Terrestrial Food Webs in the Sub-Antarctic: Island Effects

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Summary. The tundra-like ecosystems of the Sub-Antarctic islands differ from those of the Arctic, in that they occur on small, very isolated landmasses. The effects of isolation, the climate and the paucity of vertebrate consumers on the food webs of the islands are reviewed. There are no native land mammals and few land birds, unlike in Arctic regions. The success of introduced mammals provides interesting insights into the functioning of Sub-Antarctic terrestrial ecosystems. The diets of land birds are reviewed. Data from Marion Island suggest that there is a comparatively large amount of food available to birds but few species exploit it, due to isolation and climatic constraints. Although there are few invertebrate species, they are key elements in food webs but their trophic roles are poorly understood. The few data available show some evidence of broad habitat use by invertebrates, possibly a response to low species diversity. The review highlights the lack of comprehensive studies of the dynamic structure and functioning of terrestrial food webs in the Sub-Antarctic.

1 Introduction

The structure and dynamics of certain tundra ecosystems are now fairly well documented, as a result of the International Biological Programme's (I.B.P.) focus on the tundra biome. Only 3 of the 23 I.B.P. tundra study sites were in the southern hemisphere: at Signy Island, South Georgia, and Macquarie Island (Bliss et al. 1981). Consequently, southern hemisphere tundra systems are poorly understood, relative to those in Arctic or northern alpine regions.

Sub-Antarctic terrestrial ecosystems have been difficult to categorize in a global scheme. In general appearance the habitats resemble Arctic or alpine tundra, but there are important differences, notably the lack of perma-frost. I have adopted the broad-scale approach used in the I.B.P. programme (Bliss et al. 1981), and have included the Sub-Antarctic among tundra-like regions where low temperatures, high precipitation and wind preclude the development of forests (Wielgolaski 1972; Smith 1977a). Smith (to be publ.) has produced a revised classification of Sub-Antarctic vegetation types.

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Tundra-like habitat covers very little of the southern hemisphere and occurs mainly on islands, in alpine regions and in ice-free areas of the Antarctic continent. Thus, unlike the Arctic tundra which covers vast continental areas, the tundra of the southern hemisphere is insular; being surrounded by large areas of ocean, ice or temperate-zone vegetation. Island effects have been suggested as influencing many aspects of Sub-Antarctic life, including the low numbers of plant and animal species (Wace 1960; Gressitt 1970; Walton, to be publ.) and the low productivity of certain invertebrate (Holdgate 1977). One aim of this review is to elucidate some of the effects of insularity on terrestrial food webs in the Sub-Antarctic.

Another major difference between Arctic tundra and Sub-Antarctic systems is in the roles played by birds and mammals. This difference is of course largely due to the geographical isolation mentioned above. The I.B.P. studies revealed that, in the Arctic, a few species of birds and mammals played important roles in the flux of nutrients and energy and in determining the community structure (Wielgolaski 1975; Bliss 1977; Brown et al. 1980; Bliss et al. 1981). By contrast, the Sub-Antarctic islands support no endemic land mammals and very few land birds. The effects this has on terrestrial food webs are investigated in this paper.

Research into the structure and dynamics of terrestrial food webs is at a very early stage in the Sub-Antarctic. A qualitative description of the food web at Marion Island has been proposed (Smith 1977a) but the intensive, collaborative research which led to the quantitative models of food webs at Signy Island in the maritime Antarctic (Davis 1981; Block 1985) has not been undertaken at any Sub-Antarctic island.

The islands to be considered here are those included in Holdgate's (1977) Sub-Antarctic sub-region: South Georgia; Marion and Prince Edward islands; Iles Crozet; Iles Kerguelen; Heard Island; and, Macquarie Island. In general they are characterized by an oceanic climate with small daily and seasonal temperature range, mean temperatures above 0 °C, frequent high winds and high precipitation (Holdgate 1977). None of the islands has trees but all support extensive tundra-like vegetation dominated by low vascular plants and bryophytes. The organisms and food webs to be considered here are those supported by terrestrial primary productivity. The islands also have large populations of breeding seabirds and seals.

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2 Introduced Mammals

The Antarctic and Sub-Antarctic have no indigenous terrestrial mammals, but several species have been successfully introduced. Their history and biology were reviewed by Holdgate (1967) and Bonner (to be publ.). Many populations have not been studied adequately, notably those on the archipelagos of Kerguelen and Crozet. A review of the trophic roles of introduced mammals reveals some characteristics of the terrestrial ecosystems.

Herbivores have been very successful. At present there are Reindeer, *Rangifer tarandus*, on South Georgia and Kerguelen, feral sheep, *Ovis aries*, on Kerguelen and Iles Crozet, Corsican moufflon, *Ovis ammon musiman*, on Kerguelen and Rabbits, *Oryctolagus cuniculus*, on Kerguelen, Ile aux Cochons (Iles Crozet) and Macquarie Island (Bonner, to be publ.). In addition, horses, mules, donkeys, cattle, goats, and sheep were once kept as domestic stock at several islands but have now been removed (Bonner, to be publ.).

