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Small Mammal Differentiation on Islands

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SUMMARY

The reason for the distinctiveness of small mammals on islands has traditionally attracted some imaginative story-telling, usually invoking isolation (as a relict) followed by adaptation and/or random genetic changes. Studies of voles on Orkney, long-tailed field mice on the Hebrides and Shetland, and house mice on the Faroe archipelago show that the main factor in differentiating island races from their mainland ancestors is the chance genetic composition of the founding animals. Subsequent change has necessarily to be based on the genes and frequencies carried by this colonizing group. Probably most post-colonization change is adaptive, although possibly limited in extent both by the initial paucity of variation and by the conservative effect of intragenomic interactions. It is probably helpful to recognize that the 'founder effect' or principle commonly invoked in discussions about evolution on islands involves a founder 'event', followed by founder 'selection'. Island differentiation is not necessarily a precursor to speciation, although the wide occurrence of island endemics suggests that founder effects should not be rejected as a driving force initiating speciation. Notwithstanding, island forms provide a valuable 'laboratory' for testing new genetic combinations, a small proportion of which may prove evolutionarily exciting. Only more empirical studies will uncover their evolutionary importance.

1. INTRODUCTION

Island endemics have provided (and probably will continue to provide) a fertile bank of evolutionary 'just-so' stories. For example, Charles Darwin's vaunted Damascus Road conversion to evolution when he visited the Galapagos was in fact nothing of the sort: by the time the *Beagle* put into the Galapagos, Darwin was bored and somewhat homesick (Sulloway 1982; Berry 1984). Soon after his return to England, he published a note showing that he retained only very vague memories of the islands. All he could say about the finches (later to be eponymized as 'Darwin's finches') was that 'their general resemblance in character and the circumstance of their indiscriminately associating in large flocks, rendered it almost impossible to study the habits of particular species. They appeared to subsist on seeds' (Darwin 1837).

2. *MICROTUS* (*ORCADENSIS*) *ARVALIS* AND OTHERS

The story of the Orkney vole is a typical cautionary tale of island speciation, which shows both the pitfalls of over-enthusiastic speculation and highlights the purgative effect of continued research.

The Orkney vole was introduced to science by J. G. Millais (1904) as a new species *Microtus orcadensis*, almost twice as large as the common British vole *M. agrestis* (which does not occur in the Orkney archipelago), as well as differing in a number of pelage and skeletal traits. Oldfield Thomas at the National History Museum confirmed it as 'a most distinct species, and one of the most interesting and unexpected discoveries ever made in British mammalogy' (Thomas 1904). But Millais had not finished; the year after his original description of voles from the main Orkney island, he added a subspecies (*M. o. sandayensis*) from Sanday, one of the northern isles of Orkney (Millais 1905). This was raised to a full species by Miller (1908), who went on to describe a subspecies of it from the nearby island of Westray (*M. sandayensis westrae*) on the grounds that the voles there were slightly smaller and darker than on Sanday. Finally Hinton (1913) added two more subspecies, *M. orcadensis ronaldshaiensis* from the southern Orkney island of South Ronaldsay and *M.o. rousaiensis* from Rousay. Neither of these last two could be distinguished from typical *orcadensis* on external appearance; they were differentiated on trivial cranial proportions. Barrett-Hamilton & Hinton (1910–21) regarded all five races as subspecies of *M. orcadensis*.

The nearest British vole to the Orkney vole is on the island of Guernsey, off the other extreme of the large island of Great Britain. Miller (1909) described this as a distinct species, *Microtus sarnius*, largely because of its size. He noted (Miller 1912):

> Misled by the extreme narrowness of the very aged type skull, I at first supposed this animal to be a member of the *agrestis* group with aberrant dentition. Further material shows that it is related to the voles of the Orkney Islands and to the extinct *Microtus corneri* of the British mainland, the three living species and their fossil relative apparently belonging to an older fauna than that now inhabiting Great Britain and the mainland of Europe (Hinton, 1910).

This is where just-so speculation took off. Barrett-Hamilton argued in his magesterial *History of British Mammals*:

> The *orcadensis* group appears to have arrived in south-eastern England in late pleistocene times, probably from France by way of the Channel Islands, which explains its absence from Skandinavia. It spread though Britain, becoming specialized as it dispersed, and eventually reached the Orkney district which was then part of the mainland; later, on the severance of the Orkneys from the mainland, portions, probably the northern first, became detached as separate islands. In these segregation has played its part, and differentiation of subspecies has been the result. The persistence of *M. sarnius* in an island far to the south shows that these mice owe their survival to freedom from competition rather than to any other factor; elsewhere they have probably succumbed to such competition, helped by the attacks of carnivora.
>
> G. Barrett-Hamilton & M. Hinton (1910–21, pp. 456–7)

Bryan Beirne was even more dogmatic in a comprehensive review of *The origin and history of the British fauna* (1952). He believed that many present British species survived the Ice Ages in temperate oases to the south and west of the British Isles, for which geological evidence of their biota was lacking as 'most of it is now covered by the sea' (Beirne 1952, p. 49). He regarded the extant *Microtus* species as:

> represented by two former 'Celtic Land' populations of different ages. The oldest is represented by the Orkney short-tailed vole (*Microtus orcadensis*) and by the Guernsey short-tailed vole (*Microtus sarnius*). The former is represented by a number of subspecies which developed since the various islands of the Orkneys became separated from eachother by the sea. The more recent Celtic Land population is represented by subspecies of *Microtus agrestis*: the Scottish short-tailed vole (subspecies *M. neglectus*), of the Highlands and Bute; the Islay vole (subspecies *M. macgillivraii*), of Islay; the Eigg vole (subspecies *M. mial*), of Eigg; and the Hebridean vole (subspecies *M. exsul*), of most of the remaining islands of the Hebrides. The British short-tailed vole (subspecies *M. hirtus*) represents another population of the same main population that gave rise to the subspecies of the Highlands and Hebrides.
>
> (Beirne 1952, p. 92)

Harrison Matthews argued similarly in his standard work on *British mammals*, although he maintained a caveat, 'It is important to remember that this is an interpretation of the available evidence. It may be the whole story, but, on the other hand it may have to be modified in the future when more detailed research has been done on the genetics of voles.' Nevertheless, he seemed to have been personally convinced by the interpretation, based on both fossil and biogeographical evidence: 'The bewildering variety of fossils has been reduced to order in the classic researches of Hinton, and the living animals have been closely studied by that author, Barrett-Hamilton, Miller and others' (Matthews 1952, p. 157). In fact, the interpretation is wrong for at least five reasons.

