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On Co-Existence, Foraging Strategy and the Biogeography of Weasels and Stoats (*Mustela nivalis* and *M. erminea*) in Britain

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Summary. *Mustela nivalis* and *M. erminea*, two sympatric species of weasels of superficially similar appearance and habits, have different breeding and foraging strategies associated with the difference in their body size. *M. nivalis* is more efficient in exploiting small rodent prey, and can breed rapidly to take immediate advantage of rodent peaks, but is vulnerable to local extinction during rodent declines. *M. erminea* has more generalized food habits, and is the larger and probably the dominant species, but is limited by delayed implantation to producing only one litter a year. *M. nivalis* is therefore superior in exploitation competition, and *erminea* in interference competition. We offer the hypothesis that the co-existence of the two species is permitted by a balance of these competitive advantages determined, at a given time or place, by the heterogeneity of the environment and the distribution of the prey fauna. We use this hypothesis to explain cases where co-existence has either broken down or is not recorded (the results of simultaneous introductions to New Zealand and Terschelling Island, and of myxomatosis in Britain, and the distribution of *nivalis* and *erminea* on the offshore islands of Britain). We argue that the diversity and size distribution of the prey fauna of an island (which are both related to its area and isolation) are important in deciding the species and size of mustelids surviving there; for example, we suggest that *nivalis* was present in Ireland in immediate post-glacial times but became extinct with the lemmings.

Introduction

The two smallest mammalian carnivores, *Mustela nivalis* L. and *M. erminea* L. are superficially alike in appearance and habits, and sympatric over much of their range. Though *nivalis* is about half the size of *erminea*, both depend

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upon the same stock of prey (small mammals and birds) and their co-existence has often been noted, but never fully explained. Rosenzweig (1966) demonstrated the similarity of the diets of the three American species of *Mustela*, but could account for their widespread co-existence only by suggesting that they differed in degree of specialization on small rodents, or that the larger *Mustela* of a pair, assumed to be the poorer competitor, regularly preyed upon its smaller relative. His data were inadequate to test or distinguish between either possibility, but since both hinge on differences in body size, both could operate simultaneously. However, Wilson (1975) points out that this alone is not sufficient explanation, since other factors (e.g. the distribution of sizes of prey) greatly influence the extent of "separation" of predators of different body sizes.

The co-existence of two species with overlapping niches, especially if they are congeneric, implies that ecological overlap between them is minimized or in some way counterbalanced so that one does not always displace the other. For example, they may occupy different habitats, be active at different times, or have different foraging strategies. In British *nivalis* and *erminea*, the first two possibilities are not likely, as both live in almost any habitat and both are active at any time (Corbet and Southern, 1977), but they do have markedly different feeding and breeding strategies associated with the difference in their body size, which may reduce competition between them. However, the more similar a pair of competing species, the more vulnerable their co-existence to environmental and other disturbance (McArthur, 1972). We may expect then that the co-existence of *nivalis* and *erminea* will be unstable and liable to be influenced by the environment.

Besides the fact of their co-existence, there are some other intriguing aspects of the ecology of *nivalis* and *erminea* which invite attention. For example, when myxomatosis swept through Britain in the mid 1950s, populations of *erminea* declined steeply, while *nivalis* increased. In contrast, in two instances when both species were introduced together on to islands abounding with potential prey (*Arvicola* and *Oryctolagus*) *erminea* rapidly established itself while *nivalis* became almost or completely extinct. Again, the geographic distributions of the pair contain some curious features; for example, *erminea* occurs frequently on the offshore islands of the Holarctic, but *nivalis* only rarely.

In this paper, we offer a hypothesis on the relationship between *nivalis* and *erminea* which accounts for their co-existence in areas where they are sympatric, and at the same time suggests explanations for the different consequences for each of myxomatosis and of life on islands. Our intention is to stimulate ideas which might lead to the type of specific, carefully designed field work needed ("accurate, precise, massive and tailored to the needs of the biomathematician" – Southern, 1970) before data on real animals can approach and test theoretical ideas, including our own.

We have avoided the use of common names, as the word "weasel" means only *nivalis* in Britain and Europe, but is applied also to *erminea* in America and in Ireland. The smallest American form, *rixosa*, is considered conspecific with *nivalis* (Reichstein, 1957), but when quoting American authors we use whichever name they used. We use the term *Mustela* spp. to mean weasels in general.

We refer to two types of interspecific competition as defined by Miller (1967). In exploitative or "scramble" competition, the most efficient competitor is the one which can obtain and use the greater amount of the disputed resource. It occurs only if the resource is actually limiting. In interference, or "contest" competition, the most efficient competitor is the one which can directly or indirectly limit the access of the other to the resource. It may occur whether or not the resource is actually limiting. Classical competitive exclusion is due usually to interference (Gill, 1974).

Ecological Differences Between *nivalis* and *erminea*

1. Body Size and Home Range

Both *nivalis* and *erminea* are highly variable in body size, but when they occur together, *erminea* is always the larger. Both species show pronounced sexual dimorphism. In Britain, male *nivalis* average 116 g, females 62 g; male *erminea* 321 g, females 213 g (Corbet and Southern, 1977). The size of their home range varies with habitat, but Lockie (1966) found that, in his study area, the home range of one *erminea* male (20 ha) was disproportionately larger than those of 10 *nivalis* males (1–5 ha).

2. Foraging Strategy

Both *nivalis* and *erminea* are specialized predators of small mammals and birds, compared with, for example, their omnivorous relative the badger, *Meles meles* (Corbet and Southern, 1977). Table 1 shows that both species take the same small total number of prey types, though not at the same frequencies: *nivalis* concentrates on small rodents, while *erminea* eats more lagomorphs and birds. The data are taken from Day (1968), whose survey is still the only general comparison of the foods of *nivalis* and *erminea* in Britain, but localized samples from Sussex and Yorkshire (Potts and Vickerman, 1974; Howes, 1977) and a general study in Holland (Brugge, 1977) show similar contrasts between the two carnivores.

The different degrees of specialization within the common range of prey of the two species can be expressed objectively by calculation of their niche widths (Levins, 1968). The niche of a generalist is wider than that of a specialist. Table 1 shows that the niche of *erminea* is wider than that of *nivalis*, and to that extent *erminea* may be called a generalist in comparison with *nivalis*.

