PLANTS IN RELATION TO ANIMAL DISTRIBUTION

by

L. F. DE BEAUFORT
(Zoölogisch Museum, Amsterdam)

It needs an explanation why among the botanical papers published in this volume to honour Mrs. Weber—van Bosse on her 90th birthday a zoological contribution has been inserted. Those who have read the curriculum vitae of this wellknown botanist in the foregoing pages of this volume will not wonder, for they know that she has been keenly interested for more than half a century in the zoological work of her late husband. And so among the chorus of botanists the voice of a zoologist could hardly be missed. For many years I have enjoyed the friendship of both, and I am grateful for this opportunity to show Mrs. Weber my affection and my admiration.

When contemplating an adequate theme for this paper it occurred to me that in some way or other it had to dwell on the relations between zoology and botany and as the distribution of animals is a branch of science which has always interested both Max Weber and me, I decided on the influence which the distribution of plants has on that of animals.

Now this is a problem which has been treated over and over again. Every biologist knows how animal life is dependent, directly or indirectly, on that of plants. This relation has been studied from all aspects and I fear that I shall disappoint those, who hope to gather any new facts or thoughts from what follows. In three ways animals depend on plants. These relations are those of food, shelter, and oxygen production.

When grouping the Animal Kingdom according to their ecological distribution we distinguish a fauna of the woods, a fauna of the bushes and savannahs, of plains and steppes etc., all of them bound to habitats characterized or even formed by some kind of vegetation. On land these different ecological groups of animals are tied to the localities by the plants, and the boundaries of some kind or other of vegetation will also be those of many species of animals. Still more so when the animal feeds on the plants, and in the case of monophagous herbivores the animal will be unable to migrate beyond the boundaries of the area of the plant on which it feeds. Migration of such a species is only possible when the plant migrates or when the animal changes its diet.

In the sea it is different. Sessile plants are restricted to the coastal regions, being unable to live in great depths in consequence of the lack of light. Moreover, sessile animals compete with the plants and are often of much greater importance than the plants as shelters. The food offered

by plants to sea-animals is derived for a small part only from these sessile plants; by far the greater quantity is produced by the floating microscopical algae, the phyto-plankton. This source of food is not bound to circumscribed localities; it floats and is continuously in motion through the agency of winds and currents. It is true, that the plankton is not equally distributed over the seas and oceans, but varies in quality and quantity according to temperature and currents, but still the effect is that the ties, which bind the animals on land to circumscribed localities, are loose or even wanting here.

Sea-animals which feed exclusively on such submerged Phanerogams as *Zostera, Posidonia,* and *Halophila,* or on Algae like *Laminaria,* and *Fucus,* are rare. Among the plankton-feeders, those which feed on phyto-plankton are small animals, such as crustaceans, *Appendicularia,* and others. The reason is, that the phyto-plankton is very small for the greater part (nanno-plankton) and that only small animals can catch it. As is well known the *Appendicularia* even construct "nets" of a microscopical texture, in which the nanno-plankton is caught. When we come to larger plankton-feeders such as herrings or still larger ones such as whales, we see that animal-plankton is the chief food. Possibly some phyto-plankton is caught together with the animals, but we can safely say that the bulk of the larger plankton-feeders depend on animal-plankton and these again on phyto-plankton. The relation, therefore, is indirect, but this does not alter the statement, given above, that sea-animals are less bound to certain localities than land-animals. There are of course other factors which limit their dispersal, temperature for instance, and it stands to reason that sessile animals are left out of consideration here. There is evidence that the distribution of the last-named follows the same rules as that of plants and that they play a part in the "succession", which seems to occur here just as well as on the land.

In fresh water we find much the same relations as in the sea. Here too we can distinguish plankton-feeders and feeders on sessile plants. Plants provide shelter in a greater degree than in the sea, as sessile fresh-water animals are rarer. The chief relation between plants and animals in fresh water, however, is another, viz. the production of oxygen. This is a consequence of the smaller dimensions of the area, and the importance of this factor increases, when the size of the area decreases. It attains its maximum in a small pool or in its artificial equivalent: the aquarium, where under favourable conditions a stable relation between plants and animals can be obtained. The classification of lakes in relation to their animal population is based on the vegetation, not as food, but as oxygen producers.

Shelter is not only provided by sessile plants surrounding lakes and other stagnant waters, but also by floating plants, such as *Lemna, Pistia, Azolla* or plants with floating leaves such as *Nelumbium, Nymphaea* and many others. Underneath these leaves fishes as well as molluscs and worms find protection.

In the Atlantic the Sargassum-Sea provides a similar kind of cover.

This has been but a rapid survey of the ways in which plants affect

the distribution of animals. If space permitted, many details could be discussed, but what has been said seems sufficient to come to the conclusion, that of the three ways in which animals are dependent on plants that of food is, of course, the most important, but of the other two, shelter is the most manifest on land, and production of oxygen in fresh water.