Herbivores do not appear to be limited by food on Sub-Antarctic islands, except in certain instances where their populations have increased until they caused overgrazing and habitat destruction (Pascal 1982; Bonner to be publ.). All of the introduced herbivores exhibit food preferences and in large areas of South Georgia, Iles Crozet, Kerguelen, and Macquarie Island they have eradicated or severely overgrazed preferred plants. In the absence of preferred species, the mammals have been able to eat other plants.

The introductions of herbivorous mammals have demonstrated interesting interactions within the terrestrial communities, in a similar manner to the experimental perturbations used to demonstrate the structure and dynamics of intertidal communities (Paine 1980). Something of the nature of interspecific competition between plants has been demonstrated. Prior to the arrival of mammals, under conditions of minimal herbivory, vegetation in productive areas tended to be dominated by species which were competitively dominant but susceptible to heavy grazing by mammals (Costin and Moore 1960; Smith 1982). Reindeer at South Georgia and rabbits at Macquarie Island have destroyed large areas of formerly dominant species, allowing other species to establish themselves more prominently. At heavily grazed areas on South Georgia, *Poa flabellata* and *Acaena magellanica* have been replaced by *P. annua* which is resistant to grazing and trampling (Smith 1982). In large areas of Kerguelen, rabbits eradicated *Pringlea antiscorbutica* and *Azorella selago* (the latter by the rabbits digging burrows) which have been replaced by *Acaena magellanica* (Holdgate 1967; Pascal 1982). The use of exclosures at South Georgia has shown that some of these changes were reversible (Smith 1982), but on many islands the changes are thought to be irreversible (Holdgate 1967; Bonner, to be publ.).

The effects of herbivorous mammals on entire ecosystems have not been studied, but plant species affected by mammals are often those important to invertebrate herbivores and detritivores (e.g., *Poa flabellata, Acaena magellanica,* and *Pringlea antiscorbutica*; Brown 1964; Smith and Walton 1975). Holdgate (1967) has suggested that the "unique endemic invertebrate fauna" formerly associated with *Pringlea* and *Azorella* vegetation at Kerguelen has been reduced in range and abundance by the actions of rabbits. The Sub-Antarctic food webs are largely detritus-based and large herbivores may have significant effects on such food webs by converting plant matter into faeces rather than litter. Exclosures at South Georgia have been used to investigate the effects of grazing by reindeer on certain insects (Vogel et al., to be publ.). Similar experiments could show the resilience of terrestrial communities to perturbations caused by introduced mammals and also provide data on natural interspecific interactions.

Omnivorous mammals accidentally introduced to Sub-Antarctic islands include Brown Rats, *Rattus norvegicus*, Black Rats, *R. rattus*, and House Mice, *Mus musculus*. Domestic pigs introduced to Iles Crozet and Kerguelen in the 19th century were omnivorous, but they have been eliminated there (Holdgate 1967).

The Brown Rats on South Georgia and the Black Rats on Macquarie Island are primarily vegetarian, preferring tillers of tussock grass, but both species also eat invertebrates, such as insect larvae, and carrion (Smith and Walton 1975; Pye and Bonner 1980; Jenkin et al. 1982). The diet of the Black Rat at Kerguelen and Iles Crozet is unknown (Pascal 1982). Early suggestions that rats killed large numbers of smaller seabirds (e.g. Luke 1917) are not supported by recent work at Macquarie Island (Jenkin et al. 1982) and South Georgia (Pye and Bonner 1980), although the South Georgia Pipit, *Anthus antarcticus*, and the Pintail, *Anas georgicus*, have been adversely affected by rats (Bonner, to be publ.). Rats have not caused other serious changes to the islands and damage to tussock grass is usually restricted to small areas (Bonner, to be publ.).

Mice feed at several trophic levels in the Sub-Antarctic. At Marion Island they prefer macro-invertebrates, particularly lepidopterous larvae, but also eat seeds and carrion (Gleeson and Van Rensburg, to be publ.). Seeds of the Macquarie Cabbage, *Stilbocarpa polaris*, are the preferred food of mice at Macquarie Island but invertebrates, such as spiders and lepidopterous larvae, are also important (Berry and Peters 1975; Jenkin et al. 1982). Mice on Ile aux Cochons (Iles Crozet) feed almost exclusively on plants (Derenne and Mougin 1976). Mice are not reported to have major effects on Sub-Antarctic ecosystems, although their populations are sometimes large (Bonner, to be publ.).