The different niche widths of *nivalis* and *erminea* are related to the difference in their body sizes, as explained by the theoretical analysis of McArthur and Levins (1964). The two species each select a different proportion of the mixture of prey sizes available to both. Such selection is to be expected only where the time and energy lost because of neglecting one possible food is slight compared with the benefits of specialization. *Mustela* spp. are highly mobile predators which can efficiently specialize, so separation by differences in the degree

Table 1. Width of the food niches of *nivalis* and *erminea* in mainland Britain (data from Day, 1968)

	M. nivalis		*M. erminea*	
	n	% occ.[c]	*n*	% occ.[c]
Mammals				
Mice and voles	84	55.3	37	22.0
Rats and squirrels	4	2.6	8	4.8
Insectivores	2	1.3	1	0.6
Lagomorphs	29	19.1	47	28.0
Birds	22	14.5	56	33.3
Invertebrates	8	5.3	7	4.2
Plants (probably incidental)	3	2.0	12	7.1
Total no. of prey	152		168	
No. prey types	7		7	
B^a	2.72		4.05	
B_s^b	0.29		0.51	

[a] B = niche width; $B=(\sum p_i^2)^{-1}$ where p_i = proportion of i[th] prey in the diet (Levins, 1968)

[b] B_s = standardized niche width; $B_s=(B-1)/(n-1)$ (Hespenheide, 1975) where n = number of prey types identified. B_s increases as food habits become more generalized, and reaches unity when all foods are exploited equally

[c] Day's method of calculating frequency of occurrence contained several errors, but corrected frequency distributions are not significantly different relative to each other, from these

of specialization is feasible. The reasoning behind their conclusion, "thus, weasels [*Mustela* spp.] tend to be found in sympatric forms of many sizes" is confirmed by Day's results. It leads to the well-known general relationship between the body sizes of carnivores and their prey, as documented for the North American *Mustela* spp. by Rosenzweig (1966).

The ability of *erminea* to regularly select prey of larger sizes seldom tackled by *nivalis*[1] gives it an advantage (Wilson, 1975), especially when supplies of all sizes of prey fluctuate unpredictably (Schoener, 1971). However, if larger prey become scarce, the relative advantage of *erminea* is extinguished. The specialist strategy of *nivalis* gives it an advantage in exploitative competition as long as the abundance of small prey is sufficient. But local declines of voles are followed by emigration or local extinction of *nivalis*, until conditions become favourable again, and voles and *nivalis* recolonize in the same order. Therefore, in a heterogenous environment with a range of prey species fluctuating out of phase in time and space, *erminea* survives by switching between prey sizes, while *nivalis* survives by following the same fugitive strategy as its small prey.

The foraging strategies of the two species are illustrated by observations of their natural history. The specialist role of *nivalis* was recognized by Rubina

[1] *M. nivalis* in Mediterranean countries has the size and presumably the foraging strategy of *erminea*, and is excluded from this argument. In western North America, where *nivalis* is absent and the pair of *Mustela* spp. are *erminea* and *frenata*, *erminea* plays the role of *nivalis* in Britain, and *frenata* that of *erminea*. These are included as ecological equivalents of *erminea* and *nivalis*, though the Californian *frenata* are smaller than British *erminea*, and Californian *erminea* smaller than British *nivalis* (Fitzgerald, 1977).

Table 2. Reproductive strategies of *nivalis* and *erminea* in Britain (source: Corbet and Southern, 1977)

	M. nivalis	*M. erminea*
Earliest possible age at first littering (not conception)	3 months	1 year
Mean litter size, and range	6.2 (4–8)	q[a] (6–13)
No. litters per year	1–2	1
Approximate mean longevity of females	< 1 year	?c. 1 year
Delayed implantation	No	Yes
Maximum possible productivity of one adult female in an optimum season	30[b]	13

[a] From embryo counts, including resorbing foetuses. No records of litter size available
[b] A spring litter of 6 of equal sex ratio (King, 1975a) with the 3 early-born young females and the adult each producing a summer litter of 6: $12+(3\times3)=30$ (King, in prep. (b))

(1960) and in other studies of their food habits (Erlinge, 1975; Moors, 1975; King in prep. (a)). When small rodents become scarce, *nivalis* declines first (Nasimovich, 1949); *erminea* is more often recorded making use of secondary foods when necessary, e.g. berries (Nasimovich, 1949), insects and carrion (King, unpubl.), or worms (Osgood, 1936). Foraging strategy also explains the difference in home range size between *nivalis* and *erminea*: as Lockie (1966) explained, "this discrepancy is in part due to the fact that weasels [*nivalis*] can exploit voles more efficiently than can stoats [*erminea*], since weasels can follow the voles below the ground whereas stoats hunt on the surface and have a curtain of grass between them and their prey". Snow cover has the same effect in Finland (Nyholm, 1959). Similarly, the *M. frenata* (males 256 g; females 122 g) observed by Fitzgerald (1977) were less efficient in hunting voles than the *erminea* (males 59 g; females 45 g) hunting over the same area, and had larger home ranges.

3. Breeding Strategy

The characteristics which contribute most to a high rate of increase in a population are early maturity, more than one litter per year, large litter size, and more than one litter per adult female's lifetime, in that order (Slobodkin, 1961). Table 2 shows that, on these characteristics, the potential rate of increase of *nivalis* is considerably higher than *erminea*. In years of poor food supplies, when *nivalis* produces only one litter, there may be little difference between the two in production. However, in years when small rodents are abundant, adult female *nivalis* may breed a second time, and young females may breed in the season of their birth, enormously increasing the potential productivity of *nivalis* relative to *erminea*. By the end of a good season in Britain the potential descendants of one *nivalis* female could be about double the maximum of one *erminea* female (Table 2). If superiority in exploitative competition goes to the species which turns resources into reproductive adults the fastest (Gill, 1974), *nivalis* definitely has the advantage, at least during a vole peak.

On the other hand, *erminea* has a remarkably efficient breeding system. Young females are extremely precocious, and can be mated before leaving the nest (Müller, 1970). Assuming that ovulation is induced by copulation (Rowlands, 1972), 99% of females of all ages are pregnant with blastocysts in delay by the time the family disperses in midsummer (figures for 334 New Zealand female *erminea* collected December–April, from corpora lutea counts by King, unpubl.). The next generation is therefore already assured even if only one female survives a period of unusual mortality, or colonizes a new area. These differences in reproductive biology, as well as other anatomical details, led Pohl (1910) to suggest that the similar appearance of *nivalis* and *erminea* is only a result of convergence: *erminea* is more closely related to *Martes*, and *nivalis* to *putorius*, than either to each other.

