted and reintroduced into various areas of Eurasia. Mountain sheep of several species and races occur in North America and Eurasia but are very restricted and occur in areas of high altitude dominated by grasses and sedges (Geist, 1971), and saiga are caprids which have survived in the steppe regions of Eurasia at the southern end of *Rangifer*'s range (Bannikov, Zhirmov, Lebedeva & Fandeev, 1967). Of these present-day arctic ungulates, *Rangifer* shows the greatest niche breadth, and occurs in most habitats of the arctic-

Figure 1.3. Relationship between shoulder height and antler length of males in different species of deer (after Clutton-Brock, Albon & Harvey, 1980). Squares (A), small (≤ 2) breeding groups; circles (B), medium (3–5) groups; triangles (C), large (≥ 6) groups, including *Rangifer*.



alpine biome, excepting steeply graded mountain slopes and cliffs (White *et al.*, 1981).

Also of interest to this study is the relationship between the ecology of *Rangifer* and other contemporary cervids. The various species of tropical and temperate deer have been classified according to the sizes of their breeding groups, and *Rangifer* is amongst those species having large groups (Clutton-Brock *et al.*, 1980, 1982). Characteristics that favour polygyny include large body size of males relative to females and large size of antlers in males. These characteristics are more enhanced in species living in large groups, as shown for *Rangifer* in Figure 1.3. Amongst temperate and Arctic species only medium and large breeding group sizes are represented (Table 1.2). *Alces alces* is the next most northerly species, which also belongs to a monotypic genus that is holarctic in its distribution. It lives in cold northern forests but some confusion exists because it is referred to as 'moose' in North America and 'elk' in Europe. Members of the genus *Cervus* occur in both North America and Eurasia, and are temperate and tropical in their distribution. However, only two of the nine species are of major interest in temperate areas: red deer (*Cervus elaphus*) and wapiti (*C. elaphus canadensis*), which is usually referred to as the 'elk' in North America. Hereafter, I will refer to *A. alces* as moose and *C. e. canadensis* as wapiti, in the hope of avoiding further confusion. Single genera occur in each of North America and Eurasia and their only representatives are white-tailed deer, *Odocoileus virginianus*, mule or black-tailed deer, *O. hemionus*, and roe deer, *Capreolus capreolus*, which all inhabit various niches in temperate woodlands. A final monotypic genus, the fallow deer (*Dama dama*), originated in the Mediterranean area, but is often included amongst temperate species, having been introduced widely to forest and open areas of Eurasia and North America. The marked degree of polygyny seen amongst reindeer and caribou will be discussed in chapters of Part II in relation to the other species of temperate cervid.

1.2 Habitats and ecology

The various sub-species of *Rangifer* occur at latitudes varying from 45° to 80°N (Figure 1.2) and in habitats ranging from taiga woodlands to High Arctic islands. At these latitudes, snow and cold are dominant factors in the lives of terrestrial animals for much of the year (Pruitt, 1960b; Formosov, 1964). In adapting to them, *Rangifer* has evolved many interesting morphological characteristics (Skjenneberg & Slagsvold, 1968; Kelsall, 1968; Baskin, 1970; Banfield, 1977). Their

Table 1.2. Arctic and temperate species of contemporary cervids, showing their breeding group size (B, 3–5; C, ≥ 6), and habitat type (from Clutton-Brock, Guinness & Albon, 1982), and origin (Holarctic, Nearctic, and Palearctic)

Species	Breeding group size	Open country	Broken canopy forests, woodland or fringe	Closed-canopy forests	Origin
<i>Rangifer tarandus</i> (reindeer and caribou)	C	_____	_____	_____	H
<i>Cervus elaphus canadensis</i> (wapiti)	C	_____	_____	_____	N
<i>Cervus elaphus</i> (red deer)	C	_____	_____	_____	P
<i>Dama dama</i> (fallow deer)	C	_____	_____	_____	P
<i>Odocoileus virginianus</i> (white-tailed deer)	B	_____	_____	_____	N
<i>Odocoileus hemionus</i> (mule deer, black-tailed deer)	B	_____	_____	_____	N
<i>Alces alces</i> (moose)	B	_____	_____	_____	H
<i>Capreolus capreolus</i> (roe deer)	B	_____	_____	_____	P

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winter coat is long and dense, and comprised of air-filled guard hairs and a close underfur for extra insulation. Their crescentic hooves are unusually large and facilitate both travel across snow and boggy ground, and also digging through the snow for winter forage. Their legs are long and powerful enabling the species to cover large distances and also to swim strongly.

Woodland sub-species are relatively sedentary and have short altitudinal migrations (Edwards & Ritcey, 1960). In the High Arctic, Spitzbergen reindeer now have a restricted range on Svalbard (Hjeljord, 1973; Tyler, 1987a), but Peary caribou frequently travel between islands on sea-ice (Miller, Russell & Gunn, 1977). Migrations are most extensive in continental tundra sub-species (Geller & Borzhanov, 1984), and especially in barren-ground caribou which cover remarkable distances of up to 1000 km on each migration in moving to the tundra in the spring and returning to taiga woodland in autumn (Kelsall, 1968). Calves are born in the tundra during, or at the end of, the spring migration in May or June. They are extremely precocious and capable of travel within a few hours of birth and are the only species of cervid not to have a spotted coat at birth.

Migrations, whether short or extensive, are necessary to exploit seasonal differences in availability of forage. Tundra vegetation is highly nutritious in its short summer growing season and fly harassment is reduced in open, windswept areas (Klein, 1970a; White *et al.*, 1975). During winter, when forage is unavailable over much of the tundra, reindeer and caribou have to find access to food that is beneath snow shallow enough for them to dig through. *Rangifer* is able to live over much of the north because it has adapted to a winter diet in which lichens (Figure 1.4) usually predominate, and there is little competition with other Arctic herbivores for this niche (Klein, 1980a). As lichens have slow growth rates and recover their former abundance several decades after extensive damage due to grazing or trampling (Palmer & Rouse, 1945; Pegau, 1970a), there is a delicate interaction between *Rangifer* and its habitat. This has led several authors (Leopold & Darling, 1953; Andreev, 1977) and many traditionalists to assume that lichens play a central role in limiting numbers of reindeer and caribou in many areas of the holarctic. The underlying mechanism of population regulation presumably lies in long-term cycles of lichen abundance, overutilisation and recovery.

The climate of Arctic regions also shows long-term fluctuations, and *Rangifer* generally shows marked and cyclical fluctuations in its numbers

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Figure 1.4. 'Reindeer' lichens of the genus *Cladonia* in conifer woodlands in Norway. Reindeer and caribou are the only northern ungulate to occupy the lichen-based food niche in the Arctic.

