THE
AMERICAN NATURALIST

Vol. XCIII May-June, 1959 No. 870

HOMAGE TO SANTA ROSALIA
or
WHY ARE THERE SO MANY KINDS OF ANIMALS?*

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When you did me the honor of asking me to fill your presidential chair, I accepted perhaps without duly considering the duties of the president of a society, founded largely to further the study of evolution, at the close of the year that marks the centenary of Darwin and Wallace's initial presentation of the theory of natural selection. It seemed to me that most of the significant aspects of modern evolutionary theory have come either from geneticists, or from those heroic museum workers who suffering through years of neglect, were able to establish about 20 years ago what has come to be called the "new systematics." You had, however, chosen an ecologist as your president and one of that school at times supposed to study the environment without any relation to the organism.

A few months later I happened to be in Sicily. An early interest in zoogeography and in aquatic insects led me to attempt to collect near Palermo, certain species of water-bugs, of the genus Corixa, described a century ago by Fieber and supposed to occur in the region, but never fully reinvestigated. It is hard to find suitable localities in so highly cultivated a landscape as the Concha d'Oro. Fortunately, I was driven up Monte Pellegrino, the hill that rises to the west of the city, to admire the view. A little below the summit, a church with a simple baroque facade stands in front of a cave in the limestone of the hill. Here in the 16th century a stalactite encrusted skeleton associated with a cross and twelve beads was discovered. Of this skeleton nothing is certainly known save that it is that of Santa Rosalia, a saint of whom little is reliably reported save that she seems to have lived in the 12th century, that her skeleton was found in this cave, and that she has been the chief patroness of Palermo ever since. Other limestone caverns on Monte Pellegrino had yielded bones of extinct pleistocene Equus, and on the walls of one of the rock shelters at the bottom of the hill there are beautiful Gravettian engravings. Moreover, a small relic of the saint that I saw in the treasury of the Cathedral of Monreale has a venerable and

*Address of the President, American Society of Naturalists, delivered at the annual meeting, Washington, D. C., December 30, 1958.

petrified appearance, as might be expected. Nothing in her history being known to the contrary, perhaps for the moment we may take Santa Rosalia as the patroness of evolutionary studies, for just below the sanctuary, fed no doubt by the water that percolates through the limestone cracks of the mountain, and which formed the sacred cave, lies a small artificial pond, and when I could get to the pond a few weeks later, I got from it a hint of what I was looking for.

Vast numbers of Corixidae were living in the water. At first I was rather disappointed because every specimen of the larger of the two species present was a female, and so lacking in most critical diagnostic features, while both sexes of the second slightly smaller species were present in about equal number. Examination of the material at leisure, and of the relevant literature, has convinced me that the two species are the common European *C. punctata* and *C. affinis*, and that the peculiar Mediterranean species are illusionary. The larger *C. punctata* was clearly at the end of its breeding season, the smaller *C. affinis* was probably just beginning to breed. This is the sort of observation that any naturalist can and does make all the time. It was not until I asked myself why the larger species should breed first, and then the more general question as to why there should be two and not 20 or 200 species of the genus in the pond, that ideas suitable to present to you began to emerge. These ideas finally prompted the very general question as to why there are such an enormous number of animal species.

There are at the present time supposed to be (Muller and Campbell, 1954; Hyman, 1955) about one million described species of animals. Of these about three-quarters are insects, of which a quite disproportionately large number are members of a single order, the Coleoptera.[1] The marine fauna although it has at its disposal a much greater area than has the terrestrial, lacks this astonishing diversity (Thorson, 1958). If the insects are excluded, it would seem to be more diverse. The proper answer to my initial question would be to develop a theory at least predicting an order of magnitude for the number of species of 10^6 rather than 10^8 or 10^4. This I certainly cannot do. At most it is merely possible to point out some of the factors which would have to be considered if such a theory was ever to be constructed.

Before developing my ideas I should like to say that I subscribe to the view that the process of natural selection, coupled with isolation and later mutual invasion of ranges leads to the evolution of sympatric species, which at equilibrium occupy distinct niches, according to the Volterra-Gause principle. The empirical reasons for adopting this view and the correlative view that the boundaries of realized niches are set by competition are mainly indirect. So far as niches may be defined in terms of food, the subject has been carefully considered by Lack (1954). In general all the indirect evi-

[1] There is a story, possibly apocryphal, of the distinguished British biologist, J. B. S. Haldane, who found himself in the company of a group of theologians. On being asked what one could conclude as to the nature of the Creator from a study of his creation, Haldane is said to have answered, "An inordinate fondness for beetles."

dence is in accord with the view, which has the advantage of confirming theoretical expectation. Most of the opinions that have been held to the contrary appear to be due to misunderstandings and to loose formulation of the problem (Hutchinson, 1958).