1. There is no geological evidence that conditions permitting the survival of temperate species persisted in or around the British Isles during the Pleistocene (West 1973; Yalden 1982; Jones & Keen 1993).

2. The fossil vole *M. corneri*, conceived by Hinton as an intermediate and possible ancestor of the Guernsey and Orkney species, is an artefact. *Microtus* mandibles are not assignable to species, and all those from (subfossil) cave deposits in Britain which have been identified as belonging to *M. corneri* are associated without exception with *M. agrestis* skulls; *M. corneri* skulls should almost certainly be referred to *M. ratticeps* (*M. oeconomus*), a living species mainly of the tundra (Sutcliffe & Kowalski 1976), which was common on mainland Britain during the Pleistocene (Stuart 1974).

3. There is no evidence of a landbridge between Orkney and Scotland after the retreat of the Pleistocene ice (Berry 1985; Davidson & Jones 1985). The assumption that there was depends on assumptions about species distributions and is therefore tautologous. For example, Steers (1953) wrote 'there must have been a connection to account for the similarity of fauna between the islands and the mainland' (cf. Elton 1947).

4. *M. orcadensis* is conspecific with the widespread *M. arvalis* of the European mainland. The two forms are morphologically similar and cross-breed with no difficulty (Zimmerman 1959).

5. The claim that *M. agrestis* out-competed *M. (orcadensis) arvalis* and led to the latter's elimination from the British mainland is unlikely because the two species coexist over much of mainland Europe. Furthermore, *M. agrestis* has a more northerly limit than *M.arvalis*, which suggests that it would have preceded *M. arvalis* in post-pleistocene colonization, and hence have reached northern Britain (including Orkney, if the latter was connected to Scotland) before *M. arvalis*.

In the face of these objections it is impossible to maintain the 'classical' assumption about isolation and subsequent differentiation. All modern scholars now accept that voles colonized Orkney after the islands separated from Scotland, presumably via human agency. The colonization event must have occurred early in the human history of Orkney, because subfossil voles have been recovered from the neolithic settlements of Skara Brae and Quanterness, around 6000 years BP (Corbet 1979; T. M. Clegg, personal communication). Comparison of Orkney voles with ones from continental Europe using non-metrical skeletal frequencies shows that the Orkney races are more closely related to populations from southern Europe (Iberian or Mediterranean) than to ones from northern Europe; in contrast, Guernsey voles are very similar to north European animals (Berry & Rose 1975). These data imply that the Guernsey population may be a relict of the time before the island separated from Brittany, but that the Orkney vole was carried thither from southern Europe, perhaps by early megalith builders whose origins seem to have been in the Mediterranean (Wainwright 1962).

The 'Orkney vole' type of legend has recurred repeatedly. The traditional interpretation of island differentiation of the long-tailed field mouse (*Apodemus sylvaticus*) shares with it many features and a similar cast of myth-makers.

Apodemus sylvaticus extends over much of Eurasia with little differentiation. At its Atlantic edge it explodes on British islands into three species and 14 subspecies. The forms (*A. hirtensis* on St. Kilda, *A. hebridensis* from the Outer Hebrides, and *A. fridariensis* from Fair Isle) are all large races, distinguished from each other by small skeletal and pelage traits. Barrett-Hamilton & Hinton (1910–1921) comment that 'the characters which distinguish them are slight, and all three might be regarded as mere subspecies of *A. sylvaticus* were it not for the fact that *A. hebridensis* and *A. fridariensis* have in turn undergone a further differentiation into a number of recognizable and distinct insular races'. Matthews (1952) developed this idea: 'the island races may be regarded as local developments from the primitive *A. sylvaticus* stock of the region, which appeared to have resulted from the segregation of this stock upon small islands'.

Beirne (1952) interpreted the island species as the results of temporally different colonizations, along the same lines as his beliefs about the differentiation of *Microtus orcadensis*. He wrote, 'The long-tailed field mice of the genus *Apodemus* apparently invaded (the British Isles) on three occasions. The first invasion is represented by *Apodemus fridariensis* of Shetland; *Apodemus hirtensis* of St Kilda; and *Apodemus hebridensis* of the Hebrides. They represented a population that inhabited the northern part of the Celtic Land (a hypothetical and now submerged area to the south and west of the British Isles, which was not glaciated during the Pleistocene) and which was later divided into a number of smaller populations which in turn developed independently of each other: at least three subspecies of *Apodemus fridariensis* and five of *Apodemus hebridensis* are known. A later invasion is represented by *Apodemus flavicollis* and post-glacial invasion by *Apodemus sylvaticus*'.

Darling (1947) attempted to combine a relict explanation with adaptation. He believed that in the Hebrides, '*Apodemus* is considered to be a true relic. It is probable that the island races form a broken cline'. The unlikeliness of these interpretations was shown by Berry *et al.* (1967) who found that the relationships between the *Apodemus* races on the Small Isles of the Inner Hebrides (Rhum, Muck, Eigg and Canna) could most easily be explained by the colonization of one island (Eigg), and the independent introduction of mice from this island to the others.

