

part of Iceland? Perhaps they are not. In Walker's view, the sheets are only exposed in this part of Iceland because the erosion here has been particularly severe. He proposes that the sheet swarm actually "constitutes a widespread and integral part of the structure of Iceland and is not merely a local phenomenon". Elsewhere it is not seen because it lies below sea level.

He then goes on to identify this widespread swarm with crustal layer 3. Of the four main crustal layers identified seismically beneath Iceland, layers 0, 1 and 2 have been interpreted reasonably as basalt lavas and associated rocks. But the nature of layer 3, which has an average thickness of 6 km and begins at an average depth of 3.5–4.0 km, is still unknown. Certainly a layer 3 of basic intrusive material should have the right P wave velocity ( $6.35 \text{ km s}^{-1}$ ). The next step should therefore be to test Walker's hypothesis by measuring seismic velocities within the sheet swarm in south-east Iceland. It is unfortunate that all previous seismic profiles were run outside the swarm or in parts of it where the concentration of sheets is very low.

## Group selection

from Robert M. May

MANY animals seem to exhibit altruistic behaviour, whereby individuals sacrifice their own interests for the good of the group. The 'warning cries' uttered by some birds are an example: the individual puts his own life at greater risk for the benefit of his fellows. Many other apparent examples are to be found in the patterns of behaviour with which animals regulate their population density.

But natural selection acts on individuals, not groups. It has been argued that 'group selection' (the evolution of traits which are advantageous at the group level, but disadvantageous at the individual level) cannot take place within the classical Darwinian framework.

In many cases, closer study reveals that seemingly altruistic behaviour directly benefits the individual as well as his group, thus removing any paradox. In other cases, group selection can be seen to derive from kin selection: the altruist's actions are of direct advantage to his relatives, and therefore his gene type is favoured by his action, even if his own life is not. As W. D. Hamilton has pointed out, social insects probably exhibit extreme examples of kin selection. In the Hymenoptera, females are more closely related to their sisters than to their daughters, and so from a genetic point of view they do better to care for a sister than

to devote an equal amount of care to their own offspring.

There remain, however, examples of apparent group selection which cannot be evaded by the above arguments. Maynard Smith, Levins, Boorman and Levitt and others have tried to construct mathematical models which exhibit the phenomenon. These models envisage a population distributed over many islands or other such environmental patches, with occasional migration between patches. They seek to show that when a 'selfish gene' appears it will (by classical individual selection) take over the local population, but that the consequent disadvantage to this group as a whole may cause its extinction before the selfish gene can spread to the other populations. All these models require the most delicate tuning if the desired effect is to be exhibited, and none of them constitutes a truly plausible explanation for group selection.

Recently, two different models have been proposed, both of which exhibit group selection in a robust fashion.

The first of these was suggested by May, and has independently been elaborated at monograph length by Gilpin (*Group Selection in Predator-Prey Communities*, Princeton University Press, 1975). These models take advantage of specifically nonlinear aspects of predator-prey or plant-herbivore interactions, which can produce stable oscillatory patterns in population density. Small advantages to the selfish individual can now be nonlinearly magnified into disastrously large amplitudes of population oscillation for his group. The result is that group selection can be rapid and powerful; although selfish genes continue to appear by mutation, the groups in which they appear are quickly extinguished before they spread.

A simpler and more compelling mechanism has been pointed out by Wilson (*Proc. natn. Acad. Sci. U.S.A.*, 72, 143–146; 1975). As in essentially all these models, first suppose the total population is constituted of several isolated groups. Periodically these populations are mixed together and then re-dispersed. (One may think of the annual episodes of winged dispersal among so many insects.) The population contains two genotypes: altruists,  $a$ , and selfish non-altruists,  $b$ . Wilson notes that it can be that in each group the altruists suffer higher mortality than the non-altruists, but that nevertheless the overall proportion of altruists in the population can increase from generation to generation.

This statistical paradox is familiar in other areas, for example medical biometrics, and is best illustrated with a numerical example. To fix ideas, let  $a$  be birds which give warning cries,

thereby decreasing the average mortality in their group at the expense of increasing their own mortality rate relative to the selfish  $b$ . Suppose we have two patches: the first containing  $25a$  and  $75b$ , the second  $75a$  and  $25b$ . Initially  $a$  therefore constitutes 50% of the population. The birds in the first patch suffer higher mortality by virtue of the smaller complement of altruists; just before the next dispersal phase there are, say, 30 individuals,  $6a$  and  $24b$ . The second group does better, coming down to, say, 70 individuals,  $50a$  and  $20b$ . Note that in both groups the fraction of altruists,  $a$ , has decreased (from 25% to 20% in the first, and from 75% to 71% in the second), but that the altruistic genotype has increased in the population as a whole (from 50% to 56%).

Wilson's model has the quality of *a posteriori* obviousness which characterises so much of the best in science. It illustrates group selection, pure and simple.

## Emplacement of intrusions

from G. M. Brown

THE geological evolution of the British Isles is a long and complex story but one period is particularly well understood, due to a prodigious amount of scientific investigation since the 1920s. Relatively recently in geological time, about 60 million years ago in the early Tertiary, active volcanoes erupted in what is now north-west Britain. Vast outpourings of basaltic lava were succeeded by the emplacement of a very complex array of igneous bodies in the form of dykes, cone sheets, ring dykes and other intrusive masses. The rock types are variable but include, predominantly, the products of medium to slow crystallisation of basaltic and granitic magmas. The intrusive complexes are believed to represent generally the eroded cores of central-type volcanoes that developed, as in Iceland, on and within the plateaux of the earlier flood lavas. Remnants of the flood lavas are preserved particularly well in Antrim but also in the Scottish Inner Hebrides. The later, central volcanic complexes constitute the bulk of many of the Hebridean islands such as Arran, Rhum, Mull and Skye, as well as Ardnamurchan (mainland Scotland) and the Mourne and Carlingford mountain regions in northern Ireland.

The volcanic regions have been mapped in ever-increasing detail, including geophysical measurement, by British geologists; and a host of laboratory studies has been conducted on the phase petrology, mineralogy and