In any study of evolutionary ecology, food relations appear as one of the most important aspects of the system of animate nature. There is quite obviously much more to living communities than the raw dictum "eat or be eaten," but in order to understand the higher intricacies of any ecological system, it is most easy to start from this crudely simple point of view.

FOOD CHAINS

Animal ecologists frequently think in terms of food chains, of the form *individuals of species* S_1 *are eaten by those of* S_2, *of* S_2 *by* S_3, *of* S_3 *by* S_4, etc. In such a food chain S_1 will ordinarily be some holophylic organism or material derived from such organisms. The simplest case is that in which we have a true *predator chain* in Odum's (1953) convenient terminology, in which the lowest link is a green plant, the next a herbivorous animal, the next a primary carnivore, the next a secondary carnivore, etc. A specially important type of predator chain may be designated Eltonian, because in recent years C. S. Elton (1927) has emphasized its widespread significance, in which the predator at each level is larger and rarer than its prey. This phenomenon was recognized much earlier, notably by A. R. Wallace in his contribution to the 1858 communication to the Linnean Society of London.

In such a system we can make a theoretical guess of the order of magnitude of the diversity that a single food chain can introduce into a community. If we assume that in general 20 per cent of the energy passing through one link can enter the next link in the chain, which is overgenerous (cf. Lindeman, 1942; Slobodkin in an unpublished study finds 13 per cent as a reasonable upper limit) and if we suppose that each predator has twice the mass, (or 1.26 the linear dimensions) of its prey, which is a very low estimate of the size difference between links, the fifth animal link will have a population of one ten thousandth (10^{-4}) of the first, and the fiftieth animal link, if there was one, a population of 10^{-49} the size of the first. Five animal links are certainly possible, a few fairly clear cut cases having been in fact recorded. If, however, we wanted 50 links, starting with a protozoan or rotifer feeding on algae with a density of 10^6 cells per ml, we should need a volume of 10^{26} cubic kilometers to accommodate on an average one specimen of the ultimate predator, and this is vastly greater than the volume of the world ocean. Clearly the Eltonian food-chain of itself cannot give any great diversity, and the same is almost certainly true of the other types of food chain, based on detritus feeding or on parasitism.

Natural selection

Before proceeding to a further consideration of diversity, it is, however, desirable to consider the kinds of selective force that may operate on a food chain, for this may limit the possible diversity.

It is reasonably certain that natural selection will tend to maintain the efficiency of transfer from one level to another at a maximum. Any increase in the predatory efficiency of the n^{th} link of a simple food chain will however always increase the possibility of the extermination of the $(n-1)^{th}$ link. If this occurs either the species constituting the n^{th} link must adapt itself to eating the $(n-2)^{th}$ link or itself become extinct. This process will in fact tend to shortening of food chains. A lengthening can presumably occur most simply by the development of a new terminal carnivore link, as its niche is by definition previously empty. In most cases this is not likely to be easy. The evolution of the whale-bone whales, which at least in the case of *Balaenoptera borealis*, can feed largely on copepods and so rank on occasions as primary carnivores (Bigelow, 1926), presumably constitutes the most dramatic example of the shortening of a food chain. Mechanical considerations would have prevented the evolution of a larger rarer predator, until man developed essentially non-Eltonian methods of hunting whales.

Effect of size

A second important limitation of the length of a food chain is due to the fact that ordinarily animals change their size during free life. If the terminal member of a chain were a fish that grew from say one cm to 150 cms in the course of an ordinary life, this size change would set a limit by competition to the possible number of otherwise conceivable links in the 1-150 cm range. At least in fishes this type of process (metaphoetesis) may involve the smaller specimens belonging to links below the larger and the chain length is thus lengthened, though under strong limitations, by cannibalism.

We may next enquire into what determines the number of food chains in a community. In part the answer is clear, though if we cease to be zoologists and become biologists, the answer begs the question. Within certain limits, the number of kinds of primary producers is certainly involved, because many herbivorous animals are somewhat eclectic in their tastes and many more limited by their size or by such structural adaptations for feeding that they have been able to develop.