However, neither the relict nor the human introduction theory provide in themselves any particular reason why the island races should be so different from each other. The islands support large populations of mice (of the order of several thousands) too large for genetic drift to be important. Detailed comparisons of samples using standard taxonomic traits (pelage and morphometrics) reveal no discernible pattern of differentiation (Delany & Healy 1964). Berry (1969) extended the Inner Hebrides study, and found that the relationships between island populations made more sense in terms of history than of traditional biology: Eigg was a political centre with Scandinavian links from the early days of human organization in northern Britain. In the 8th century the Vikings raided there; by the 13th century the island was a seat of the Lord of the Isles. The Vikings must have had considerable dealings with Eigg in their exploratory journeys before they turned to conquest. In contrast, Rhum seems never to have been permanently occupied before the 17th century.

If there were mice on Eigg from the early days of human settlement, it is not difficult to picture a few animals being introduced when someone landed, perhaps taking over livestock in a boat with mice hiding in the straw or foodstuff. If this is what happened, any new population established could be instantly differentiated from the one whence it came because of the chance collection of alleles and frequencies in the founding group: it is therefore understandable why the Rhum population is so distinct, yet probably relatively recent in its occupation of the island.

Eigg is important in considering the inter-relationships of the Outer Hebridean mouse populations, because the latter show a complicated pattern of affinities, all of them, like the Small Isles races, being closer to either Eigg or Norway than to the Scottish mainland. Clearly there has been no simple introduction and spread of field-mice in the Hebrides: Lewis/Harris is distant from every sample except South Uist, whose closest affinities are directly with Norway; North Uist is not at all like South Uist, and is closer to Eigg than anywhere; Barra and Mingulay are closely related to each other, and to Eigg; the Shetland populations are more closely related to Norway than elsewhere (Berry 1969). The Uists became divided from each other comparatively recently, yet their mouse populations are genetically very distinct. The relationships overall fit closely with the expectations of separately founded populations, and not at all with the possibility that the mice are relicts.

Handford & Pernetta (1974) have criticized this way of looking at relationships, on the grounds that: (i) rates of evolution are the same for all populations; (ii) all populations are evolving in the same direction; and (iii) colonizing groups are very similar to one another.

There is no evidence for any of these axioms, but the crucial one is the last one. Although we know of no trait that makes colonizing groups more adventurous than their peers, they will certainly be heterozygous at

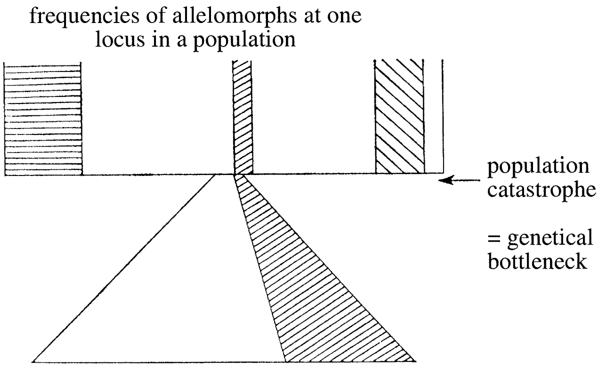

Figure 1. The founder effect. The shading represents different alleles existing at different frequencies in parental and post-bottleneck populations.

many of their loci, meaning that any small number of animals will almost inevitably differ in both allele content and allele frequencies from any other sub-sample of the same population (figure 1). When it was believed that individuals were normally homozygous at all but a few polymorphic or mutant loci, it would have been reasonable to assume that colonizing groups were similar to each other; now we know that heterozygosity is rampant, this assumption will usually be wrong.

When *Apodemus* on southern British islands (where they may have survived the Pleistocene) are considered, their divergence from nearby mainland neighbours can be accounted for by a reasonable combination of chance introduction following extinction (Alderney, Sark, Herm and Tresco), and survival as relicts from previously widespread populations (Jersey, Guernsey and St Mary's) (Berry 1973). If a group of organisms is introduced into an area already occupied by a similar species, it would be much more difficult for them successfully to establish themselves, or contribute materially to the gene-pool. Probably *Apodemus* only managed to colonize the Hebrides and Shetland as late as the time of Viking domination and certainly not before they were cut off from the mainland at the end of the Pleistocene.

A similar but less speculative explanation can be applied to the house mice (*Mus musculus*) of the Faroes, a group of about 20 islands lying mid-way between Norway and Iceland. There is no possibility of any land connection between these islands and anywhere else; and they were heavily glaciated during the Pleistocene. The only small mammals are house mice, first described scientifically by Eagle Clarke (1904), who wrote of a collection from Nolsøy (one of the smaller islands) that they were 'remarkable for their great size, indeed, they are veritable giants, being considerably larger than the type and of any of its numerous geographical races'. He classified these animals as a new subspecies, *faeroensis*, distinguished solely by 'immense size'. On the same grounds, Miller (1912) promoted the race to specific rank since it 'differs so conspicuously from all other members of the (species) group.'

This distinctiveness is of considerable interest because there is no plausible way that mice could have reached the islands except by being brought by humans, who only arrived there just over 1000 years ago. The earliest known human inhabitants were 8th Century Irish hermits, but the archipelago was not properly settled until Norse colonizers began to arrive in the 9th Century (Wylie 1987). The first mention of mice occurs in a general account of Faroese life by a local minister (1673), but a more detailed statement by Landt (1800) recorded that all the northern islands of Faroe, together with Koltur, Hestur, Skuvøy, Dimun and Mykines were free of both rats and mice. Evans & Vevers (1938) list mice on seven islands (Fugløy, Mykines, Nolsøy, Sandøy, Esturøy, Streymøy and Suđurøy). Writing soon afterwards, Degerbøl (1942) gave the same distribution, with the exception that he cites mice as occurring also on Hestur. Finally Reinert (1971) reported that mice are found on six islands only, no longer existing on Eysturøy.