Of the surviving introduced mammals, only the House Cat, *Felis catus*, is a true carnivore. Cats occur on Marion Island, Ile aux Cochons (Iles Crozet), Kerguelen and Macquarie Island. They have had a serious impact on the populations of small petrels (Van Aarde 1980; Pascal 1982; Jenkin et al. 1982) but their effect on terrestrial food webs is not known. Their greatest impact might be to cause changes in the amounts of energy and nutrients supplied to the terrestrial systems by the petrels (Williams 1978). Cats kill very few of the birds which feed in the terrestrial food webs, such as Lesser Sheathbills, *Chionis minor*, (Van Aarde 1980;

Derenne and Mougin 1976) and Wekas, *Gallirallus australis*, (Jones 1977), but they have been implicated in the extinction of the Banded Rail, *Rallus philipensis*, and the Parakeet, *Cyanoramphus novaezelandiae erythrotis*, at Macquarie Island (Jenkin et al. 1982). In general, cats are only important top predators within terrestrial food webs when preying on other introduced mammals, and they are supported more frequently by marine birds.

There are remarkably few records of introduced mammals failing to colonize Sub-Antarctic islands. Cats and rabbits failed at South Georgia and this is probably due to the climate, which is colder than at the other Sub-Antarctic islands where one or both species have been successful (Holdgate 1967; Bonner, to be publ.). Mink, *Mustela vison*, failed to colonize Ile du Chat, at Kerguelen, in 1956, apparently because the founder population (1 male and 2 females) was too small (Bonner, to be publ.). Some introduced populations (e.g., dogs at Macquarie Island) have been exterminated by humans.

The successes of introduced mammals are clear indications that there were suitable food resources at most Sub-Antarctic islands which were unexploited or underexploited by the indigenous birds and invertebrates. Research on introduced mammals, currently focused on their primary effects on the fauna and flora and on eradication methods, could profitably include investigations into the effects of the mammals on whole communities.

3 Roles of Birds in Terrestrial Food Webs

Birds are a component of the terrestrial food web on all Sub-Antarctic islands. Their occurrence and diets are summarized in Table 1. The diets of most species are poorly known. Marine species, such as skuas, *Catharacta* spp. and giant petrels, *Macronectes* spp., which prey on other seabirds on the islands have been omitted, since they are not strictly

Table 1. Diets of birds using land-based food resources on Sub-Antarctic Islands

Species	Island	Food from tundra habitats	Food from the shoreline	Other food
South Georgia Pipit *Anthus antarcticus*	South Georgia	Insects; Collembola; other arthropods[a,b]. Plant seeds[c]	Beached marine crustaceans[a]	–
European Starling *Sturnus vulgaris*	Macquarie	Insects; earthworms; berries; (seeds?)[a]	Beached marine organisms[a]	–
Common Redpoll *Carduelis flammea*	Macquarie	Seeds of several plants; (insects?)[a,e]	–	–
Weka *Gallirallus australis*	Macquarie	Insects; earthworms; other arthropods[a,d,e]. Some plant matter[a,e]	Kelp fly larvae; beached fish and marine invertebrates[a,j]	Rodents; rabbit young; carrion; birds' eggs and chicks[a,d,e]
Wattled Sheathbill *Chionis alba*	South Georgia	Not studied	Not studied	Carrion; birds' eggs and chicks; kleptoparasitized food[a]
Lesser Sheathbill *Chionis minor*	Marion and Prince Edward	Insects; earthworms; other arthropods; snails[f]	Kelp fly larvae, beached marine animals; intertidal invertebrates; algae[f]	Carrion; birds' eggs and chicks; kleptoparasitized food; placentae; excreta[f]
Lesser Sheathbill *Chionis minor*	Îles Crozet, Kerguelen	Similar to Marion Island; not well-studied[f]	Similar to Marion Island; not well-studied[f]	Similar to Marion Island[f]
Lesser Sheathbill *Chionis minor*	Heard Island	Not studied	Similar to Marion Island; not well-studied[f]	Similar to Marion Island[f]
Kelp Gull *Larus dominicanus*	Marion and Prince Edward and others(?)	Lepidoptera larvae; earthworms; possibly other invertebrates[g]	Intertidal and shallow subtidal organisms[a]	Carrion; possibly birds eggs and chicks; seal placentae[a]
Kerguelen Tern *Sterna virgata*	Marion, Prince Edward, Îles Crozets, Kerguelen	Diptera; spiders; other invertebrates[a]	Not recorded	Marine organisms[a]
South Georgia Pintail *Anas georgica*	South Georgia	Nematodes; other invertebrates(?)[h]	Algae; crustaceans[a,h]	Marine and freshwater invertebrates; algae[h]; Carrion[i]
Speckled Teal *Anas flavirostris*	South Georgia	Insects and small arthropods[h]	Not recorded	Mainly plant material from freshwater ponds; Invertebrates[a]
Kerguelen Pintail *Anas eatoni*	Kerguelen, Îles Crozet	Seeds; roots; other plant matter; earthworms; insects[a]	Crustaceans; small fish etc. from tidal flats[a]	–
Grey Duck *Anas superciliosa*	Macquarie	Not recorded	Kelp fly larvae (and other foods?)[a]	Aquatic plants and animals?[a]

References: [a] Watson (1975); [b] Smith and Walton (1975); [c] Holdgate (1977); [d] Jenkin et al. (1982); [e] N.P. Brothers (in litt. 1980, 1983); [f] Burger (1981); [g] Burger (1978); [h] Weller (1975); [i] Parmelee (1980); [j] Jenkin (1975)

part of the terrestrial food webs. However, they do play a role in the introduction of energy and nutrients into the islands (Gillham 1961; Smith 1978a; Siegfried 1982).