Effects of terrestrial plants

The extraordinary diversity of the terrestrial fauna, which is much greater than that of the marine fauna, is clearly due largely to the diversity provided by terrestrial plants. This diversity is actually two-fold. Firstly, since terrestrial plants compete for light, they have tended to evolve into structures growing into a gaseous medium of negligible buoyancy. This has led to the formation of specialized supporting, photosynthetic, and reproductive structures which inevitably differ in chemical and physical properties. The ancient Danes and Irish are supposed to have eaten elm-bark, and sometimes sawdust, in periods of stress, has been hydrolyzed to produce edible carbohydrate; but usually man, the most omnivorous of all animals, has avoided

almost all parts of trees except fruits as sources of food, though various individual species of animals can deal with practically every tissue of many arboreal species. A major source of terrestrial diversity was thus introduced by the evolution of almost 200,000 species of flowering plants, and the three quarters of a million insects supposedly known today are in part a product of that diversity. But of itself merely providing five or ten kinds of food of different consistencies and compositions does not get us much further than the five or ten links of an Eltonian pyramid. On the whole the problem still remains, but in the new form: why are there so many kinds of plants? As a zoologist I do not want to attack that question directly, I want to stick with animals, but also to get the answer. Since, however, the plants are part of the general system of communities, any sufficiently abstract properties of such communities are likely to be relevant to plants as well as to herbivores and carnivores. It is, therefore, by being somewhat abstract, though with concrete zoological details as examples, that I intend to proceed.

INTERRELATIONS OF FOOD CHAINS

Biological communities do not consist of independent food chains, but of food webs, of such a kind that an individual at any level (corresponding to a link in a single chain) can use some but not all of the food provided by species in the levels below it.

It has long been realized that the presence of two species at any level, either of which can be eaten by a predator at a level above, but which may differ in palatability, ease of capture or seasonal and local abundance, may provide alternative foods for the predator. The predator, therefore, will neither become extinct itself nor exterminate its usual prey, when for any reason, not dependent on prey-predator relationships, the usual prey happens to be abnormally scarce. This aspect of complicated food webs has been stressed by many ecologists, of whom the Chicago school as represented by Allee, Emerson, Park, Park and Schmidt (1949), Odum (1953) and Elton (1958), may in particular be mentioned. Recently MacArthur (1955) using an ingenious but simple application of information theory has generalized the points of view of earlier workers by providing a formal proof of the increase in stability of a community as the number of links in its food web increases.

MacArthur concludes that in the evolution of a natural community two partly antagonistic processes are occurring. More efficient species will replace less efficient species, but more stable communities will outlast less stable communities. In the process of community formation, the entry of a new species may involve one of three possibilities. It may completely displace an old species. This of itself does not necessarily change the stability, though it may do so if the new species inherently has a more stable population (cf. Slobodkin, 1956) than the old. Secondly, it may occupy an unfilled niche, which may, by providing new partially independent links, increase stability. Thirdly, it may partition a niche with a pre-existing species. Elton (1958) in a fascinating work largely devoted to the fate of species accidentally or purposefully introduced by man, concludes that in very

diverse communities such introductions are difficult. Early in the history of a community we may suppose many niches will be empty and invasion will proceed easily; as the community becomes more diversified, the process will be progressively more difficult. Sometimes an extremely successful invader may oust a species but add little or nothing to stability, at other times the invader by some specialization will be able to compete successfully for the marginal parts of a niche. In all cases it is probable that invasion is most likely when one or more species happen to be fluctuating and are underrepresented at a given moment. As the communities build up, these opportunities will get progressively rarer. In this way a complex community containing some highly specialized species is constructed asymptotically.

Modern ecological theory therefore appears to answer our initial question at least partially by saying that there is a great diversity of organisms because communities of many diversified organisms are better able to persist than are communities of fewer less diversified organisms. Even though the entry of an invader which takes over part of a niche will lead to the reduction in the *average* population of the species originally present, it will also lead to an increase in stability reducing the risk of the original population being at times underrepresented to a dangerous degree. In this way loss of some niche space may be compensated by reduction in the amplitude of fluctuations in a way that can be advantageous to both species. The process however appears likely to be asymptotic and we have now to consider what sets the asymptote, or in simpler words why are there not more different kinds of animals?

