

# Disease and Evolution\*

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RIASSUNTO. – Negli esempi addotti dai biologi per mostrare come la selezione naturale agisce, la struttura o la funzione presa in esame è per lo più collegata con la protezione contro forze naturali a vverse, contro predatori, oppure con la conquista di alimento o dell'altro sesso. L'A. mostra che la lotta contro le malattie, e in particolare contro le malattie infettive, ha rappresentato un fattore evolutivo molto importante e che alcuni dei suoi risultati sono diversi da quelli raggiunti attraverso le forme consuete della lotta per l'esistenza.

RÉSUMÉ. – Les exemples portés par les biologistes pour montrer comment la sélection naturelle opère tiennent compte d'ordinaire de structures ou de fonctions liées à la protection contre des forces naturelles hostiles, contre des prédateurs, ou bien liées à la conquête de la nourriture ou du sexe opposé. L'A. montre que la lutte contre les maladies, et en particulier contre les maladies infectieuses, a représenté un facteur évolutif très important et que quelques-uns parmi ses résultats diffèrent bien de ceux qui ont été atteints par les formes ordinaires de la lutte pour la vie.

SUMMARY. – Examples quoted by biologists, in order to show how natural selection is working, almost present structures or functions concerned either with protection against natural forces or against predators, or with purchase of food or mates. The Author suggests that the struggle against diseases, and especially infectious diseases, has been a very important evolutionary agent and that some of its results have been rather unlike those of the struggle for life in its common meaning.

It is generally believed by biologists that natural selection has played an important part in evolution. When however an attempt is made to show how natural selection acts, the structure or function considered is almost always one concerned either with protection against natural «forces» such as cold or against predators, or one which helps the organism to obtain

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food or mates. I want to suggest that the struggle against disease, and particularly infectious disease, has been a very important evolutionary agent, and that some of its results have been rather unlike those of the struggle against natural forces, hunger, and predators, or with members of the same species.

Under the heading infectious disease I shall include, when considering animals, all attacks by smaller organisms, including bacteria, viruses, fungi, protozoa, and metazoan parasites. In the case of plants it is not so clear whether we should regard aphids or caterpillars as a disease. Similarly there is every gradation between diseases due to a deficiency of some particular food constituent and general starvation.

The first question which we should ask is this. How important is disease as a killing agent in nature? On the one hand what fraction of members of a species die of disease before reaching maturity? On the other, how far does disease reduce the fertility of those members which reach maturity? Clearly the answer will be very different in different cases. A marine species producing millions of small eggs with planktonic larvae will mainly be eaten by predators. One which is protected against predators will lose a larger proportion from disease.

There is however, a general fact which shows how important infectious disease must be. In every species at least one of the factors which kills it or lowers its fertility must increase in efficiency as the species becomes denser. Otherwise the species, if it increased at all, would increase without limit. A predator cannot in general be such a factor, since predators are usually larger than their prey, and breed more slowly. Thus if the numbers of mice increase, those of their large enemies, such as owls, will increase more slowly. Of course the density-dependent check may be lack of food or space. Lack of space is certainly effective on dominant species such as forest trees or animals like *Mytilus*. Competition for food by the same species is a limiting factor in a few phytophagous animals such as defoliating caterpillars, and in very stenophagous animals such as many parasitoids. I believe however that the density-dependent limiting factor is more often a parasite whose incidence is disproportionately raised by overcrowding.

As an example of the kind of analysis which we need, I take Varley's (1947) remarkable study on *Urophora jaceana*, which forms galls on the composite *Centaurea nigra*. In the year considered 0.5% of the eggs survived to produce a mature female. How were the numbers reduced to  $\frac{1}{200}$  of the initial value?

If we put  $200 = e^k$ , we can compare the different killing powers of various environmental agents, writing  $K = k_2 \div k_1 \div k_3 \div \dots$ , where  $k_r$  is a measure of the killing power of each of them. The result is given in Table 1. Surprisingly, the main killers appear to be mice and voles (*Mus*,