The South Georgia Pipit is the only indigenous species which is a true land bird. Despite its unique status and the fact that it is threatened by rats (Pye and Bonner 1980), there has been no intensive field study of this bird. The European Starling, *Sturnus vulgaris*, and the Common Redpoll, *Carduelis flammea*, are Holarctic species which were introduced to New Zealand, and which have spread to several small islands to the south. Both species are now common and have persisted for more than 50 years at Macquarie Island (Jenkin et al. 1982).

Terrestrial foods are vital to the survival of the Pipit, Starling, and Redpoll. The Sheathbills and the Weka are primarily scavengers and predators at seal and seabird colonies, but also rely heavily on terrestrial food at certain times. Terrestrial foods appear to be a less important food for the Kelp Gull, *Larus dominicanus*, Kerguelen Tern, *Sterna virgata*, and the four species of dabbling ducks (Table 1). All of these species rely on marine or freshwater organisms for food. The diet of the recently established Mallard, *Anas platyrhynchos*, at Macquarie Island is unknown.

The macro-invertebrates appear to be the most important terrestrial food eaten by birds in the Sub-Antarctic (Table 1). Plant seeds are apparently abundant at some Sub-Antarctic localities (Dorne 1977; Tallowin 1977) but are not important food for birds, except for Common Redpolls at Macquarie Island. Plant foliage and roots are unimportant and apparently are eaten only by the Weka and Kerguelen Pintail, *Anas eatoni*. The Upland Goose, *Chloephhaga picta*, a grazing species, has been introduced twice to South Georgia but was extirpated (Watson 1975). All of the birds which use terrestrial foods are obliged to eat intertidal and marine species in some seasons. The South Georgia Pipit, for example, is forced by heavy snow to leave the tussock grass in winter to forage along the shoreline, and the birds apparently suffer heavy mortality at this time (Parmelee 1980).

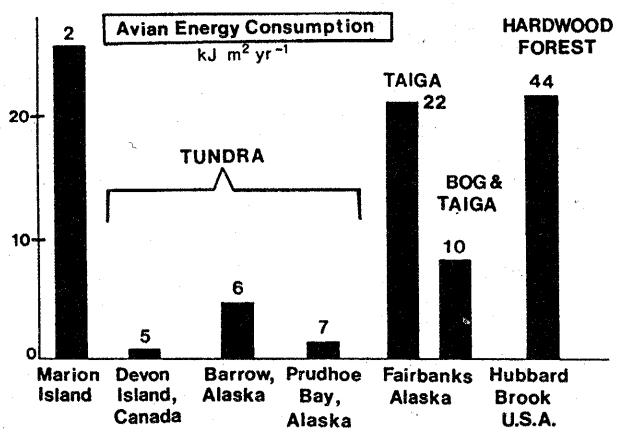

Fig. 1. Energy consumption by birds eating terrestrial invertebrates in the coastal lowlands at Marion Island (Burger 1978) compared to that of birds in northern tundra, taiga, and hardwood forests. *Numbers above columns* indicate the numbers of avian species involved. Data from Pattie (1977) and Norton et al. (1975): Truelove Lowland, Devon Island; MacLean (1980): Barrow; Norton et al. (1975): Prudhoe Bay; West and DeWolfe (1974): Fairbanks; Homes and Sturges (1973): Hubbard Brook, New Hampshire, USA

The roles of birds as consumers in Sub-Antarctic terrestrial ecosystems have received little attention, but should not be ignored. Predation by Lesser Sheathbills and Kelp Gulls on terrestrial invertebrates at Marion Island was important to both predators and prey (Burger 1978, 1981, 1982). The macro-invertebrates supported 33% of the 3,500 Sheathbills during the winter when the more preferred food in penguin and seal colonies was much less abundant. The Sheathbills exhibited acute habitat selectivity, foraging predominantly in those vegetation types in which invertebrates were most abundant and accessible (Burger 1982). The availability of invertebrates in winter probably reduced the Sheathbills' mortality rates, to the extent that the population appeared to be near or at the island's carrying capacity and limited by the availability of suitable nesting territories in penguin colonies (Burger 1979, 1981). The importance of invertebrates in the population dynamics of the Kelp Gull is unknown. Sheathbills and Kelp Gulls ate about 8% of the standing crop of invertebrates annually, within a 100 ha study site, and possibly a similar proportion over the whole of Marion Island (Burger 1978). Intensive foraging by Sheathbills in localized areas caused depletions of invertebrate populations.