4. Dominance Relationships

In both *erminea* and *nivalis* the female is much smaller than the male, and is subordinate except when with young (Lockie, 1966; Erlinge, 1977a). If animals exhibit the same behavioural responses in interspecific as in intraspecific encounters (as suggested for rodents by Grant, 1972), we may expect the larger *Mustela* species to be dominant over the smaller ones. The literature supports this suggestion. In Russia, *nivalis* is common only where *erminea* is absent (Parovschikov, 1963; Heptner et al., 1967), or *nivalis* takes refuge in vole runways which are too small (4–6 cm diameter) for *erminea* to enter (Nasimovich, 1949). Fitzgerald (1977) observed apparently reciprocal distributions of *erminea* and *frenata* in California, and McCabe (1949) of mink (*M. vison*) and *rixosa*. Among the larger mustelids, Erlinge (1972) documented the restriction of mink by *Lutra* in Swedish lakes and rivers; in Russia there is open antagonism between sable (*Martes zibellina*) and mink, and the latter always lose (Shaposhnikov, 1956).

An individual or species may be selected either because its own capabilities are superior, or because it can somehow impair those of its competitors (Gill, 1974). The daily food requirements of *erminea* are greater than those of *nivalis* (Corbet and Southern, 1977; Moors, 1977); so, in a fluctuating environment, social dominance is a safer strategy than specialization for *erminea*, and gives it superiority in interference competition with *nivalis*.

Co-Existence of *nivalis* and *erminea* in the Field

Having summarized the ecological differences between *nivalis* and *erminea* which may permit co-existence, we now examine field examples illustrating occasions and places where co-existence has been disturbed, or is not recorded. A comparison between the examples could help define what conditions are required for co-existence, and thereby imply what conditions maximize competition. Two of the examples are recent historical events, and one is a geographical distribution presumably related to events in the evolutionary past. The study of long-term

(>20 years) population interactions of vertebrates usually requires too great a scale of time and location for *ad hoc* experimental studies, so we have used instead data from natural experiments. Though these are uncontrolled, they have the required length of perspective.

a) Simultaneous Introductions

Because of their reputation as efficient predators of rabbits and voles, mustelids have several times been introduced on to islands. The experiments in colonization and population dynamics which followed were unintentional and the processes largely unrecorded, but in the best-known cases the results were so clear that exact measurements are not crucial to perceiving the outcome.

1) Terschelling Island. During afforestation in 1910–1930, pines, oaks and alders were planted on 600 ha (about 5%) of the Dutch island of Terschelling. Culverts dug to drain the plantations provided favourable habitat for watervoles (*Arvicola terrestris*), and from about 1920 the increased number of watervoles began to damage trees and gardens on the island. Bounties, mouse typhoid and poison failed to control them, so in 1931, 102–104 *nivalis* and 6–9 *erminea* were liberated on the island. Mammalian prey species available are listed in Table 3. By 1934 *nivalis* had disappeared, even though the number introduced should have been adequate for successful colonization. *M. erminea*, on the other hand, with an initial stock of less than 10 animals, increased prodigiously; they multiplied to at least 180 by 1934, decreasing later as the watervoles disappeared. By 1937 *erminea* had established a fluctuating but apparently permanent population, and the watervoles were extinct (van Wijngaarden and Bruijns, 1961).

2) New Zealand. The history of the introduction of exotic mammals into New Zealand has been summarized by Wodzicki (1965). Three species of *Mustela* were brought in to control the massive increase of rabbits in the newly established pastures. The *nivalis* and *erminea* came from wild stock caught in various parts of Britain, but as *M. putorius* was by 1880 extinct in most of the country (Langley and Yalden, 1977), domestic ferrets (*M. putorius furo*) were reared for release. Tremendous numbers of mustelids were liberated on the worst-affected pastoral areas. In 1885 alone, about 3,000 *erminea* and *nivalis* were sent from Lincolnshire. The N.Z. Department of Agriculture bred ferrets for release until about 1897, and mustelids were legally protected until 1907. By that time it had become clear that, besides failing to control the rabbits, the new arrivals had found the native birds easier to catch, since they were not adapted to avoid predators as were the rabbits and other mammalian prey available, all of which were also introduced (Table 3).

As in Terschelling, *nivalis* started in New Zealand with a distinct numerical advantage, but did not thrive. It is not extinct in New Zealand, but its distribution is restricted and numbers are low (Wodzicki, 1965). *M. erminea* is now widespread and common in many habitats, including native forests, where *nivalis*

Table 3. Distribution on some islands of mammalian prey for mustelids, excluding species introduced after 1900

	Mainland Britain	Ireland	New Zealand	Terschelling
Area (km^2)	230,000	82,000	260,000	110
Sorex araneus	×			×
S. minutus	×	×		×
Neomys fodiens	×			
Talpa europaea	×			
Erinaceus europaeus	×	×	×	×
Clethrionomys glareolus	×			
Microtus agrestis	×			
Arvicola terrestris	×			× [a]
Apodemus sylvaticus	×	×		×
A. flavicollis	×			
Mus musculus	×	×	×	×
Micromys minutus	×			
Muscardinus avellanarius	×			
Rattus rattus	×	×	×	
R. norvegicus	×	×	×	×
R. exulans			× [a]	
Oryctolagus cuniculus	×	×	×	×
Lepus capensis	×		×	
L. timidus	×	×		
Sciurus vulgaris	×	×		
S. carolinensis	×	×		
Trichosurus vulpecula			×	
Total	20	10	8	8
Weight range 0–100 g	11 (55%)	4 (40%)	2 (25%)	4 (50%)
100–1000 g	6 (30%)	4 (40%)	3 (38%)	3 (38%)
>1000 g	3 (15%)	2 (20%)	3 (38%)	1 (12%)
Prey size index $\frac{\sum \log_e \text{(average weight)}}{\text{(total no. prey types)}}$	4.57	4.96	6.07	4.14[b]

[a] Common at the time mustelids were introduced, extinct or rare now

[b] Includes the 3 species of insectivores which are not usually eaten by mustelids, though whether or not they are on Terschelling is unknown. This figure therefore might under-represent the mean size of prey actually available on Terschelling

and *p. furo* are usually rare or absent (King, unpubl.). *M. p. furo* is locally common in farmland.