Degerbøl (1942) described distinct races on at least four islands: Nolsøy, Mykines, Fugløy and Streymøy. The last mentioned were regarded by Degerbøl as intermediate between typical *M. m. musculus* and *M. m. faeroensis*. He discussed the possibility that the Faroese characters might be diluted by a 'constant influx of *M. m. musculus* from ships', but concluded it was 'more likely that these mice are fairly pure representatives of the original Faroe mouse, originating through isolation for a long space of time, while the big Nolsøy mice have then developed by adaptation to the leaping life on the bird cliffs (i.e. as a kind of ecological race)'.

The belief of Degerbøl that differentiation of and within the Faroe mouse race is the result of adaptation, is typical. Annandale (1905) wrote 'The evolution of a peculiar breed or local race need not have taken very long, for we know that this species has great powers of adapting itself to its environment'. Huxley (1942) regarded the Faroe mouse situation as a significant example of particularly rapid evolution. After discussing evidence that subspeciation usually takes about 5000 years, he commented 'The facts concerning rats and mice show that subspeciation may sometimes occur much more quickly. In particular, the Faroe house-mouse *Mus musculus faeroensis*, which was introduced into the islands not much more than 250 years ago, is now so distinct that certain modern authorities have assigned full specific status to it'. Matthews (1952) has argued similarly: 'These island races are particularly interesting in showing the rate at which isolated wild populations can develop new genetic characteristics for it is definitely known that their forerunners could not have been introduced into the Faroes less than 250 years or more than 1000 years ago.'

In fact the situation is both more complicated and more informative: of the six Faroe Islands where mice occur, Fugløy and Mykines were recorded as having no mice before 1800, and Hestur only acquired them between 1938 and 1942 (Degerbøl 1942). Notwithstanding all the island races are very distinct on the basis of morphometrics, non-metrical skeletal traits, and allozyme frequencies (Berry *et al.* 1978).

The most variable population comes from Sandøy, one of the southern Faroe Islands. The southern islands are more fertile and intensively farmed than the northern ones, and it seems plausible that the original establishment of mice on Faroe was on Sandøy, and that mice spread from there to the other islands. On the basis of distance statistics both Hestur and Nolsøy were probably colonized from their large neighbour, Streymøy.

On historical grounds, the most likely agents for introducing house mice to the Faroes were the Vikings. But it is impossible to avoid the conclusion that the Hestur race (at least) is an example of virtually instant subspeciation. The obvious mechanism for this is the 'founder effect'.

3. THE FOUNDER EFFECT

The death knell to the just-so stories about island evolution as far as British small mammals are concerned was a short paper by Corbet (1961), in which he pointed out that neither geological nor distributional data support the assumptions of differentiation after isolation, and that most of the island races must have originated through human agency. Corbet's argument can be applied generally. For example, there are both 'native' and introduced rats on the Galapagos archipelago. There are three groups of native rats: the extinct genus *Megaorysmys*, apparently derived from a thomasomyine of mainland South America; *Nesoryzomys*, which has no close relatives among the mainland rats nearest to it (which are the highly diverse rice rats *Oryzomys*); and a single living species of *Oryzomys*, *O. bauri*, which is morphologically and allozymically virtually identical with the mainland *O. xantheolus*. (Another island species *O. galapagoensis*, has become extinct within historical times). This implies two successful introductions in the far distant past, plus a more recent introduction of *Oryzomys* (Patton 1984).

Allozymic, morphometric and non-metrical skeletal traits all show the same set of inter-island relationships in the 'introduced rat' *Rattus rattus*, and can be interpreted as indicating another three groups of introductions, corresponding to different periods of human activity in the islands: the first in the late 1600s, the most recent during World War II. After the primary introductions, gene flow between the islands seems to have been slight (Patton *et al.* 1975). Analysis of mitochondrial DNA polymorphisms in nine subspecies of *Peromyscus maniculatus* on the Californian Channel Islands indicates at least four separate colonizations from the mainland, all probably within the last 500000 years (Ashley & Wills 1987).

'Natural', 'native' or 'endemic' are imprecise terms, describing little more than time. The Polynesian or Maori rat, *Rattus exulans*, is frequently described as 'native' on Pacific islands, yet it must have been introduced either intentionally (it is eaten by the Maori in New Zealand) or accidentally in the days before European influence (Lever 1985; King 1990). Although there are many examples of relict populations of small mammals (e.g. Stewart & Baker 1992), most island populations that have been studied in detail seem to have been the result of colonization at some time in the not too far distant past (Crowell 1986; Patterson & Atmar 1986). One assumes that such colonizers will be few in number and, with mammals at least, that multiple colonizations are uncommon (*contra* MacArthur & Wilson 1967, p. 155) although it is rarely possible to be definite. The colonizing event means that the population will go through a bottleneck in numbers with potentially major effects on genetic variation. A founding event results in intermittent genetic drift (so named by Waddington 1957, p. 86), which is likely to be much more drastic than the more normally assumed persistent drift, where alleles change in frequency relatively slowly (at a rate inversely dependent on the effective breeding size of the population). The whole future reaction and adjustment of the colonizing group will depend largely on the alleles and their frequencies in the original members. Even if further immigration brings in fresh variation, by the time it occurs the original founders are likely to have increased in number and range, reducing the impact of fresh individuals.

The importance of the initial founding population has been consistently undervalued by population biologists. The dominating influence on island biology in recent years has been Robert MacArthur and Edward Wilson's theory of island biogeography (1963, 1967). But they were interested almost entirely in diversity, not differentiation. Their 1967 book contains a chapter (36 pp.) on 'Evolutionary changes following colonization' but it concentrates wholly on adaptive adjustment; in this they followed Mayr (1954), who saw the founder effect as disturbing the genetic cohesion generally assumed to hold species together. Wilson (1969) confirmed this bias, concentrating on changes in species composition with time and on interspecific relationships. Without denigrating or arguing against these effects, and accepting that natural selection may affect island biotas as much as – if not more than – continental ones, it is nonetheless difficult to avoid the conclusion that the main differentiation of island forms is usually the result of the chance colonizers of each population, and only secondarily due to subsequent adaptation.

