Biogeography

How do flightless mammals colonize oceanic islands?

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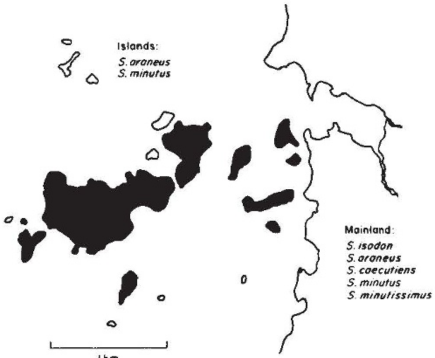
OCEANIC islands support only a subset of an adjacent mainland's species, biased towards species with obvious means of crossing water, such as flight. On the most remote islands like New Zealand and Hawaii the sole native terrestrial mammals are bats, whereas those islands with the richest mammal faunas are ones that had well-documented Pleistocene land bridges to continents, such as Britain and Borneo[1]. Thus, it is disconcerting to find that oceanic islands up to the distance of the Galapagos (1,000 km from South America) have any native flightless mammals at all. There has been a long debate over whether such mammals arrived via vanished land bridges undocumented by independent geological evidence, or whether they can somehow, although very rarely, cross water gaps. Several recent studies make the surprising discovery that overwater dispersal of flightless mammals occurs sufficiently often to measure[2–6].

The least implausible mechanisms by which mammals could cross water are by swimming, rafting on floating vegetation or (at high latitudes) rafting on ice floes or crossing frozen straits in the winter. Evidence for water-crossing could include finding a mammal species on an island recently lacking that species, tagging an individual mammal at one site and recovering it on a separate island, and actually observing an individual in transit. All three types of evidence were reported recently by Pokki[2], who studied voles on coastal islands of the Tvarminne Archipelago, Finland. Of 2,175 voles that he tagged on islands, 98 were recaptured on other islands removed by open-water distances of up to 620 m, and four voles made two inter-island moves. Because most moves were made during the ice-free late summer, dispersal was inferred to have been by swimming, supported by lucky direct observations by two other Finnish scientists.

In Lake Sysmä, Finland, Hanski[3] caught 60 shrews on islands that had no breeding populations and that those individuals could thus only have reached by crossing water. One island on which all the shrews were trapped out in 1983 supported a single pregnant female in the spring of 1984, which must have moved to that island after mating elsewhere. Thus, a single colonist could found a population. A shrew can swim for at least 1 h and cover 1 km (see figure, for example). Hanski was not lucky enough to come across shrews swimming between islands, but other interested 'observers' often do: the stomachs of 2,486 trout yielded 270 shrews!

On Maine coastal islands (northeastern United States), Crowell[4] recorded newly founded populations of 13 mammal species, which must thus have crossed water in recent decades. The species ranged in size from bear and deer to beaver, raccoon, muskrat, bobcat, fox, rabbit and hare down to voles, mice and shrews. Deer, moose and otter were actually observed swimming across straits up to 12-km wide.



An archipelago in Lake Koitere, East Finland. Dark islands, *Sorex araneus* occurred with *S minutus* in 1983; light islands, *S. araneus* occurred alone (from ref. 3).

As a direct test of the role of dispersal across ice, Lomolino[5] searched for mammal tracks while driving a snowmobile over the frozen St Lawrence River, Canada, in winter. Energetic considerations of winter travel favour large animals, as the ratio of energy reserves to energy costs per kilometre of travel increases with size, whereas problems of heat loss decrease with size. For instance, treadmill experiments show that at near-freezing temperatures a 40-g vole can run 6 km and an 18-g shrew only 1 km. In fact, Lomolino found winter-ice tracks of large mammals to be disproportionately commoner and to go further than tracks of small mammals. In particular, there were six times more vole tracks than shrew tracks, although shrews were more widespread on the mainland.

Those size-related dispersal considerations may account for why voles occur on St Lawrence islands more than 1 km from the shore, whereas shrews only occur on islands less than 700 m from the shore. Size-dependent selection of immigrants may also explain why body size increases with distance for insular populations of both voles and shrews. Energetic limits on dispersal were further illustrated by the fact that at the end of Lomolino's longest recorded mole track (1 km; 8 times the mean track length), under sub-freezing conditions, was a dead mole.

Many differences between the species composition of island and mainland mammal faunas depend on species differences in over-water dispersal ability. For example, on St Lawrence islands the winter-active mammal species that disperse across ice are over-represented, whereas species that hibernate during the winter ice season are under-represented. Similarly, the increase of swimming endurance with body size favours voles over deer mice on islands of the US Atlantic coast[4,5], and favours large rather than small shrew species on Finnish lake islands[3].

If dispersal is sufficiently frequent, however, extinction also becomes a determining factor of insular species composition, and Lomolino could interpret species differences in occurrence on islands (incidences) in terms of species differences in ratios of immigration to extinction rates. Thus, perhaps the most surprising result of the recent studies is that populations of not just birds but even of some flightless mammals on islands several kilometres offshore approach immigration/extinction equilibria, as postulated in the MacArthur–Wilson theory of island biogeography[2–5].

For islands tens or hundreds of kilometres offshore, dispersal events will naturally be much rarer. (For example, one successful colonization every few hundred thousand years from Indonesia would have sufficed to build up the mammal fauna of those Philippine islands lying beyond the Palawan land bridge[6].) Large water gaps imply not only less frequent crossings but also a different mechanism of crossing, namely rafting instead of swimming. Whereas swimming favours large over small colonists, rafting favours small over large colonists. In fact, 19 of the 20 endemic flightless mammal species of Luzon[6], all those of the Galapagos and all flightless placental species of Australia are small rodents[1]. Hence, rafting has left its signature on the native mammal faunas (and perhaps snail faunas, soon to be discussed in a News and Views article by Peter Moore) of distant oceanic islands, just as swimming and ice travel have moulded the faunas of close islands. □

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