b) Myxomatosis in Britain

Myxomatosis reached southern England in late 1953 (Fenner and Ratcliffe, 1965). It had spread throughout the country by 1955, and its immediate effect was to reduce the population of rabbits by about 90%. The consequences for carnivores of this staggering ecological experiment went largely unrecorded, though its effects on the tawny owl. (*Strix aluco*) and the buzzard (*Buteo buteo*) have been described by Southern (1970) and Moore (1956), respectively. Although we have few accurate data on populations of mustelids before and after the epidemic, the results were sufficiently clear-cut to show on the crudest estimates, the vermin records from game estates. Records from all over the country agree that populations of *erminea* were immediately and substantially reduced. *M. nivalis* was little effected at first, because although there was a general shortage of prey in 1955–56, caused by the concentration of all remaining predators on small rodents, *nivalis* could follow voles and mice into their runways and nests, and thus have the advantage over even the most assiduously hunting foxes and raptors. But in the years after the epidemic, the herbaceous vegetation of Britain was thicker and greener than before (Fenner and Ratcliffe, 1965) and 1957 was a year of great abundance for mice and voles. Exceptionally many *nivalis* were killed on most game estates that year (Jefferies and Pendlebury, 1968). Since 1955 the ratio of *nivalis* to *erminea* killed has been reversed on many estates, from about 1:2 before myxomatois, to 2:1 since (Craster, 1970; Hewson, 1972). According to Hewson this reversal was due to a statistically significant decline in *erminea* and an insignificant increase in *nivalis*. However, as Hewson pointed out, the lighter female *nivalis* are likely to be under-represented in samples taken by steel traps; and further, traps at a given density will catch a lower proportion of the total population of *nivalis* than of *erminea*, because of the difference in the sizes of their home ranges (King, 1975a). These two factors could tend to underestimate the increase in *nivalis*, yet the records from one estate in Norfolk show that the average number of *nivalis* killed per year more than doubled, from 15 in the 7 years before the outbreak (1947–53) to 38 in the 7 years when *erminea* was at its lowest ebb (1957–63) (King, in prep. (b)).

c) The Biogeography of nivalis and erminea in Britain

1) Niche Overlap and Competition for Food. The overlap in diet between *nivalis* and *erminea* (Table 1) could be a source of competition when preferred prey are scarce or alternatives lacking. The potential overlap of their food niches is extensive, judging by the values of niche overlap (α) calculated from the formula of Levins (1968) (Appendix 1).

The degree of niche overlap implied by these figures does not necessarily measure the real degree of competition between *nivalis* and *erminea* in Britain, for two reasons. First, the actual overlap is probably reduced by the different hunting behaviour and micro-habitat of the two species, presumably developed because of competition in the past. The calculated figures are therefore maxima and are based on the rather small samples from only one study (Day, 1968). Secondly, niche overlap is not a direct measure of the intensity of exploitative competition; it is a necessary but not sufficient condition for such competition, and is neither necessary nor sufficient for interference competition (Pianka, 1976). Colwell and Futuyma (1971) have pointed out that niche overlap can logically be used to prove either the presence or the absence of exploitative competition. The literature illustrates this anomaly. Data showing overlaps were interpreted by Erlinge (1972) to show that competition was occurring between *Lutra* and *M. vison* and was significant; by Herrera and Hiraldo (1976) to show that competition was not occurring among several species of Scandinavian owls, otherwise selection would not tolerate the overlap; and by Clem (1977) to show that it occurred between *Martes americana* and *M. pennanti* in winter but might be mitigated by habitat separation. Niche overlap leads to competition only when resources are limiting. Nasimovich (1949) states that there was no competition between *nivalis* and *erminea* in Russia when voles were abundant, and there were enough microtines available in Scandinavia for all the owl species to feed on them together (Herrera and Hiraldo, 1976). At present there are no data with which to evaluate the niches of *nivalis* and *erminea* in relation to the density of prey. The high values of α show only that competition for food between British *nivalis* and *erminea* is potentially important in certain circumstances; it may both increase the chances of local extinction of one of the pair, and reduce the chances of recolonization, especially of islands (see Appendix 1 for further details).

2) Distribution of erminea and nivalis in the British Isles. The British Isles (Fig. 1) are a group of over 400 islands ranging in area from rocky stacks to 230,000 km^2. In Fig. 2, the number of mammalian prey species available for mustelids are plotted against the area of all the major islands. Potential prey (listed for the mainland in Table 3) include all species from shrews to hares, excluding other carnivores and those mammals too large or unavailable to mustelids (data from Corbet, 1971). The plot is not intended to illustrate the biogeographical relationship between number of species and area, as it refers only to mustelid prey species. Rather, it shows that mustelids do not occur on islands below a certain size, and that this restriction is probably related to the number of prey species available. We have not calculated the distribution of bird species, which could be important alternative prey for mustelids on islands with few mammals (as, for example, in New Zealand). However, it is clear from Lack (1942) that the pattern of decreasing number of species with area and isolation is similar in land-birds and mammals.

The spread of points in Fig. 2 is wide because diversity of prey has been plotted only against area. In fact, diversity is affected by other factors: distance from the source of colonizing species (illustrated in British insular rodents by Grant, 1970), the period of time available for colonization, and environmental factors on the island. The British offshore islands show every combination of these three influences, and are therefore a rather heterogeneous group. The southern parts of England were probably free of ice throughout most of the Pleistocene (Fig. 1), and islands south of them, e.g. Wight and the Channel Isles, are landbridge islands. Most of the rest are oceanic islands in the sense of McArthur (1972) (i.e., they had to be colonized across water) and were released from the ice in chronological order northwards. The most northerly (the Orkneys and Shetlands) and the furthest offshore (the Outer Hebrides) therefore have the fewest species.