This conclusion has been repeatedly challenged (most determinedly by E. B. Ford, arguing particularly from genetical changes in *Maniola jurtina* populations in the Scillies (q.v. Ford 1975, pp. 61–77); Ford's ideas have persisted because, as MacArthur & Wilson (1967, p. 156) point out, they were based on 'one of the few adequate analyses of ecogenetic variation in insular populations' when modern views of island evolution were forming). Williamson (1981, pp. 131–8) points out that founder effect differentiation depends on anecdotal suppositions (which form ideal bases for 'just-so stories'); he suggested that the differentiation of island mouse races could be explained by 'adaptation to the colder and damper situation found on islands'. This was tested by Davis (1983) by comparing house mice from the mainland of Great Britain with mice from the Orkney, Shetland and Faroe archipelagoes. His null hypothesis was that a major 'maritime island' effect would result in island populations being more similar to each other than to mainland populations. Using a discriminant factor

Table 1. *Inherited allozymic variation (heterozygosity) in island and mainland populations of small mammals of the same species (after Kilpatrick 1981; Berry 1986; Frankham 1996)*

(*N* is number of populations studied.)

	mainland	island	
	mean heterozygosity per locus (range)	mean heterozygosity per locus (range)	reduction in heterozygosity (%)
Macrotus waterhousii	0.021 (0–0.043)	0.040	–
Macaca fuscata	0.019 (0–0.035)	0.013 (0.03–0.018)	31.6
Spermophilus spilosoma	0.090 (0.049–0.160)	0.009	90.0
Peromyscus eremicus	0.040 (0.006–0.079)	0.009 (0–0.022)	77.5
Peromyscus leucopus	0.080 (0.076–0.084)	0.071 (0.052–0.078)	11.3
Peromyscus maniculatus	0.088 (0.054–0.124)	0.068 (0.010–0.131)	22.7
Peromyscus polionotus	0.063 (0.050–0.086)	0.052 (0.018–0.086)	17.5
Sigmodon hispidus	0.022 (0.017–0.025)	0.021	4.6
Microtus pennsylvanicus	0.142 (0.120–0.171)	0.056 (0.023–0.114)	60.6
Mus domesticus	0.091 (0.032–0.114)	0.041 (0–0.079)	55.0
Rattus fuscipes	0.047 (0.020–0.100)	0.011 (0–0.040)	76.6
Rattus rattus	0.031	0.026 (0.008–0.056)	16.1

analysis similar to that employed by Williamson, Davis found that the island groups were very different from each other, but more like Caithness (northeast Scotland) than other British mainland samples. In other words, his data showed a regional geographic influence rather than an island effect, thus effectively disproving his null hypothesis. Another study comparing populations with different chromosomal (Robertsonian) fusions in Caithness and several Orkney islands found that there was an overall genetic similarity between all the populations, despite the fact that some of the populations differed considerably in their chromosomal constitutions (Nash *et al.* 1983). Genetic (chromosomal) differences which in some cases must have arisen since isolation, did not obscure the general relationships between the populations in the area.

Island small mammals are almost always less variable than mainland populations of the same species (table 1); most data are based on allozymic comparisons, but the small amount of information from mtDNA and nuclear DNA studies gives a similar result (Frankham 1996). Leberg (1992) has shown experimentally in mosquito fish (*Gambusia holbrooki*), and argued theoretically, that allele frequencies and the incidence of polymorphisms are more sensitive indications of a bottleneck in numbers than is mean heterozygosity, but that does not alter the argument. Reduced variability would be expected as a direct consequence of a founding event by a small number of individuals, but it could also arise as a result of post-colonization drift. Kilpatrick (1981) has analysed the contribution of different loci to the reduction in variation. He found that island populations were often homozygous for the most common mainland allele, and that the major differences between mainland and island were usually through an increase in the most common mainland alleles. He compared also the amount of differentiation between so-called fast and slow evolving loci (Sarich 1977): 83% more genetic variation occurred in island populations among 'fast' as opposed to 'slow' evolving loci; in mainland populations this figure was 36%. The amount of difference was largely due to increased levels of genetic differentiation among insular populations at 'slow' loci. This again would seem to be a founder effect as all loci will be affected equally by a colonization bottleneck, but it also indicates the possible operation of post-colonization adaptive changes. Kilpatrick concluded that 'accumulated evidence suggests founder effect as the major evolutionary force responsible for the reduction of genetic variation and differentiation of insular populations (but) additional data are needed to substantiate the relative importance of founding effects and to determine the relative importance of other evolutionary forces'.