LIMITATION OF DIVERSITY

It is first obvious that the processes of evolution of communities must be under various sorts of external control, and that in some cases such control limits the possible diversity. Several investigators, notably Odum (1953) and MacArthur (1955), have pointed out that the more or less cyclical oscillations observed in arctic and boreal fauna may be due in part to the communities not being sufficiently complex to damp out oscillations. It is certain that the fauna of any such region is qualitatively poorer than that of warm temperate and tropical areas of comparable effective precipitation. It is probably considered to be intuitively obvious that this should be so, but on analysis the obviousness tends to disappear. If we can have one or two species of a large family adapted to the rigors of Arctic existence, why can we not have more? It is reasonable to suppose that the total biomass may be involved. If the fundamental productivity of an area is limited by a short growing season to such a degree that the total biomass is less than under more favorable conditions, then the rarer species in a community may be so rare that they do not exist. It is also probable that certain absolute limitations on growth-forms of plants, such as those that make the development of forest impossible above a certain latitude, may in so acting, severely limit the number of niches. Dr. Robert MacArthur points out that the development of high tropical rain forest increases the bird fauna more than that of mam-

mals, and Thorson (1957) likewise has shown that the so-called infauna show no increase of species toward the tropics while the marine epifauna becomes more diversified. The importance of this aspect of the plant or animal substratum, which depends largely on the length of the growing season and other aspects of productivity is related to that of the environmental mosaic discussed later.

We may also inquire, but at present cannot obtain any likely answer, whether the arctic fauna is not itself too young to have achieved its maximum diversity. Finally, the continual occurrence of catastrophes, as Wynne-Edwards (1952) has emphasized, may keep the arctic terrestrial community in a state of perennial though stunted youth.

Closely related to the problems of environmental rigor and stability, is the question of the absolute size of the habitat that can be colonized. Over much of western Europe there are three common species of small voles, namely *Microtus arvalis*, *M. agrestis* and *Clethrionomys glareolus*. These are sympatric but with somewhat different ecological preferences.

In the smaller islands off Britain and in the English channel, there is only one case of two species co-occurring on an island, namely *M. agrestis* and Clethrionomys on the island of Mull in the Inner Hebrides (Barrett-Hamilton and Hinton, 1911–1921). On the Orkneys the single species is *M. orcadensis*, which in morphology and cytology is a well-differentiated ally of *M. arvalis*; a comparable animal (*M. sarnius*) occurs on Guernsey. On most of the Scottish Islands only subspecies of *M. agrestis* occur, but on Mull and Raasay, on the Welsh island of Skomer, as well as on Jersey, races of Clethrionomys of somewhat uncertain status are found. No voles have reached Ireland, presumably for paleogeographic reasons, but they are also absent from a number of small islands, notably Alderney and Sark. The last named island must have been as well placed as Guernsey to receive *Microtus arvalis*. Still stranger is the fact that although it could not have got to the Orkneys without entering the mainland of Britain, no vole of the *arvalis* type now occurs in the latter country. Cases of this sort may be perhaps explained by the lack of favorable refuges in randomly distributed very unfavorable seasons or under special kinds of competition. This explanation is very reasonable as an explanation of the lack of Microtus on Sark, where it may have had difficulty in competing with *Rattus rattus* in a small area. It would be stretching one's credulity to suppose that the area of Great Britain is too small to permit the existence of two sympatric species of Microtus, but no other explanation seems to have been proposed.

It is a matter of considerable interest that Lack (1942) studying the populations of birds on some of these small British islands concluded that such populations are often unstable, and that the few species present often occupied larger niches than on the mainland in the presence of competitors. Such faunas provide examples of communities held at an early stage in development because there is not enough space for the evolution of a fuller and more stable community.

NICHE REQUIREMENTS

The various evolutionary tendencies, notably metaphoetesis, which operate on single food chains must operate equally on the food-web, but we also have a new, if comparable, problem as to how much difference between two species at the same level is needed to prevent them from occupying the same niche. Where metric characters are involved we can gain some insight into this extremely important problem by the study of what Brown and Wilson (1956) have called *character displacement* or the divergence shown when two partly allopatric species of comparable niche requirements become sympatric in part of their range.