In contrast to the Sub-Antarctic, the roles of birds in Arctic tundra have received considerable attention (e.g., Pattie 1977; MacLean 1980). Birds are conspicuous members of tundra food webs, although they are not always important in total energy or nutrient flux of the ecosystems. In Fig. 1 the annual energy consumption by Lesser Sheathbills and Kelp Gulls at a coastal site at Marion Island is compared with data from certain tundra, taiga, and forest areas. The site at Marion Island was representative of vegetated coastal lowland, which is more productive than the island's other habitats. Avian energy consumption within this area far exceeded that within tundra areas and was comparable to that of taiga and northern hardwood forests. This comparatively high intake at Marion Island is made possible by the high biomass of macro-invertebrates, which is several times greater than the biomass of invertebrates at tundra and bog sites used in the I.B.P. tundra programme (Fig. 2).

Although energy consumption by birds is high at Marion Island, virtually all of it goes to only two species, the Lesser Sheathbill and the Kelp Gull. A third species, the Kerguelen Tern eats negligible amounts of invertebrates at Marion Island (Burger 1978). By contrast, many more bird species are found regularly in Arctic tundra and taiga communities (Fig. 1) and often are members of relatively complex food webs (Pattie 1977). The paucity of bird species in terrestrial food webs in the Sub-Antarctic seems due to two primary factors: isolation and the climate.

Sub-Antarctic islands are among the most isolated in the world. In addition, the Antarctic continent is not a source region for terrestrial species and the environments at other

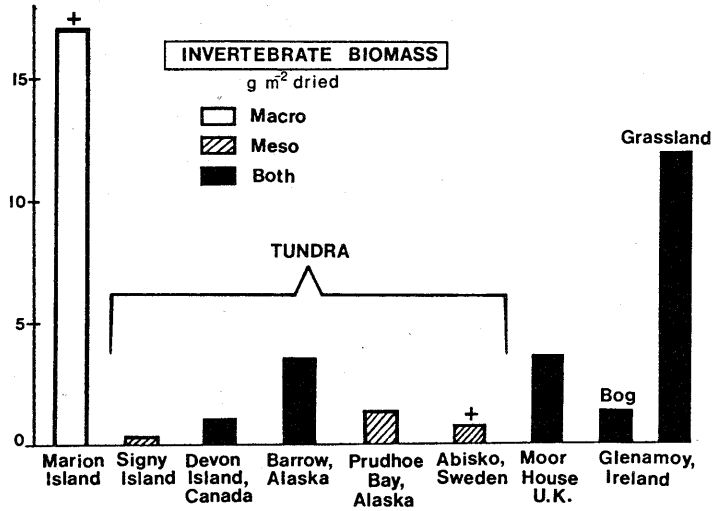

Fig. 2. The biomass of terrestrial macro-invertebrates (earthworms, molluscs, weevils, and spiders) at the coastal lowlands at Marion Island compared to that of macro- and meso-invertebrates at I.B.P. tundra biome study sites. Data from Burger (1978): Marion Island; Davis (1981): Signy Island; Ryan (1977): Truelove Lowland, Devon Island; MacLean (1980): Barrow; MacLean (1975): Prudhoe Bay; Rosswall et al. (1975): Abisko; Heal et al. (1975): Moor House; Moore et al. (1975): Glenamoy

potential source regions, the southern continents, are generally unlike those of the islands. Despite their isolation, Sub-Antarctic islands regularly receive vagrant land birds (Table 2). Most of these are not potential colonists, being migrants which breed in the northern hemisphere or birds from temperate continental regions not suited to the islands. Nevertheless, these records indicate that the isolation does not totally preclude colonization by land birds.

Abbott (1974) investigated factors affecting numbers of land bird species on Sub-Antarctic and cool-temperate islands. The number of plant species per island accounted for 71% of the variability in the number of bird species. Island area, the number of insect species and the distance from a mainland were also correlated with the number of avian species, but were less important. Abbott (1974) proposed that temperature was the ultimate factor determining numbers of plant species, and the plants in turn determined the numbers of land bird species by providing cover and food. Biotic factors on the islands were thus suggested to be the proximate factors affecting land birds.

Sub-Antarctic islands provide abundant food for land-based birds but most of it is available for limited seasonal periods (e.g., food from seal and seabird colonies) or is made unavailable by snow-cover (soil and litter invertebrates and seeds). Food from seals and seabirds is exploited successfully, in the absence of specialized terrestrial predator-scavengers, by seabirds (two species of giant petrels, two skuas and one gull). These species, unlike land birds, can switch to marine prey when seals and seabirds are unavailable.