4. COLONIZATION AND ESTABLISHMENT

If one accepts that most island populations arise from colonization rather than through survival as relicts, the hazards of ecological establishment and adjustment have to be seen as important factors, stressing individuals and hence acting as likely selective agents (Berry 1996*a*). Entry into an area free of competitors, predators and presumably parasites is easier than into a habitat already occupied by species likely to interact with the invaders. There are plenty of examples of small mammal colonies being established and thriving to make labouring this point unnecessary (e.g. Crowcroft 1966; Lidicker 1976). Of more evolutionary interest are situations where a population has either failed to establish itself or become extinct. Grant (1972) reviewed a large number of distributional and experimental studies of interactions between rodent species and was wholly convinced that competitive interaction (mainly) for space was a general phenomenon. Even such an efficient colonizer as the house mouse may be affected in this way: Berry *et al.* (1982) describe two attempts to establish populations on Scottish islands which were unsuccessful due to food lack in one case and competition from *Rattus norvegicus* in the other. Detailed case-studies have reported the disappearance of flourishing island house mouse populations as a result of competition from *Microtus californicus* (Lidicker 1966) and *Apodemus sylvaticus* (Berry & Tricker 1969); both resulted from a failure to recruit young individuals into the population, rather than through increased adult mortality. In the latter case, the extinct mice were the only British house mice to have been given taxonomic differentiation, as *Mus* (*musculus*) *muralis* (Barrett-Hamilton 1899). Dueser & Porter (1986) examined competition between seven small mammal species on a large (60 km long) island off the Maryland coast. They found that each species was fairly closely confined to specific habitats. They estimated the intensity of competition between pairs of species on the basis of changes in population density of the two in areas where they met. On this measure, house mice were 'at the bottom of the competitive hierarchy. *Mus* is an inferior competitor in comparison with native rodents in natural habitats' and was found most commonly in marginal rodent habitat, 'xeric grassland on and immediately behind the seaward foredunes where there is sparse cover, low plant and structural diversity, low biomass and productivity, a shifting substrate and frequent disturbance'. Notwithstanding, the species was found on at least five of the small islands in the vicinity (all of which were occupied by at least one additional species) whereas two strongly competitive species (*Peromyscus leucopus* and *Zapus hudsonius*) were absent from nine of the ten islands for which there were data (Dueser & Brown 1980). Dueser & Brown (1980) concluded that 'extinction rates are relatively high and colonization rates are relatively low for small mammals in this physically rigorous environment'.

Hanski and his colleagues have studied the persistence (including both colonizing ability and extinction rate) of three species of shrews (*Sorex araneus*, *S. caecutiens* and *S. minutus*) on 108 islands in three lakes in Finland. They found the species differed in their migratory capability, the larger species having an advantage, apparently because of larger body size (higher swimming rate, longer starvation time; see Peltonen & Hanski 1991). However, on arrival at an empty island, the smallest species (*S. minutus*) proved to have the largest colonization success, for reasons that are not known but may include their smaller per capita food requirements. Populations of the larger species (*S. araneus* and *S. caecutiens*) had a higher survival rate than populations of the smallest species (*S. minutus*) on small islands, probably a consequence of the short starvation time of small species and their consequent vulnerability to environmental stochasticity (Hanski 1992). Hanski (1993) has extended his analysis of island occupancy patterns to other sets of data (such as those of Lomolino, 1993, on small mammals on islands in Lake Huron, U.S.A.) and shown that similar conclusions emerge. He bases his methodology on combining MacArthur & Wilson's (1967) equilibrium model of island species number with models based on metapopulation dynamics (Hanski & Gilpin 1991).

Studies such as these are almost always carried out without any genetic characterization of the individuals involved; Hanski & Kuitunen (1986) provide one of the few exceptions to this, and their data show differentiation between island but not mainland populations, even though their island populations were small and short-lived. Small mammals provide ideal material for combining genetical with ecological studies; perhaps a better integration of disciplines may come from the growing interest in life history evolution (Berry & Bronson 1992).

5. FOUNDER EFFECT, PRINCIPLE AND SELECTION

The introduction of the 'founder effect' into evolutionary literature was due to Ernst Mayr in his *Systematics and the origin of species*, one of the books which forged the neo-Darwinian synthesis. He wrote:

> The reduced variability of small populations is not always due to accidental gene loss, but sometimes to the fact that the entire population was started by a single pair or by a single fertilized female. These 'founders' of the population carried with them only a very small proportion of the variability of the parent population. This 'founder' principle sometimes explains even the uniformity of rather large populations, particularly if they are well isolated and near the borders of the range of the species.
> (Mayr 1942, p. 237)

This founder suggestion was Mayr's addition to the received wisdom of half a century ago that island differentiation was the result of drift in small populations. He saw the most important property of a founder population as its 'sudden conversion from an open to a closed population.... at once completely emancipated from the parental population' and hence subject to radically new selection pressures (Mayr 1963, p. 532). He believed this would lead to a 'genetic revolution', producing a new species. My contention is different: that the key significance of founding populations is that they provide a mechanism for rapid (= sudden) changes in gene frequencies and genome content, and this gives a new platform for subsequent adjustment. Sewall Wright seems to be the only person to have argued similarly. In a letter to Victor McKusick (24 May, 1977), he wrote: 'The effects attributed to the "founder" principle by Mayr (gene loss, reduced variability) are the most obvious but the least important of the three I had stressed. I attributed most significance to wide random variability of gene frequencies (*not fixation or loss*) expected to occur simultaneously in tens of thousands of loci....' (Provine 1989, p. 57). This contrasts with the common discussions about founder effects, which tend to focus on allele loss. For example, MacArthur & Wilson (1967, p. 154) wrote, 'The founder principle is actually no more than the observation that a propagule should contain fewer genes than the entire mother population.' In view of these differences of emphasis, it is probably useful to follow Halkka, Raatikainen & Halkka (1974) and use the term 'founder principle' to include a 'founder event' (which leads to genetic impoverishment, elimination of immigration, and –

Table 2. *Change in size of island mammals in comparison with their mainland nearest relative (number of species) (after Foster 1964)*

	smaller	same	larger
Insectivores	4	4	1
Lagomorphs	6	1	1
Rodents	6	3	60
Carnivores	13	1	1
Artiodactyls	9	2	0

almost certainly – changed gene frequencies) and subsequent 'founder selection'.