I have collected together a number of cases of mammals and birds which appear to exhibit the phenomenon (table 1). These cases involve metric characters related to the trophic apparatus, the length of the culmen in birds and of the skull in mammals appearing to provide appropriate measures. Where the species co-occur, the ratio of the larger to the small form varies from 1.1 to 1.4, the mean ratio being 1.28 or roughly 1.3. This latter figure may tentatively be used as an indication of the kind of difference necessary to permit two species to co-occur in different niches but at the same level of a food-web. In the case of the aquatic insects with which I began my address, we have over most of Europe three very closely allied species of Corixa, the largest *punctata*, being about 116 per cent longer than the middle sized species *macrocephala*, and 146 per cent longer than the small species *affinis*. In northwestern Europe there is a fourth species, *C. dentipes*, as large as *C. punctata* and very similar in appearance. A single observation (Brown, 1948) suggests that this is what I have elsewhere (Hutchinson, 1951) termed a fugitive species, maintaining itself in the face of competition mainly on account of greater mobility. According to Macan (1954) while both *affinis* and *macrocephala* may occur with *punctata* they never are found with each other, so that all three species never occur together. In the eastern part of the range, *macrocephala* drops out, and *punctata* appears to have a discontinuous distribution, being recorded as far east as Simla, but not in southern Persia or Kashmir, where *affinis* occurs. In these eastern localities, where it occurs by itself, *affinis* is larger and darker than in the west, and superficially looks like *macrocephala* (Hutchinson, 1940).

This case is very interesting because it looks as though character displacement is occurring, but that the size differences between the three species are just not great enough to allow them all to co-occur. Other characters than size are in fact clearly involved in the separation, *macrocephala* preferring deeper water than *affinis* and the latter being more tolerant of brackish conditions. It is also interesting because it calls attention to a marked difference that must occur between hemimetabolous insects with annual life cycles involving relatively long growth periods, and birds or mammals in which the period of growth in length is short and of a very special nature compared with the total life span. In the latter, niche separation may be possible merely through genetic size differences, while in a pair of ani-

TABLE 1

Mean character displacement in measurable trophic structures in mammals (skull) and birds (culmen); data for Mustela from Miller (1912); Apodemus from Cranbrook (1957); Sitta from Brown and Wilson (1956) after Vaurie; Galapagos finches from Lack (1947)

	Locality and measurement when sympatric	Locality and measurement when allopatric	Ratio when sympatric
Mustela nivalis	Britain; skull ♂ 39.3 ♀ 33.6 mm.	(*boccamela*) S. France, Italy ♂ 42.9 ♀ 34.7 mm. (*iberica*) Spain, Portugal ♂ 40.4 ♀ 36.0 (*hibernica*) Ireland ♂ 46.0 ♀ 41.9	♂ 100 : 128 ♀ 100 : 134
M. erminea	Britain; " ♂ 50.4 ♀ 45.0		
Apodemus sylvaticus	Britain; " 24.8	unnamed races on Channel Islands 25.6–26.7	100 : 109
A. flavicollis	Britain; " 27.0		
Sitta tephronota	Iran; culmen 29.0	races east of overlap 25.5	100 : 124
S. neumayer	Iran; " 23.5	races west of overlap 26.0	
Geospiza fortis	Indefatigable Isl.; culmen 12.0	Daphne Isl. 10.5	100 : 143
G. fuliginosa	Indefatigable Isl.; " 8.4	Crossman Isl. 9.3	
Camarhynchus parvulus	James Isl.; " 7.0	N. Albemarle Isl. 7.0	James 100 : 140 : 180
	Indefatigable Isl.; " 7.5	Chatham Isl. 8.0	100 : 129
C. psittacula	S. Albemarle Isl.; " 7.3	Abington Isl. 10.1	Indefatigable 100 : 128 : 162
	James Isl.; " 9.8	Bindloe Isl. 10.5	100 : 127
	Indefatigable Isl.; " 9.6		
C. pallidus	S. Albemarle Isl.; " 8.5		
	James Isl.; " 12.6	N. Albemarle Isl. 11.7	S. Albemarle 100 : 116 : 153
	Indefatigable Isl.; " 12.1	Chatham Isl. 10.8	100 : 132
	S. Albemarle Isl.; " 11.2		
			Mean ratio 100 : 128

mals like *C. punctata* and *C. affinis* we need not only a size difference but a seasonal one in reproduction; this is likely to be a rather complicated matter. For the larger of two species always to be larger, it must never breed later than the smaller one. I do not doubt that this is what was happening in the pond on Monte Pellegrino, but have no idea how the difference is achieved.