Abbott (1974) suggested that the numbers of land birds on the southern islands might be determined by the accessibility of arthropods (and he should have included earthworms) to birds, rather than the numbers of arthropod species present. Snow-cover and frozen ground are known to affect the accessibility of available invertebrates to Pipits on South Georgia (Parmelee 1980) and Sheathbills on Marion Island (Burger 1979, 1981), thereby affecting their survival. Accessibility to seeds should be similarly affected. Thus, Abbott's (1974) proposal that the climate (temperature) was the ultimate factor affecting the number of land birds might also operate through the effects of climate on

Table 2. Numbers of land bird vagrants recorded at South Georgia and the Prince Edward Islands (Marion and Prince Edward)

	South Georgia[a]		Prince Edward Islands[b]	
	Species	Individuals	Species	Individuals
Palaearctic/Nearctic Migrants				
Waders (Charadriidae, Scolopacidae)	4	13	8	22
Swallows (Hirundinidae)	2	7	1	15
Others	1	1	5	7
Totals	7	21	14	44
Resident S. American/African Birds				
Egrets (Ardeidae)	3	56–66	2	9
Doves (Columbidae)	0	0	2	7
Others	1	1	2	2
Totals	4	57–67	6	18
Unidentified Species	0	0	5+	12
Overall Totals	11	78–88	25+	74
Years	1943, 1958, 1960, 1961, 1970–1982		1974–1983	

[a] Prince and Payne 1979; Prince and Croxall 1983
[b] Burger et al. 1980; Berruti and Schramm 1981; Newton et al. 1983

the accessibility of invertebrates, seeds and perhaps other terrestrial foods.

4 Invertebrates in Terrestrial Food Webs

Invertebrates are by far the most important heterotrophs within undisturbed terrestrial food webs in the Sub-Antarctic. Bacteria and other microbial groups, Protozoa, oligochaetes, Collembola, mites, spiders, and insects are major components of terrestrial communities, and nematodes, rotifers, molluscs, enchytraeids, and tardigrades are often present but not consistently common. The invertebrates occur in several habitats: intertidal zones; among piles of kelp and other jetsam on the shore; within colonies of seabirds and seals; and, in a fairly wide spectrum of terrestrial plant communities (Holdgate 1977; Sømme, to be publ.).

Research on these invertebrates has been centred on taxonomy and geographical distribution (e.g., Gressitt 1967, 1970; Dreux 1971; Deharveng 1981; Travé 1981), physiology (e.g., Block 1982; Vannier 1982), habitat use and life-histories (e.g., Brown 1964; Davies 1973; Travé 1977, 1982) and a few autecological studies (e.g., Paulian 1953; Smith 1977b; Davies 1982). Their diets and food webs are poorly known (Sømme, to be publ.). There are certainly insufficient data to construct quantitative food webs for any island.

Some effects of insularity are evident in the invertebrate communities, which influence their roles in terrestrial food webs. Gressitt (1970) found that the arthropod faunas of Sub-Antarctic islands were disharmonic, relative to Arctic tundra, and that several major groups were absent, possibly due to insularity. The numbers of free-living arthropods on the islands are consistently fewer than those at northern tundra sites at higher latitudes (Table 3), despite the high primary productivity and less extreme climate in the Sub-Antarctic. Both Gressitt (1970) and Abbott (1974) suggested that the physical and biotic environments of the islands

Table 3. Numbers of free-living arthropods on Sub-Antarctic islands (Gressitt 1970) and at I.P.B. Arctic, Sub-Arctic and sub-alpine tundra sites (Ryan 1981)

Sub-Antarctic islands		IBP Tundra sites	
South Georgia (55°S, 36°W)	96	Devon Island, Canada (75°N, 84°W)	167+
Marion Island (47°S, 37°E)	33	Point Barrow, Alaska (71°N, 156°W)	280+
Îles Crozet (46°S, 50°E)	81	Tareya, Taimyr, U.S.S.R. (72°N, 89°E)	395+
Îles Kerguelen (49°S, 65°E)	58	Kevo, Finland (70°N, 27°E)	452+
Heard Island (53°S, 73°E)	27	Stordalen mire (Abisko) Sweden (68°N, 19°E)	115+
Macquarie Island (54°S, 158°E)	95	Hardangervidda (Finse) Norway (60°N, 7°E)	296
		Hardangervidda (Stigstuv) Norway (60°N, 8°E)	260

Table 4. Habitat preferences of 30 species of surface-dwelling arthropods from Île de la Possession, Îles Crozet, January–April 1968 (from Davies 1973)

Habitat	Weevils	Spiders	Others	Total
Moorland only	0	1	5	6
Abundant in moorland and rare in fellfield	1	1	2	4
Total moorland species	1	2	7	10
Fellfield only	5	2	1	8
Abundant in fellfield only and rare in moorland	1	0	0	1
Total fellfield species	6	2	1	9
Moorland and fellfield	0	2	9	11

governed the invertebrate faunistic composition and not island area or distance from a source region as implied by the MacArthur and Wilson (1967) island-biogeography model. Hence, careful studies of the food webs and niches of the terrestrial invertebrates are needed to make meaningful conclusions about island biogeography in the Sub-Antarctic.