It is the effects of founder selection (or genetic revolution *sensu* Mayr) that have attracted most debate. For example Barton & Charlesworth (1984) have sought to define conditions by which a species (defined as an equilibrium gene-pool, stable towards the introgression of foreign genes) can move from one 'adaptive peak' to another. They conclude that:

> the generally small chance of achieving reproductive isolation or marked phenotypic change in a single founder event means that founder effects themselves probably do not provide the explanation (for speciation). It is impossible to separate the effects of isolation, environmental differences, and continuous change by genetic drift from the impact of population bottlenecks in these cases. Since all of these factors promote divergence by a variety of processes, it is not clear that the additional influence of founder effects need be invoked.
> (Barton & Charlesworth 1984, p. 158)

In other words, the founder effect might contribute in particular instances, but is not necessary for speciation. Although Barton & Charlesworth ask 'what is the mechanism driving divergence?', they do not consider the allele-changing effect of the founder event.

Notwithstanding, it seems worth insisting that founder events may often provide the conditions to facilitate speciation (Wright 1942, p. 244). One of the difficulties about the sort of models of speciation considered by Barton & Charlesworth is that 'our imagination is limited by viewing populations as being at equilibrium, and by neglecting the complicated geometry that channels evolution' (Barton, 1989). It is this latter neglect that Mayr (1954) and Waddington (1957) in very different (and admittedly qualitative) ways were attempting to remedy. Interestingly, Mayr cited Charles Elton (1930) in his original 'founder statement' (which is, of course, based on biology rather than theory). Elton derived many of his ideas from the study of microtine fluctuations (Sheail 1987). He believed that speciation could result from bottlenecks produced by fluctuations in numbers: which is, of course, exactly what a founding propagule is. He was also innately distrustful of theoretical models. He wrote about the assumption of ecological equilibrium, 'It has the disadvantage of being untrue. "The balance of nature" does not exist.' (Elton 1930, p. 17).

It seems worthwhile pursuing the idea that the start given to differentiation by a small founding group may affect the genetic possibilities of their descendants, and sometimes lead to a new species. There is no doubt about the first, and plenty of evidence for founder selection, although not in the detail suggested by Mayr (1954). For example, one of the commonest characteristics of island mammals is a change in size relative to their mainland relatives: in general, large animals get smaller and small animals (notably rodents) get bigger (table 2). The usual explanation for this is that large animals are chronically food restricted on islands, whereas small ones can increase to a more physiologically efficient size when not constrained by ground predators or competitors. Angerbjörn (1986) has shown that the body size of *Apodemus sylvaticus* on European islands is not affected by climate, island size, or distance from the mainland but is greater if either its usual competitors (*A. flavicollis* and *Clethrionomys glareolus*) or ground predators (*Mustela erminea*, *M. nivalis*, *M. foina* or *Vipera berus*) are absent.

The size difference can be quite marked: *A. sylvaticus* from St. Kilda are on average about twice the weight of mainland British mice. Moreover the size adjustment may be rapid. House mice on the island of Stockholm were about 25% heavier than their mainland ancestors after ca. 60 generations in isolation, and this increase could have occurred much earlier (Berry 1964). The large island size is inherited (Wallace 1981). House mouse populations contain a great deal of variance for size (Crowcroft & Rowe 1961).

It is impossible without knowing the genetic composition of the colonizers to distinguish between the chance characteristics of the founding propagule and subsequent adaptation. For example, in his original description of two of the Faroese house mouse populations, Clarke (1904) spoke of the 'remarkable coarseness' of their feet, 'a modification which has been probably brought about by the rough nature of their haunts'. This fall into the 'just-so' explanation category. Hebridean field mice vary from 'reddish' on Rhum to 'greyish' on St Kilda. There are no obvious differences in background coloration on different islands, and the most likely explanation is that different alleles were represented in the founders on the different islands. However, an informative parallel emerges from a laboratory study of nest-building in house mice, one of the few unequivocally adaptive traits in small mammals which has been investigated (Lynch 1992). Laffen (cited by Lynch 1994) has shown that the genetic determinants of nest building efficiency are different in different selected lines derived from the same stock; in other words adaptation is serendipitous as well as pragmatic.

The evidence for the effect of founder heterogeneity is much firmer in human populations. For example, retinitis pigmentosa in Tristan da Cunha, porphyria variegata in South Africa, Huntington's disease and nephrogenic diabetes insipidus in New England, and other inherited conditions, can all be traced back to alleles carried by the colonizing groups (reviewed by Berry 1972). A small mammal example is the high frequency (over 60%) of midline skeletal defect (= spina bifida occulta) in Skokholm house mice: this is rare in most wild-living mice, but occurs nowadays in

Table 3. *Allele frequencies in a* Mus domesticus *population after an experimental release on the Isle of May; the population on the island contained none of the alleles before the introduction (from Berry et al. 1991)*

	Eday (source of introduced animals)	frequencies in released animals	estimated averages post-introduction*	frequencies six years post-introduction
Hbb^d	0.214	0.170	0.010	0.071
$Car\text{-}2^b$	0.423	0.221	0.020	0.171
Ada^b	0.187	0.160	0.020	0.021
Gda^b	0.536	0.620	0.040	0.338
$Es\text{-}3^b$	1.000	1.000	0.070	0.613
$Es\text{-}10^a$	0.100	0.080	0.005	0.029
N	96	77	–	120

* The resident population at the time of release was estimated to be *ca.* 1000 mice.

ca. 10% of the mice in the area from which the original founders came (Berry 1964).