In the foregoing pages the influence of plants on the distribution of animals has been dealt with from an ecological point of view. What we have discussed is how the distribution of animals depends on that of plants at the present time. Another question is, how this relation worked in past ages. This problem deals with a chapter of historic biogeography. What we have been looking at was a static process and we have silently assumed that the circumstances under which the plants and animals live remained unchanged. It is hoewever, well known that changes of climate, changes in the distribution of land and sea, and orogenetic events have a very important influence on distribution and that many facts in the present distribution cannot be understood without taking these factors into account.

Changes of climate can make a country uninhabitable for some plants or animals. On land, plants will probably have first been affected. If we look at what has happened in the Northern Hemisphere after the pleistocene ice-ages we see that after the retreat of the ice the abandoned land has been invaded, first by a fauna similar to that which now lives in the tundra, then, when the temperature rose, by a fauna similar to that of the steppes, and finally by a forest fauna. It stands to reason that these faunae have inhabited tundra's, steppes, and forests. Although this was denied by some scientists in the past century, I think that nobody holds their side nowadays. Now tundra, steppe, and forest are principally botanical notions and so we may conclude that in this case the countries freed from the ice have been invaded, by plants first, the animals adapted to the peculair vegetation following. As the plants, being the basic food, stand at the bottom of every plant and animal community, nothing else could be expected.

So we can state that plants and animals migrate together, but that the plants advance first. It is well to remember this. When speaking of territories invaded by a new fauna we are apt to think of an army, advancing in enemy country, but this comparison is misleading. In an advancing army the soldiers fight their way, their food follows, here the food (the plants) prepare the ground and the animals follow.

Of course we must not think that these are processes succeeding each other. Such an invasion is a very slow and gradual proceeding and only when we pick out one animal-species or other and trace its migration we can demonstrate how it follows the spreading of the plants on which it depends, either as food or as cover.

Topographical changes which affect the distribution of life are, broadly speaking, of two kinds. An area, forming a biogeographical unit, can be split into two separate ones by the rising of mountains or by the invasion of the sea, and formerly separate ones can be united by the retreat of the sea or by the abrasion of mountains.

In the first-named case isolation occurs. The influence of isolation on the development of new species together with the conservation of primitive types is well known and the peculiar and primitive flora as well as fauna of Australia or New Zealand shows that both plants and animals undergo the influence of isolation in the same way. How the evolution of plants affects that of animals in such an isolated area, we can only speculate on. Probably a certain equilibrium is maintained, as we may deduct from the fact, that harmony is disturbed when foreign plants or animals are imported in such a country.

In the second case, the connection of two areas hitherto separated, the flora and fauna of both will advance into the new connecting territory, a proceeding comparable to the migration discussed above. A certain degree of mixing will take place and in case the "living stock" of both differs, this mixing will be accompanied with a struggle. By "living stock" I mean flora and fauna together; as far as I know there is no technical term for this notion. This struggle must be a very complicated one, and certainly not of plants against plants and animals against animals only.

We need not dwell at length on what happens when the non-biotic circumstances which control life in the sea change. Such changes can be of temperature, of salinity or of another chemical nature, or they can be topographical ones, for instance the separation or the union of two seas. The course of events in the coastal flora and fauna will be much the same as on land, and the pelagic fauna, with its pelagic and highly movable basic food supply, will not be affected so seriously as on land.

Lastly, in fresh water, we must distinguish between stagnant water and streams. Lakes, as is well known, have a short life, considered from a geological point of view, for they gradually change into marshes. The part played by the vegetation during these changes is well known, and so the influence of plants on animal distribution is clear enough here. River systems are continually changing too. Meanders will be cut off, turn into stagnant waters and suffer the same fate as lakes. Adjacent river systems can get connections and the "living stock" of both will mix, but as fresh water animals are seldom so dependent on special plants, either as food or as shelter, as is the case on land, the influence of plants on the fresh water fauna will not be of great importance.

Resuming we can say that everywhere, but principally on land, climatic or topographical mutations do not affect the fauna directly, but indirectly through changes in the flora. In historic zoogeography this has not always been realised. This branch of science is a young one, and its methods are often clumsy. When two zoogeographical regions are compared, generally a few systematic groups of animals are picked out, with which the author is well acquainted. Although I agree that interesting results have been obtained that way, it is obvious that they must be incomplete and fragmentary. To give an example: a certain group of animals is well represented in region A, but is wanting in B. This can be due to the fact, that there is a geographical barrier which prevents the group from migrating from A to B, but it is also possible,

that the plant- and animal-community, in which the group fits, is lacking in B. What is necessary is a comparative study of the plant- and animal-communities occurring in the regions we want to investigate. This looks like an impossible task. It will take many years before we shall have reached a clear insight into the complicated relations, existing even in simple communities, and once this has been achieved, we are still far from our goal, for only then can we start the comparison of the faunae and florae of the different regions. However, there is no reason to be discouraged. The work to be done is full of interest and it has to be done by scientists in all parts of the world. Botanists as well as zoologists, workers on systematics as well as ecologists will have to co-operate and work is waiting in the laboratory as well as in the field.

It may be thought futile to develop such plans when the world is on fire, but we look with confidence to the future.