The effects of insularity on invertebrate niche dimensions in the Sub-Antarctic are poorly known, although Tréhen et al. (1985) showed that lumbricid earthworms and Diptera exhibit some habitat specialization at Ile de la Possession, Iles Crozet. Using somewhat broader habitat criteria, Davies (1973) showed that weevils and spiders on the same island were apparently habitat-specific, but that many other arthropods were not (Table 4). One-third of the species (11 of the 30) were considered to be regular inhabitants of both fellfield and moorland, habitats which differed greatly. Fellfield has well-drained, rocky soil of low organic content with a sparse cover (usually $< 10\%$) of low cushion-plants, moss and grass tufts; moorland comprises poorly drained organic peat soils with almost complete vegetation cover including quite tall (0.5 m) plants (Davies 1973). A significant portion of the arthropod fauna thus exhibits very broad habitat tolerances.

Similar conclusions can be drawn from a study of macroinvertebrates at Marion Island (Burger 1978). Nineteen vegetation types were sampled on the coastal plain, which differed in plant species composition, physiognomy, the chemical composition of the plants, slope, aspect, soil water content, and soil organic content (Huntley 1971; Smith 1977c, 1978b,c, 1979; Burger 1978; Gremmen 1982). Accordingly, the biomass of invertebrates varied greatly (60-fold) between vegetation types, ranging from 0.7 to 46.9 g m^{-2} (dry wt.) (Burger 1978). Despite this, most invertebrate taxa were found within most vegetation types (Table 5). Furthermore, the ranking of the 19 vegetation types, with respect to biomass, was similar for all invertebrates. This was tested using a Friedman two-way analysis of variance (Siegel 1956:166). The null hypothesis, that the ranking of habitats by each organism was independent, was rejected ($X_r^2 = 46.1$, d.f. = 1, $P < 0.001$). Thus, for a wide

Table 5. Annual mean biomass (dry g m^{-2}) of terrestrial invertebrates in each of 19 vegetation types at Marion Island (from Burger 1978)[a]

Vegetation type[b]	Earthworms	Earthworm cocoons	Lepidoptera larvae	Weevil larvae and pupae	Weevil adults	Spiders	Snails	Slugs
Mires								
1	9.2	0.2	0.3	0.1	0.1	0	0	0
2	15.1	0.3	2.6	0.2	0.01	0.2	0	0.4
3	0.1	0	0.1	0.3	0.1	0.1	0	0
4	9.8	0.2	0.3	1.3	0.4	0.02	0	0
5	0.9	0.02	0.1	0.3	0.1	0.2	0	0
6	15.8	0.3	0.5	0.3	0.1	0.1	0.3	0
7	2.4	0.04	0.1	0.2	0.04	0.01	0	0
8	13.9	0.3	0.5	0.4	0.1	0.2	1.3	0
Slopes								
9	2.1	0.1	0.04	0.1	0.1	0.1	0.2	0.3
10	7.5	0.2	0.1	0.5	0.2	0.1	0.1	2.0
11	7.1	0.1	0.5	0.1	0	0.1	0.3	2.9
Saltspray Zone								
12	3.1	0.01	0.7	0.3	0.1	0	0	0.1
13	8.5	0.2	0.4	0.2	0.1	0.2	0	0
14	8.0	0.3	0.9	0.3	0.1	0.1	0	0
Manured Areas								
15	34.6	1.9	1.0	0.6	0.2	0.1	0	0
16	21.3	0.2	0.8	0.4	0.1	0.4	1.2	0.1
17	17.4	0.4	2.0	0.8	0.1	0.1	0	0
18	43.1	1.3	1.0	0.8	0.4	0.3	0	0.1
Fellfield								
19	6.1	0.1	0.2	0.5	0.1	0.01	0.2	0
Weighted mean[c]	14.6	0.4	0.6	0.4	0.1	0.1	0.3	0.2

[a] Lepidoptera adults and pupae, which occurred in only four vegetation types and which were inadequately sampled by the method used here have been omitted

[b] See Burger (1978) for descriptions of vegetation types

[c] Pooled data weighted in proportion to the % area of each vegetation type in the study area (Burger 1978)

range of vegetation types there were similar assemblages of macro-invertebrates which responded similarly to the differences between the habitats.

Gressitt (1970) also made generalized statements that animals in the Sub-Antarctic tend to occupy a wide variety of habitats. None of the studies mentioned here has had a primary objective of examining invertebrate niches and food webs in the light of modern island-biogeography theory. The Sub-Antarctic islands lend themselves well to comparative studies in this field.