As far as founder selection *sensu stricto* is concerned, there is almost no evidence for this in small mammals, although there are plenty of examples of strong selection in island populations (Endler 1986; Berry 1987). An attempt to detect and measure founder selection in a fully genetically characterized foundation population by Berry *et al.* (1982) was a complete failure because of the inability to establish viable populations. However, an experiment in which house mice were introduced into an existing population on a small (80 ha) island in which certain inherited traits were absent showed an increase in these traits (allozyme alleles, Robertsonian translocations, mtDNA and Y-chromosome variation) to a stable level after about four years (table 3) (Berry *et al.* 1991; Jones *et al.* 1995). It was not possible to identify the factors affecting fitness, but there can be no doubt that the observed genetical changes were not random. The increase and spread of the Robertsonian translocations was unexpected because Robertsonian heterozygotes have a reduced fertility and the rate of non-disjunction was doubled in wild-caught heterozygotes when compared to the parental groups (Scriven 1992; cf. Winking 1986, Searle, 1991). There were clearly genetical forces operating, which involve many parts of the genome, and which may approach a genetic revolution *sensu* Mayr. Bonhomme *et al.* (1989) believe that studies on the stable hybrid zone between *Mus* (semi)species in Europe and lack of genome homogeneity between wild-caught mouse samples in Japan indicate the effectiveness of intragenomic cohesion.

Conversely, there is a marked lack of evidence for random genetic changes in island small mammals, apart from the stochastic changes of founding colonization. Indeed it is worth pointing out how rare are well-documented examples of genetic drift in any wild population. Berry, Berry, Anderson & Scriven (1992) describe fluctuations at an allozyme locus (*Hbb*) in a house mouse population on a small (250 ha) Orkney island, but this was a very small population rarely exceeding a hundred individuals and probably on the verge of ecological viability. Petras & Topping (1983) present calculations to show that models incorporating strong selection explain well the distribution of alleles at the same locus in both Skokholm and Canadian populations, contrary to their earlier assumption of randomness from the same data.

Direct evidence of reproductive barriers which might indicate incipient speciation are sparse, but have not often been sought. Godfrey (1958) crossed British *Clethrionomys glareolus* races and discovered hybrid vigour in the F_1 but small F_2 and backcross litters, as would be expected if some sort of coadaptation was important. He found that animals from different races discriminated in favour of mates of their own race on the ground of scent i.e. racial integrity was maintained (or strengthened) by behaviour. A rather similar result was obtained by Zimmerman (1959) when he hybridized *Microtus arvalis* from Orkney and Germany: the F_2 offspring were smaller and less vigorous than both the F_1 and the parental forms. Inbreeding in small mammals has been reviewed by Smith (1993); it is not uniformly deleterious. Mayr (1963, p. 534) has pointed out that a founder event may remove undesirable recessive alleles and hence reduce the common effects of inbreeding.

6. SIGNIFICANCE AND CONSERVATION

Island races are particularly subject to extinction: Ceballos & Brown (1995) record that 81% (65/80) of known mammal extinctions over the past 500 years have been on islands; Reid & Miller (1989) note that island species form 22% (48/216) of endangered or vulnerable mammals. This sensitivity has been analysed for a number of situations (see Heaney & Patterson 1986). However it is something which ought to be expected if islands are, as it were, testing grounds for new genetic combinations rather than the result of more definitive evolution. Williamson (1981) calculated that only one colonization every 25000 years leads to speciation in Hawaiian *Drosophila*. Mayr (1963, p. 513) has taken a similar line, but extrapolated it to a belief in the evolutionary significance of island races:

1. 'Do peripheral isolates frequently (or usually) produce new species and evolutionary novelties? No.
2. Are new species and evolutionary novelties usually produced by peripheral isolates? Yes, as peripheral isolates are produced fifty to five hundred times as frequently as new species. Hence most peripheral isolates do not evolve into a new species, but when a new species evolves, it is almost invariably from a peripheral isolate.'

The evidence from island small mammals is that significant differentiation often arises as a result of a founder event. From a conservation point of view, this differentiation is little more than an accident of sampling. But it does not mean that island races should be treated merely as curiosities. In Mayr's words:

> Islands are an enormously important source of information and an unparalleled testing ground

> for various scientific theories. But this very importance imposes an obligation on us. Their biota is vulnerable and precious. We must protect it. We have an obligation to hand over these unique faunas and floras with a minimum of loss from generation to generation. What is once lost is lost forever because so much of the island biota is unique. Island faunas offer us a great deal scientifically and aesthetically. Let us do our share to live up to our obligations for their permanent preservation.
>
> E. Mayr (1967, pp. 359–374)

Kilpatrick (1981) adds an experimental edge:

> Manipulations of insular populations with partially known genomes and repeated sampling of these populations prior and subsequent to manipulation should allow determination of the relative importance of founder effect, genetic drift, gene flow and selection in determining the genetic structure on insular populations.
>
> C. W. Kilpatrick (1981, pp. 28–59)

Almost certainly conservationists have over-reacted to variation loss (Berry 1996*b*). Bryant and his colleagues have shown that manipulating house fly populations so that they go through small bottlenecks in number nevertheless leaves substantial potential variation remaining for evolutionary adaptation (Bryant *et al.* 1990). Brakefield (1991) comments, 'the existence of coadaptation between genes and of forms of non-additive genetic contributions to quantitative variation are likely to make variability within populations more resistant to loss than would be expected on the basis of theory developed largely from the perspectives of genes acting independently from each other and in a purely additive manner.'

It would be premature to generalize too much from such experiments, but it is worth emphasizing that island small mammals provide ideal opportunities for similar manipulation. Sadly most are still virgin territory, observed from afar by geneticists, ecologists, theoreticians secure on their own pedestals; the main linkage to them remains the corrosive and persisting mists of evolutionary story tellers. And, as MacArthur & Wilson (1967) point out, 'the actual contribution of the "founder effect" to evolution can be assessed only by empirical field studies.'

Darwin (1871) commented that 'False facts are highly injurious to the progress of science, for they often endure long; false views, if supported by some evidence do little harm, for everyone takes a salutary pleasure in proving their falseness; when this is done, one path towards error is closed and the road to truth is often at the same time opened.' He also wrote (1872) 'Great is the power of steady misinterpretation.' Research has helped considerably to clarify our understanding of insular evolution, but there is much work still to be done, particularly on the persistence of 'founding genomes' and on the importance and strength of intragenomic interactions.

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