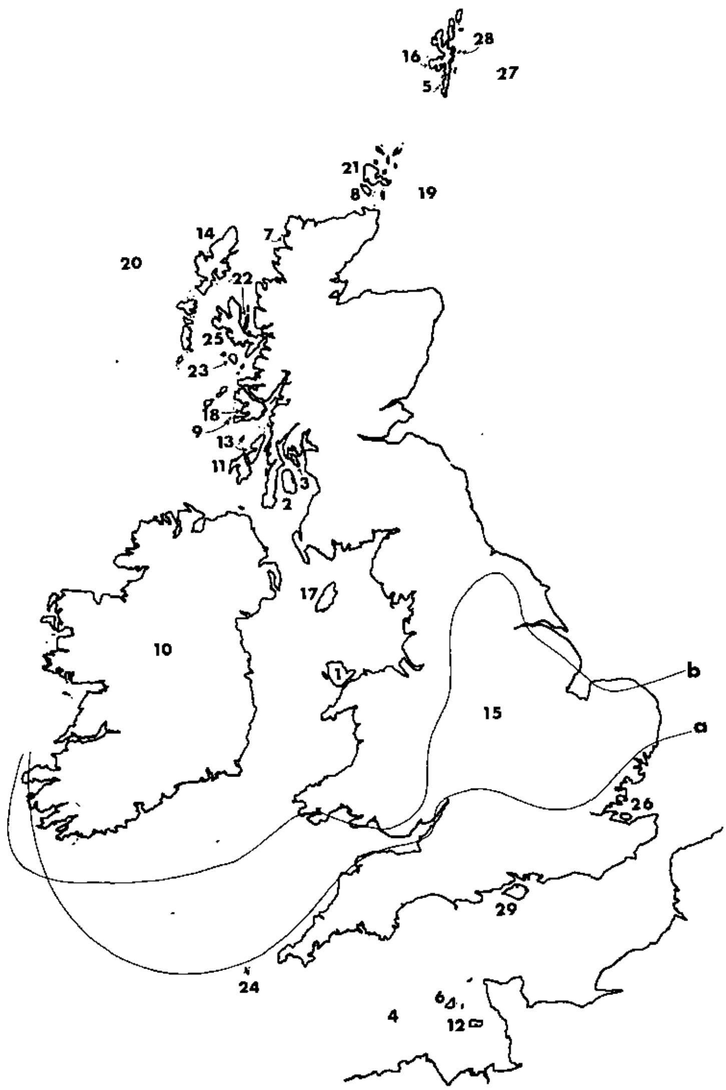

Fig. 1. The British Isles, with islands named in the text numbered as follows: 1. Anglesey; 2. Arran; 3. Bute; 4. Channel Islands group; 5. Colsay; 6. Guernsey; 7. Handa; 8. Hoy; 9. Iona; 10. Ireland; 11. Islay; 12. Jersey; 13. Jura; 14. Lewis; 15. mainland Britain; 16. mainland Shetland; 17. Man; 18. Mull; 19. Orkneys group; 20. Outer Hebrides group; 21. Pomona; 22. Raasay; 23. Rhum; 24. Scillies group; 25. Skye; 26. Sheppey; 27. Shetlands group; 28. Whalsay; 29. Wight. The narrow lines show (*a*) the maximum extent of glaciation in the Pleistocene era and (*b*) the extent in the last (Devensian) glacial period

The scatter of islands on Fig. 2 may be divided into three classes. All those smaller than a critical size, about 90 km^2, support no mustelids. The only exception is Guernsey (60 km^2); however, the biogeography of the Channel Islands is perhaps different from the rest of the British group, as their nearest mainland is not England, but France (Fig. 1). Of the 16 islands larger than

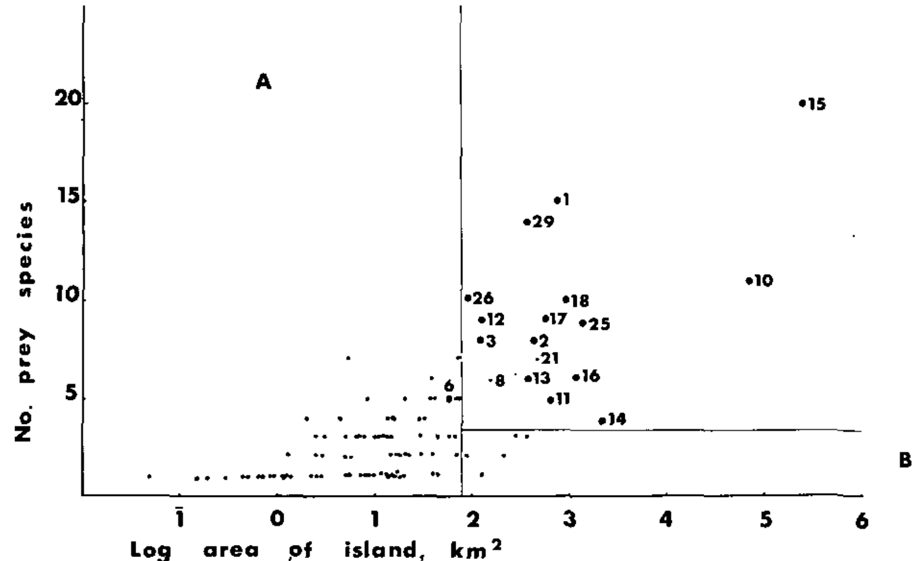

Fig. 2. The number of prey species for mustelids plotted against area in the British islands. Mustelids do not occur on islands (*smaller symbol*) which are too small (**group A**) or on which there are too few prey (**group B**). Islands on which mustelids occur are numbered as in Fig. 1, and listed in the text

90 km^2, excluding mainland Britain, and having four or more mammalian prey species, 14 support at least one species of mustelid (the two exceptions, Hoy and Pomona, are both in the Orkneys). Islands with fewer than 4 prey species, even if large, have no mustelids, and these (group B in Fig. 2) are all in the Outer Hebrides or Shetland groups. Hence we can say that the approximate minimum conditions for a British island to support a persisting population of mustelids are an area greater than 90 km^2, and at least 4 mammalian prey species, and that the probability that such an island will have mustelids decreases with its isolation and increasingly northerly position.

The present distribution of mustelids on the 14 islands is as follows:

a) *nivalis* alone: none

b) *erminea* alone: Jersey, Guernsey, Islay, Jura (60–600 km^2); also mainland Shetland (1,000 km^2), introduced in the seventeenth century or earlier (Venables and Venables, 1955)

c) *nivalis* and *erminea:* Wight and Skye (380 and 1,600 km^2); also Anglesey (700 km^2) and Sheppey (90 km^2), both bridged

d) *putorius furo* alone: Bute (120 km^2), introduced

e) *p. furo* and *erminea:* Man (570 km^2), Mull (900 km^2); *p. furo* introduced

f) *p. furo* and feral American mink (*M. vison*): Arran (430 km^2) and Lewis (2,000 km^2), both species introduced

g) *Martes* and *erminea:* Ireland (82,000 km^2)

Historical records of mustelids on islands around the British coast show that they may at times be found on the smaller islands, but do not persist for long. For example, *erminea* has been recorded on Whalsay (20 km^2), Iona (10 km^2), Handa (< 1 km^2) and Colsay (< 1 km^2), and both *erminea* and *nivalis* on Raasay (70 km^2), in the past (Harvie-Brown and Buckley, 1892; Evans and Buckley, 1899; Harvie-Brown and McPherson, 1904; Venables and Venables, 1955). Some of these records refer to single animals (e.g., on Handa) but others could have been breeding populations: a report by H.D. Graham in 1852 states that *erminea* was "very common in Iona ... where it appears to be especially destructive to the Ringed Plover" (Harvie-Brown and Buckley, 1892). Millais (1905) stated, without citing sources, that *erminea* was present on Rhum (110 km^2) and Bute, and that it had been introduced into both Orkney and Shetland. When he wrote, *erminea* was still present on Colsay, and "until recently" on Whalsay, though it had by then become extinct again in Orkney. He also records *nivalis* on Islay and Bute. G.E. Martel (pers. comm.) reports that although *erminea* was common in Guernsey about 20 years ago, none has been seen recently.