Sub-Antarctic terrestrial food webs are primarily detritus-based (Holdgate 1977; Smith 1977a). Lumbricid earthworms have been found to be important elements in the food webs at Marion Island (Burger 1978), Iles Crozet (Tréhen et al. 1985) and possibly also Macquarie Island (Jenkin 1975) and Kerguelen (Bouché 1982). They are widespread but not abundant in the loamy soils and tussock peat at South Georgia (Smith and Walton 1975). At Marion Island, *Microscolex kerguelenarum* is spectacularly successful, comprising 68% of the total numbers and 87% of the total biomass of macro-invertebrates (Burger 1978), and occurring in all 19 vegetation types sampled (Table 5). This clearly is an ideal island colonist which, having overcome the considerable problems of reaching a remote island, has successfully exploited a wide range of different habitats. Earthworms are scarce or absent at most Arctic tundra sites (MacLean 1981; Ryan 1981), except for certain areas in the U.S.S.R (Rosswall and Heal 1975). Perma-frost, present in the Arctic tundra but not in the Sub-Antarctic, is perhaps a limiting factor for earthworms.

5 Arctic and Sub-Antarctic Tundra: Some Comparisons

Tundra communities in the Arctic and those on Sub-Antarctic islands have many differences. This is expected, given their disparate global positions, geological histories, surface areas, and floras and faunas. Major differences are the reduced climatic seasonality, lack of perma-frost, low summer temperatures, high rainfall and a longer growing season in the Sub-Antarctic. Both regions, however, have broadly similar vegetation structures dominated by low phanerogams, bryophytes and lichens (Rosswall and Heal 1975). Energy and nutrient flux occur mainly through detritus food webs in

both regions (Holdgate 1977; MacLean 1980). Comparisons between these regions highlight some of the factors apparently important in structuring terrestrial food webs in the Sub-Antarctic.

Batzli et al. (1980, 1981) have reviewed the herbivore-based trophic systems in Arctic tundra. Mammals, and to a lesser extent birds, were the dominant herbivores. Homeotherms have an advantage, because they can remain active and productive at low temperatures and tend to have higher assimilation efficiencies than poikilotherms. Microtine rodents, ungulates and geese have substantial effects on the vegetation structure, diversity and productivity and are important in energy and nutrient flux at several Arctic localities. Invertebrate herbivores tend to be uncommon, appear to have little impact on the vegetation and are limited by the severe Arctic climate (Haukioja 1981). H. Remmert (pers. comm.) has proposed that herbivorous ectotherms are more susceptible to cold than other trophic groups.

The climate, particularly the lack of warmth and the prevailing strong winds, also limits herbivory by invertebrates in the Sub-Antarctic (Gressitt 1970). Insects are common above ground only in very sheltered places. Thus, the climate at the islands is important in shaping terrestrial food webs. Vertebrate herbivores, better able to tolerate the climate, are precluded by the geographical isolation of the islands, but have been very successful if introduced by humans.

One of the consequences of having few invertebrate and no native vertebrate herbivores is that plants at the Sub-Antarctic islands seem to be particularly susceptible to macroherbivory (Holdgate 1967). The plants seem to have been under no selection pressure to evolve effective chemical, morphological or life-history adaptations to reduce herbivory. Introduced mammals have thus had devastating effects on some islands. Plant-herbivore interactions and possible anti-herbivore adaptations have received scant attention in the Sub-Antarctic, but have been well studied in high northern latitudes and the proceedings of a special symposium on this topic have been published recently (see Oikos 40 (3), May 1983). Arctic and Sub-Arctic plants possess a wide range of adaptations to restrict herbivory (Haukioja 1981; McNaughton 1983; Tuomi et al. 1983).

Detritus-based food webs are more complex than grazing food webs in both the Arctic and the Sub-Antarctic. In low Arctic tundra, 93%–99% of the primary production becomes dead organic matter (DOM) and much accumulates as peat (MacLean 1980). The detritivores here are mainly enchytraeid worms, Collembola, mites and Diptera. They are preyed upon by few invertebrate carnivores, but support a large and diverse assemblage of migratory birds during the summer (MacLean 1980). In the Sub-Antarctic, virtually all of the plant productivity goes to DOM, some of which supports invertebrate detritivores (Holdgate 1977; Smith 1977a). The detritus food-webs appear to be truncated, relative to the Arctic, because so few bird species are involved. Thus, the isolation of the islands, by restricting colonization or migration of birds, affects the structure of these food webs.

6 Conclusions

The terrestrial ecosystems of the Sub-Antarctic have not been studied sufficiently to reveal the dynamics of their food webs. We also know little about the factors which affect the faunal communities and thus shape the food webs. The combined effects of isolation and the inclement climate appear to be important ultimate factors but the proximate factors remain unclear. Simple observations and experiments could do much to improve our understanding of these food webs. The diets, habitat use and life cycles of the dominant organisms, the invertebrates, are largely unknown. The intensive research at Signy Island in the maritime Antarctic, which led to the construction of quantitative food-web models (Davis 1981), should be emulated in the Sub-Antarctic.

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