I want to emphasize the complexity of the adaptation necessary on the part of two species inhabiting adjacent niches in a given biotope, as it probably underlies a phenomenon which to some has appeared rather puzzling. MacArthur (1957) has shown that in a sufficiently large bird fauna, in a uniform undisturbed habitat, areas occupied by the different species appear to correspond to the random non-overlapping fractionation of a plane or volume. Kohn (1959) has found the same thing for the cone-shells (Conus) on the Hawaiian reefs. This type of arrangement almost certainly implies such individual and unpredictable complexities in the determination of the niche boundaries, and so of the actual areas colonized, that in any overall view, the process would appear random. It is fairly obvious that in different types of community the divisibility of niches will differ and so the degree of diversity that can be achieved. The fine details of the process have not been adequately investigated, though many data must already exist that could be organized to throw light on the problem.

MOSAIC NATURE OF THE ENVIRONMENT

A final aspect of the limitation of possible diversity, and one that perhaps is of greatest importance, concerns what may be called the mosaic nature of the environment. Except perhaps in open water when only uniform quasi-horizontal surfaces are considered, every area colonized by organisms has some local diversity. The significance of such local diversity depends very largely on the size of the organisms under consideration. In another paper MacArthur and I (Hutchinson and MacArthur, 1959) have attempted a theoretical formulation of this property of living communities and have pointed out that even if we consider only the herbivorous level or only one of the carnivorous levels, there are likely, above a certain lower limit of size, to be more species of small or medium sized organisms than of large organisms. It is difficult to go much beyond crude qualitative impressions in testing this hypothesis, but we find that for mammal faunas, which contain such diverse organisms that they may well be regarded as models of whole faunas, there is a definite hint of the kind of theoretical distribution that we deduce. In qualitative terms the phenomenon can be exemplified by any of the larger species of ungulates which may require a number of different kinds of terrain within their home ranges, any one of which types of terrain might be the habitat of some small species. Most of the genera or even subfamilies of very large terrestrial animals contain only one or two sympatric species. In this connection I cannot refrain from pointing out the immense scientific importance of obtaining a really full insight into the ecology of the large mammals of Africa while they can still be studied under natural conditions. It is

indeed quite possible that the results of studies on these wonderful animals would in long-range though purely practical terms pay for the establishment of greater reservations and National Parks than at present exist.

In the passerine birds the occurrence of five or six closely related sympatric species is a commonplace. In the mammal fauna of western Europe no genus appears to contain more than four strictly sympatric species. In Britain this number is not reached even by Mustela with three species, on the adjacent parts of the continent there may be three sympatric shrews of the genus Crocidura and in parts of Holland three of Microtus. In the same general region there are genera of insects containing hundreds of species, as in Athela in the Coleoptera and Dasyhelea in the Diptera Nematocera. The same phenomenon will be encountered whenever any well-studied fauna is considered. Irrespective of their position in a food chain, small size, by permitting animals to become specialized to the conditions offered by small diversified elements of the environmental mosaic, clearly makes possible a degree of diversity quite unknown among groups of larger organisms.

We may, therefore, conclude that the reason why there are so many species of animals is at least partly because a complex trophic organization of a community is more stable than a simple one, but that limits are set by the tendency of food chains to shorten or become blurred, by unfavorable physical factors, by space, by the fineness of possible subdivision of niches, and by those characters of the environmental mosaic which permit a greater diversity of small than of large allied species.

CONCLUDING DISCUSSION

In conclusion I should like to point out three very general aspects of the sort of process I have described. One speculative approach to evolutionary theory arises from some of these conclusions. Just as adaptative evolution by natural selection is less easy in a small population of a species than in a larger one, because the total pool of genetic variability is inevitably less, so it is probable that a group containing many diversified species will be able to seize new evolutionary opportunities more easily than an undiversified group. There will be some limits to this process. Where large size permits the development of a brain capable of much new learnt behavior, the greater plasticity acquired by the individual species will offset the disadvantage of the small number of allied species characteristic of groups of large animals. Early during evolution the main process from the standpoint of community structure was the filling of all the niche space potentially available for producer and decomposer organisms and for herbivorous animals. As the latter, and still more as carnivorous animals began to appear, the persistence of more stable communities would imply splitting of niches previously occupied by single species as the communities became more diverse. As this process continued one would expect the overall rate of evolution to have increased, as the increasing diversity increased the probability of the existence of species preadapted to new and unusual niches. It is reasonable to suppose that strong predation among macroscopic metazoa