The pattern of the distribution of mustelids in Britain exemplifies two general principles of biogeography: strict carnivores can establish permanent populations only on relatively large islands, and (as documented in rodents by Grant, 1970) ecologically similar species are unlikely to be found together on islands below a certain size.

A Hypothesis on the Co-Existence of *nivalis* and *erminea*

We offer the following hypothesis to explain the co-existence of *nivalis* and *erminea*. *M. erminea*, the larger species, is more of a generalist than *nivalis*, and is dominant over *nivalis* in interspecific encounters. On the other hand, *erminea* cannot enter the nests and runways of small rodents, and is limited by delayed implantation to producing only one litter per season. *M. nivalis* specialises on small rodents, which it is more efficient in exploiting than is *erminea*. It has a high potential rate of increase, and can breed rapidly to high densities where or when rodents are abundant. However, the dependence of *nivalis* on unstable populations of small rodents makes it vulnerable to local extinction.

The biology of the two species therefore gives *erminea* superiority in interference, and *nivalis* superiority in exploitation, which results in an unstable balance of competitive advantages determined by the environment. In a patchy environment of sufficient size, where local populations of prey fluctuate asynchronously, neither can eliminate the other except temporarily and locally. They co-exist because, in a sufficiently diverse habitat, *nivalis* can avoid confrontations with *erminea*, and *erminea* can avoid dependence on a single prey resource. This situation corresponds to the Type 2b competition of Grant (1972). As Levin (1974) put it, the only salvation for a competitively inferior species is a patchy environment permitting a fugitive strategy; both *nivalis* and *erminea* are in one sense inferior to the other, but in a diverse habitat, each can avoid competing on the other's terms.

This hypothesis explains the data presented above as follows:

a) Since there were no voles (*Microtus* or *Clethrionomys*) on Terschelling or in New Zealand, both introduced populations of *nivalis* were at a considerable disadvantage, and never likely to become large in either place. However, whereas *nivalis* became extinct on Terschelling within four years, in New Zealand it still persists in scattered localities after 95 years. The two main islands of New Zealand are very large and diverse compared with Terschelling, giving *nivalis* the environmental heterogeneity it needs to avoid *erminea* and to operate its fugitive foraging strategy. The size distribution of prey on Terschelling is more favourable for *nivalis* than is that in New Zealand (Table 3), which suggests that it might have survived at low density on Terschelling but for interference from *erminea*. Terschelling (110 km^2) is much smaller than the smallest British island (380 km^2) on which both species survive together. (The large islands in the Mediterranean where *nivalis* occurs alone are not comparable cases, as they appear to be outside the contemporary range of *erminea*.)

b) The decline of *erminea* rather than *nivalis* after the catastrophic advent of myxomatosis in Britain is best explained by the sudden change in the size distribution of prey for the two species. As McArthur and Levins (1964) explain, *erminea*, which relies on a combination of large and small prey now no longer present, was replaced by *nivalis*, which relies on a combination of small prey still available. Smaller predators are favoured if larger prey are reduced more than small ones (Wilson, 1975). The increase of *nivalis* was certainly due mainly to improved supplies of small rodents, though the removal of interference competition could have helped (Hewson, 1972).

c) The distribution of *nivalis* and *erminea* on the British offshore islands can be explained in terms of the influence of environmental heterogeneity on the balance of advantages of the two species. *M. erminea* now occurs on 11 of the 16 British islands inhabited by mustelids. *M. nivalis* occurs, co-existing with *erminea*, on only four, which are all close to the mainland and either connected to it by permanent bridges, or are large (over 380 km^2). The superiority of *erminea* in interference competition and the effect of the high value of α mean that *nivalis* cannot co-exist for long with *erminea* except on islands which are large and diverse, or easily recolonized, or both. But neither can *nivalis* survive indefinitely on smaller islands where *erminea* is absent. If there are no voles, *nivalis* apparently cannot establish; if voles are present, their irregular fluctuations make *nivalis* liable to random extinction. The balance is against *nivalis* everywhere except on the largest islands, because on smaller ones its superiority in exploitation is over-ruled by its specialist hunting strategy and its vulnerability to interference from *erminea*.

Discussion

In the argument presented here we have brought together information on several curious aspects of the ecology of *nivalis* and *erminea*, and proposed a single hypothesis to account for them. The main ideas behind it are not particularly original. The crucial importance of environmental heterogeneity in the ecology of predators has been demonstrated by many workers, for example, in the laboratory by Huffaker (1958) and in the field by Southern and Lowe (1968); and the idea of a shifting balance of competitive advantages was mentioned by Jaeger (1974) and demonstrated in tits by Dhondt (1977). But we are intrigued by the new understanding of the ecology of mustelids suggested by the concept of the interplay of feeding strategy and competitive advantages in different environments.

For example, the differences in relative density of *erminea* and *nivalis* in various parts of Britain (Matheson, 1959) could be controlled by local differences in abundance of the prey species common to the whole country. In game records, *erminea* outnumbers *nivalis* in Norfolk (King, in prep. (b)), but *nivalis* outnumbers *erminea* in Hampshire (Middleton, 1966), which could perhaps be explained if rabbits are (or were) generally more abundant in East Anglia. In different habitats, competitive advantage and local prey abundance explain variations in territory size of *nivalis* and whether co-existence with *erminea* is possible or not. In a pre-thicket pine plantation where the density of *Microtus* was 110–540 ha, territories of male *nivalis* were 1–5 ha, and vigorously defended against other *nivalis*, though several resident *erminea* shared the same ground (Lockie, 1966). In contrast, in a mature deciduous woodland, the density of *Apodemus* plus *Clethrionomys* was 21–39 ha; territories of male *nivalis* were 7–15 ha, and were less obviously defended; there were transient, but no resident *erminea* (King, 1975b). Rabbits were not present in either study area, but the voles were numerous enough in the plantation to supply the needs of both *nivalis* and *erminea* without competition, while the superiority of the woodland *nivalis* in exploiting the scarce small rodents allowed it to make a living where *erminea* presumably could not.

Ranges of female *erminea* and *nivalis* are much smaller than those of males (King, 1975b; Erlinge, 1977b): the observations of Erlinge (1977a) suggest that in *erminea* this reflects the smaller females' advantage in exploiting small rodents, which counterbalances their social subordination. In both species, females take significantly more small rodents than do males (King, 1977, and unpubl.). Rosenzweig (1966) was probably correct that both interspecific aggression and differential specialization facilitate co-existence in *Mustela* spp., though effective aggression need only be threatening, not necessarily extending to actual predation, as he suggested.

