

similar function. In these highly social insects, in which different members of the society are structurally and behaviourally specialized to perform different tasks, dispersal to new areas and the founding of new colonies is the task of the winged forms.

A third form of polymorphism exhibited by insects is life-history polymorphism as exhibited among butterflies, dragonflies, and wasps. In all of these insects the wingless larvae are the feeding phase and disperse little, whereas the adults are the dispersal phase and feed little. In fact, the adults of some insects, such as mayflies, do not feed at all, but disperse, mate, lay eggs, and die.

There are exceptions to the statement that larval insects disperse little, which introduces a fourth kind of polymorphism, termed behavioural polymorphism. In a population of the larch budmoth (*Zeiraphera griseana*) in Switzerland, there are at least two types of larva that differ in structure and behaviour. One is intolerant to crowding; it disperses readily and is usually the first to appear on the principal food plant, larch trees. The other is tolerant to crowding and disperses little. The proportion of these two types in the population varies from time to time in accordance with the overall density. A balance of advantages and disadvantages allows the two forms to persist together without one replacing the other.

As indicated by the above example, natural selection does not always favour the individuals that disperse the most. If the chances of dispersing and finding a new, suitable, and unexploited environment are very low, selection will act against the strong dispersers. Such seems to be the case in highly restricted and well-isolated environments such as oceanic islands and mountain tops. In these environments the number of flightless birds and insects is striking, and is much greater than in continental regions. Charles Darwin pointed out that the possession of large wings and well-developed powers of flight could be a disadvantage to animals on oceanic islands, particularly small ones, because an occasional strong wind might carry an already airborne animal away from the island and out to sea. The zoogeographer P.J. Darlington has emphasized that wings are also used in flight from predators, but predators are scarce or absent on these islands, so the need for dispersal powers within the island environment is not as great as within continental environments.

Passive dispersal. Organisms are dispersed passively by three principal agents: wind, water, and other organisms.

Dispersal by wind and by water. The capability of wind to transport organisms is well known, but the extent and the scale of such transportation is only now becoming clear. Microscopic organisms, such as viruses and protozoa, are readily carried by the wind, but even some of the smaller vertebrate animals such as frogs can be carried along on strong winds. Spiders, mites, and insects have been collected on airplane flights across the Pacific Ocean at distances up to 3,000 kilometres (1,900 miles) from land. Because of the method of capture, specimens are dead, so there is no means of distinguishing whether they were or were not living when they were collected. Nevertheless, in view of these remarkable results, it is no longer surprising that even the most isolated islands have an extensive insect fauna. There are, for example, close to 4,000 insect species native to the geographically rather remote Hawaiian Islands. It has been suggested that these species evolved from 250 ancestral types that could have been windborne from continents.

In a similar way, winds carry insects from lowland regions to mountain tops, where they may be deposited in the snow. Those incapable of existing in this climatically rigorous environment (probably almost all) are eaten by the native arthropod fauna. In fact, the native arthropods may be dependent upon this wind-drifted food, just as some stream-dwelling insects are dependent for food upon the organic matter drifting down from upper levels of the stream.

A study of the spotted alfalfa aphid (*Therioaphis maculata*) in California indicates that an amazingly large number of organisms are passively transported by wind. Mil-

lions of these winged aphids alone float passively with the current in the spring months.

Structural adaptations facilitating dispersal by wind are strongly developed in some groups of spiders. Gossamer, the silk secreted by the spider, is blown by the wind, and the spider, attached to it, is carried along, assisted sometimes by rising air currents.

Water currents carry organisms in the same manner as wind. In the aquatic environment, however, the terrestrial organisms must stay afloat, avoid becoming saturated with water, and maintain their internal salt balance. Some outstanding examples of long distance passive dispersal by ocean currents are known. Marine invertebrates are carried from West Africa to South and Central America on the main equatorial current of the Atlantic. Some water in this current comes from the Niger and Congo rivers, so it is possible for estuarine and freshwater animals to be transported to another continent by this means as well.

The distribution of several species of terrestrial animals is evidence that long distance dispersal has been achieved by major ocean currents. One dramatic example is the distribution of a flightless staphylinid beetle, *Micralymma marinum*, believed to have been carried passively from the Western hemisphere to the Eastern by means of the Gulf Stream.

The odds are considerable against terrestrial organisms surviving the ordeal of a prolonged journey in the surface waters of the sea. Some vertebrates may actively participate in the travel by swimming, thereby increasing their chances of survival. Others may cling to floating debris or natural rafts of land or ice. Pieces of river banks or fringing swamp vegetation and soil break off and are carried out to sea, particularly when flood conditions prevail, and with the rafts go the animals that were stranded on them. Pack ice, breaking loose, can similarly function as a raft for polar animals, such as polar bears, foxes, etc. A remarkable floating island was observed in the Atlantic off the coast of North America in 1892. It was estimated to be 100 feet square, with trees 30 feet high, and to have drifted at least 1,000 miles. Whether it reached land and its plant and animal passengers were able to colonize the new land is not known, but this example at least demonstrates the feasibility of distribution of organisms on rafts.

The distinction between airborne and waterborne means of dispersal is easy to make, but the two are not alternatives, because many organisms that start a journey on air complete it by water. Insects cross the Baltic Sea from Estonia to Finland, originally participating in mass flights, but reaching the other side in the water, many of them alive.

Dispersal by other organisms. The third means of dispersal—by other organisms—may be regular, in the case of a host transporting a parasite, or irregular, as in the chance attachment of one organism to another. For parasites, finding a host is a major problem, and an efficient means of dispersal from one host to another or to the environment in which another can be found, is essential. Consequently, parasites have developed remarkable specializations to the life history characteristics of the host that enable the parasite to disperse at the most favourable time. Dispersal is often assisted by the use of an additional species as a transporting agent, or carrier, from one host to another. A case in point is the myxoma virus, which parasitizes rabbits and uses mosquitoes as carriers. When aided by wind, an individual mosquito can carry the virus as far as 40 miles before infecting a rabbit; by this process of transporting and infecting, the mosquito population can disperse the virus rapidly over a large area.

Many organisms are distributed by attachment to mobile organisms. Small invertebrates such as snails and flatworms, for example, are accidentally transported on the legs of migrating birds. Undigested food items, such as the seeds of some plants, can be widely dispersed by their consumers in excrement deposited far from the source. There are numerous cases of mutualistic associations between animals and plants in which the plants are

Adaptations for dispersal