did not begin until the late Precambrian, and that the appearance of powerful predators led to the appearance of fossilizable skeletons. This seems the only reasonable hypothesis, of those so far advanced, to account for the relatively sudden appearance of several fossilizable groups in the Lower Cambrian. The process of diversification would, according to this argument, be somewhat autocatakinetic even without the increased stability that it would produce; with the increase in stability it would be still more a self inducing process, but one, as we have seen, with an upper limit. Part of this upper limit is set by the impossibility of having many sympatric allied species of large animals. These however are the animals that can pass from primarily innate to highly modifiable behavior. From an evolutionary point of view, once they have appeared, there is perhaps less need for diversity, though from other points of view, as Elton (1958) has stressed in dealing with human activities, the stability provided by diversity can be valuable even to the most adaptable of all large animals. We may perhaps therefore see in the process of evolution an increase in diversity at an increasing rate till the early Paleozoic, by which time the familiar types of community structure were established. There followed then a long period in which various large and finally large-brained species became dominant, and then a period in which man has been reducing diversity by a rapidly increasing tendency to cause extinction of supposedly unwanted species, often in an indiscriminate manner. Finally we may hope for a limited reversal of this process when man becomes aware of the value of diversity no less in an economic than in an esthetic and scientific sense.

A second and much more metaphysical general point is perhaps worth a moment's discussion. The evolution of biological communities, though each species appears to fend for itself alone, produces integrated aggregates which increase in stability. There is nothing mysterious about this; it follows from mathematical theory and appears to be confirmed to some extent empirically. It is however a phenomenon which also finds analogies in other fields in which a more complex type of behavior, that we intuitively regard as higher, emerges as the result of the interaction of less complex types of behavior, that we call lower. The emergence of love as an antidote to aggression, as Lorenz pictures the process, or the development of cooperation from various forms of more or less inevitable group behavior that Allee (1931) has stressed are examples of this from the more complex types of biological systems.

In the ordinary sense of explanation in science, such phenomena are explicable. The types of holistic philosophy which import *ad hoc* mysteries into science whenever such a situation is met are obviously unnecessary. Yet perhaps we may wonder whether the empirical fact that it is the nature of things for this type of explicable emergence to occur is not something that itself requires an explanation. Many objections can be raised to such a view; a friendly organization of biologists could not occur in a universe in which cooperative behavior was impossible and without your cooperation I could not raise the problem. The question may in fact appear to certain

types of philosophers not to be a real one, though I suspect such philosophers in their desire to demonstrate how often people talk nonsense, may sometimes show less ingenuity than would be desirable in finding some sense in such questions. Even if the answer to such a question were positive, it might not get us very far; to an existentialist, life would have merely provided yet one more problem; students of Whitehead might be made happier, though on the whole the obscurities of that great writer do not seem to generate unhappiness; the religious philosophers would welcome a positive answer but note that it told them nothing that they did not know before; Marxists might merely say, "I told you so." In spite of this I suspect that the question is worth raising, and that it could be phrased so as to provide some sort of real dichotomy between alternatives; I therefore raise it knowing that I cannot, and suspecting that at present others cannot, provide an intellectually satisfying answer.

My third general point is less metaphysical, but not without interest. If I am right that it is easier to have a greater diversity of small than of large organisms, then the evolutionary process in small organisms will differ somewhat from that of large ones. Wherever we have a great array of allied sympatric species there must be an emphasis on very accurate interspecific mating barriers which is unnecessary where virtually no sympatric allies occur. We ourselves are large animals in this sense; it would seem very unlikely that the peculiar lability that seems to exist in man, in which even the direction of normal sexual behavior must be learnt, could have developed to quite the existing extent if species recognition, involving closely related sympatric congeners, had been necessary. Elsewhere (Hutchinson, 1959) I have attempted to show that the difficulties that *Homo sapiens* has to face in this regard may imply various unsuspected processes in human evolutionary selection. But perhaps Santa Rosalia would find at this point that we are speculating too freely, so for the moment, while under her patronage, I will say no more.

ACKNOWLEDGMENTS

Dr. A. Minganti of the University of Palermo enabled me to collect on Monte Pellegrino. Professor B. M. Knox of the Department of Classics of Yale University gave me a rare and elegant word from the Greek to express the blurring of a food chain. Dr. L. B. Slobodkin of the University of Michigan and Dr. R. H. MacArthur of the University of Pennsylvania provided me with their customary kinds of intellectual stimulation. To all these friends I am most grateful.

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