The distribution of *nivalis* and *erminea* on British islands supports Grant's (1972) suggestion that first generalists and then specialists occupy islands as these increase in size and complexity and decrease in isolation. The disadvantages of the specialist strategy have been illustrated in studies of other competing pairs; for example in tits by Dhondt (1977), and in small rodents by Crowell and Pimm (1976). Mustelid distribution, together with our calculations of niche overlap (α) confirms the conclusion of McArthur (1972) that colonists rarely succeed on an island with a competitor having α as large as 0.5.

One theory explaining the distribution of *nivalis* and *erminea* in Britain (originally suggested by Hinton and outlined by Harrison Mathews, 1968) presumes that the two species did not arrive together. It suggests that when the British Isles were re-invaded by temperate fauna after the last glaciation (*c.* 12,000–8,000 years B.P.), *erminea* arrived first and colonized Ireland and some of the Scottish islands before they were cut-off by rising post-glacial sea levels. *M. nivalis*, arriving later, was able to reach only the four islands on which it is found today, which are all close to the mainland and, by implication, cut off later. But there is no reason for *nivalis* to lag so far behind the rest of the animal community in which it lived. *M. erminea* and *nivalis* are both typical members of the arctic fauna, well-adapted to cold (Segal, 1975; Moors, 1977). In Poland, a region at the same latitude as Britain and connected to it at this time across Germany, Holland and the bed of the North Sea, both *erminea* and *nivalis* were present during the last glaciation (Wojcik, 1974). *M. erminea* was certainly present in Britain during the late Devensian (the last glacial period), among a typical cold-climate fauna including *Dicrostonyx, Lemmus, Alopex, Alces* and *Rangifer* (Stuart, 1974). *M. nivalis*, or perhaps its ancestor *praenivalis* (Kurtén, 1968), was present in Norfolk in the early mid-Pleistocene (Stuart, 1974); since the ice never advanced much further south than this (Fig. 2), *nivalis* need not necessarily have been expelled from southern England by later glaciations. The absence of *nivalis* from the assemblage of arctic animals from the British late Devensian is more easily explained by the acknowledged rarity of mustelid fossils (Kurtén, 1968) than by supposed differences in migration rates.

The earlier theory is also inadequate in assuming that *nivalis* is absent from most of the islands now because it never reached them, and that islands with *erminea* now have supported them since the retreat of the glaciers. Recent studies in biogeography show that distributions are likely to be more dynamic than this.

The interesting point for us is not whether a species ever arrived, but whether it has persisted. A species present on one of the British islands could either have survived the glacial period or have colonized since then. The characteristics required of a species in each case are different. Glacial survivors must be adapted to arctic conditions. Landbridge relics cut off from the mainland must have stable populations and be good competitors to avoid extinction and, if they colonized by land in early post-glacial times, be cold-adapted as well. Colonists of oceanic islands must be efficient in both dispersal and establishment of new populations, which together define colonising ability. May the distribution of *nivalis* and *erminea* in Britain simply reflect differences in these characters?

Both *nivalis* and *erminea* are circumpolar and boreal in distribution. Corbet (1962) classified *erminea* as a glacial relict in Ireland, but described the absence of *nivalis* there as "something of a zoogeographical mystery" (Corbet, 1966). Both are widely distributed on the British mainland; both swim, *erminea* to at least 1.6 km from land (Corbet and Southern, 1977– and see Appendix 2); both could have been assisted in dispersal by man if accidentally included in agricultural cargo carried by interisland traders (Corbet, 1961; the survey of Davis (1956) reported both found in hayricks) or deliberately introduced for pest control. But *erminea* has a considerable advantage over *nivalis* in establishing a new population, because it has a more adaptable, generalist feeding strategy, and a mating system which ensures that nearly all dispersing young females are already pregnant. The same characters give *erminea* a more stable population than *nivalis*, whose distribution and abundance is largely determined by the fluctuations of its small rodent prey (Erlinge, 1974; King, in prep. (b)). That the wide-ranging *erminea* also readily makes considerable excursions in search of food is shown by reports of its occurrence on islands far too small to support a permanent population, such as the 50 × 20 m islet of Eileen Molach, 200 m from the shore of Loch Ba, Argyll (Morton Boyd, 1958), and by the incidents recounted in Appendix 2.

We conclude that the superior colonizing ability of *erminea* is sufficient to explain its wider distribution among the British islands. However, this alone does not explain two curious features of the relative distribution of the two predators. First, though *erminea* is much larger than *nivalis*, the smallest unbridged island on which it can survive is 60 km^2, compared with 380 km^2 for *nivalis;* and *nivalis* is not found on any small islands without *erminea*. Our hypothesis suggests that this is because on remote islands smaller than about 380 km^2, *nivalis* is always at a disadvantage because of its specialized feeding strategy, the effect of niche overlap, and its vulnerability to local extinction and/or to interference from *erminea*. Second, though Ireland (82,000 km^2) should be large enough to support both species, *nivalis* is absent there. We suggest that *nivalis* may once have been present in Ireland, but became extinct because a change in the size distribution of available prey removed its advantage over *erminea*. In the Devensian period the habitat in Ireland was tundra (Stuart, 1974), and a fall in sea level of 100 m below Ordnance Datum joined Ireland to southern Scotland by "a narrow isthmus at least" (*loc. cit.*). The Devensian fauna of Ireland included *Dicrostonyx torquatus, Lemmus lemmus, Lepus timidus, Alopex lagopus,* and *Mustela erminea* (Stuart, 1974). If these species could cross the landbridge, so presumably could *nivalis*. However, *Microtus and Clethrionomys,* both less cold-adapted species than *nivalis*, did not invade Britain till after Ireland was cut off in earliest post-glacial times, about 10,250 years B.P. (Corbet, 1961; Stuart, 1974). Hence, when the lemmings became extinct they were not replaced by voles, and the absence of voles tipped the balance of advantages permanently in favour of *erminea; nivalis* then joined the list of species removed as extinctions adjusted the number of resident species to the isolation and reduced land area of post-glacial Ireland. The lack of fossil material to support this suggestion is no great surprise: as Beirne (1952) remarked, "palaeontological evidence is at present of little value ... in most instances the histories [of the British species] must be reconstructed primarily on ecological, taxonomic and zoogeographical evidence".

Other geographical regions in which the number of *Mustela* spp. is reduced, besides Ireland and New Zealand, include northern North America and southern Europe. All these regions have in common a reduced diversity of prey (McNab, 1971; Herrera, 1974; Table 3). Our hypothesis suggests that the question of which species remains should be determined largely by the size distribution of the diminished prey fauna; and further, that if the isolated mustelid exhibits character release, it should be in the direction determined by that prey fauna – which may or may not be in the direction of the absent competitor. *M. erminea* shows both convergence (toward the absent *frenata* in Canada (McNab, 1971) and toward the absent *nivalis* in Ireland (Corbet and Southern, 1977)), and divergence (away from the virtually absent *nivalis* in New Zealand forests (King, unpubl.)). These curious observations are obviously worth further investigation.

Our general hypothesis on the co-existence of *erminea* and *nivalis* rests on circumstantial evidence, but it invites testing. Small mustelids are probably among the easiest mammalian predators from which to obtain the field data needed to examine theoretical ideas. They live at relatively high densities compared with other Carnivora, and field techniques to collect data on population density and food habits are available (King, 1973; King and Edgar, 1977; Erlinge, 1977b). Many details of ecological theory could be checked from mustelids. For instance, is the width of the food-niche of *erminea* influenced by the density of its preferred prey? (Wilson, 1975). Is the realized niche of *nivalis* made narrower by the absence of *erminea?* (Morse, 1974). Evidence of this kind is the only really critical test of competition (Miller, 1967). Scent-marking is an activity highly developed in small mustelids (Stubbe, 1972), and could be a highly effective mechanism for interference competition (Gill, 1974), but we do not know whether scent-marks have the same deterrent effect on invaders of other species as on conspecifics (Erlinge, 1977a). An assessment of the relative importance of intra-specific and inter-specific competition in sympatric *Mustela* spp., along the lines of that done for tits by Dhondt (1977), would help define the conditions which give each species its relative advantage. We have no reliable estimates of rate of increase or population density for either species, alone or together, so at present cannot test whether the population dynamics of one are affected by the other. The distribution of *nivalis* in Britain suggests that voles are an essential food; are mice an inadequate substitute because they do not usually reach such high population densities? Crowell's (1973) study of the biogeography of mice and voles on islands offers a fascinating comparison with the distribution of *nivalis* and *erminea*, as well as an excellent pattern for an experimental study to test our hypothesis. Even simple laboratory observations of interspecific dominance relationships (an extension of the work of Erlinge (1977a) on *erminea*), or detailed studies of the food habits of carefully defined sympatric and allopatric populations, would be helpful. In the older natural history journals there might also be many more records of other introductions (such as in Shetland), both successful and unsuccessful, which could add information on the minimum characteristics of an island necessary for the survival of a permanent population of mustelids. The history of failed introductions round the British islands could provide interesting evidence for or against our hypothesis.

Realistic models in ecology need specific field data, and a good start could be made with any one of the questions this paper has raised.

Appendix 1. Niche overlap (α)

Calculation of α

The extent of overlap by *erminea* on the food niche of *nivalis*, α_{ne}, and vice versa, α_{en}, is calculated from the formula of Levins (1968):

$$\alpha_{ne} = \frac{\sum P_e P_n}{\sum P_n^2}; \qquad \alpha_{en} = \frac{\sum P_e P_n}{\sum P_e^2}$$

where P_e and P_n are the proportions of each food type in the diet of *erminea* and *nivalis*, respectively. When the diets are identical, $\alpha = 1.0$. From the data in Table 1, $\alpha_{ne} = 0.62$, and $\alpha_{en} = 0.92$.

Significance of α

The ratio of the carrying capacities, K, of two co-existing populations is set by their respective values of α. In the present example, at equilibrium $(1/\alpha_{en})>(K_n/K_e)>\alpha_{ne}$ (McArthur, 1972; May, 1976). As α_{en} and α_{ne} approach 1.0 (i.e., as exploitation competition increases) the limits of K_n/K_e become increasingly narrow, and the carrying capacities more alike. Then, even slight changes in the species' relative competitive abilities can upset the equilibrium and lead to the exclusion of one of them. Competitive exclusion of *erminea* will take place when $K_n>(K_e/\alpha_{en})$ and of *nivalis* when $K_e>(K_n/\alpha_{ne})$.

The potentially high values of α_{en} and α_{ne} have important consequences for the co-existence of *nivalis* and *erminea*, particularly in simple or unpredictable habitats such as farmland or on islands. In these habitats, exclusion of one by the other is highly likely and there will be a pattern of recurring local extinctions. Recolonization is easy on farmland, but on islands could take years. A high α also acts to reduce the survival time of a colonizing species. Expected survival time, $T\approx(1/K\lambda)(\lambda/\mu)^K$ (McArthur, 1972) where λ and μ are the instantaneous *per capita* rates of birth and death, respectively, and K is carrying capacity. Exploitation competition, estimated roughly by α, reduces λ and K for both competing colonists. However, interference competition is likely to increase μ for *nivalis* more than for *erminea*, since *nivalis* is more susceptible to attack from *erminea* than vice versa. Hence, the survival of *erminea*, and even more of *nivalis*, may be shorter on islands colonized jointly than on those colonized singly.

An incidental result of the way the formulae are defined is that the narrower the niche, the greater the value of α and the more efficient the exploitation of resources. These figures confirm our previous view that *nivalis* is more efficient in exploitation competition than is *erminea* $(\alpha_{en}>\alpha_{ne})$. The formulae do not apply to interference competition.

Appendix 2

The following unpublished observation was made by Capt. G.C. Phillips in Baltimore Bay, on the south-west coast of Ireland, in summer 1968. He was sailing about 0.4 km offshore, in a light wind and calm sea. He saw a small "torpedo" approaching at a great rate, which swam so close that he thought it might be trying to come aboard, but it crossed his bow a metre ahead. He clearly identified it as a good-sized *M. erminea hibernica*, swimming a "determinedly straight course" for the shore of an island, Ringarogy, about 0.5 km off the mainland at that point. Its head and shoulders were well up, the latter working fast. Its tail was not visible, but he reckoned the body was about 20 cm long, a strong reddish brown. It was definitely not an otter. The mainland shore was shelving stones, so it could not have fallen in; Capt. Phillips believed that, as the rabbits on Ringarogy were still healthy and the mainland ones recently reduced by myxomatosis, the *erminea* was hungry and was purposely making for the island rabbits.

A similar incident is reported by Harvie-Brown and McPherson (1904), who state that an *erminea* was sent to them "which had been killed while swimming from Skye to the mainland". McNally (1968) saw an *erminea* escaping from a dog by "diving into a stream, and swimming across with all the aplomb of one born to this element".

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