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ANIMAL LIFE AND SOCIAL GROWTH

BY

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M. H. A.

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PREFACE

This small book is presented as a fairly simple statement of a series of interesting facts which belong together although they are not usually treated so. The student of human society has come to regard some of the facts presented in the latter part of the book as fairly within his range of interests. The modern students of scientific natural history who call themselves ecologists for short, are seldom concerned beyond the material of the first six chapters. It remains for those of us who are interested in both fields and who find their conjunction when studying the variegated phases of mass physiology to attempt to supply the cement which will hold many of the facts about the life of wild animals in their proper relation with regard to social development.

In the preparation of this book, I have purposely omitted citations to technical literature which would give in detail the various facts cited or support the point of view taken. Reference to much of the literature of the subject can be found in recent volumes of the journal, *Ecology*; in Allee and Schmidt's American edition of R.

Hesse's *Animal Geography* (C. C. Thomas, 1932) or in Allee's *Animal Aggregations, A study in General Sociology* (University of Chicago Press, 1931).

I wish to acknowledge indebtedness to many workers who may recognize their ideas in a new dress and, perhaps, in unexpected company; to Kenji Toda for drawing the figures and to V. E. Shelford and Marjorie Hill Allee for reading the manuscript critically.

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CHAPTER I

THE ANIMAL COMMUNITY

Animals live in communities. No living thing, plant or animal, is solitary; animals especially are knit together by many ties. Even the most solitary of the sexual animals must meet in intimate union with another member of its species though it perishes as a result. Among animals that reproduce asexually there are distinct evidences of social life, which are particularly obvious in the case of colonial animals that remain throughout life physically attached to each other; frequently these forms have such direct communication from one to another that food eaten by any one may be shared by many. Social life is not an incident or an accident among animals; it is not the special privilege of some few that stand high in the evolutionary scale such as men, deer, birds, bees and ants, but it is a normal constant, universal fact. So in effect wrote the Frenchman, Espinas, over fifty years ago.

More recently Wheeler, the American student of social insects, has seconded him with: "Most animals and plants live in associations, herds, colonies or societies and even the so-called 'solitary' species are necessarily more or less co-operative members of groups or associations of individuals of different species. Living beings not only struggle and compete with one another for food, mates and safety, but they also work together to insure to one another these same indispensable conditions for development and survival."

Such descriptions of animal communities suggest that in their organization they resemble individual animals. Obviously there is no close resemblance between these more or less loosely knit animal communities and such a well organized animal as a bee or a dog or a man, but all animals are not so closely under the control of their central nervous systems. With sponges and other lower animals it is difficult to determine how much of the living tissue belongs to one individual and how much to another. Even in fairly well organized animals such as starfishes, the different parts of the body may work in decided opposition to each other rather than in co-operation. When a starfish is placed on its back, three of the arms may be working vigorously to turn in one direction and be actively opposed by the other two, or the arms may be attempting to right the animal by working in three or even in five directions at the same time.

After a period of such divided effort, one set of arms wins out and the animal is turned in their direction.

Even more disastrous for the animal involved, are the numerous cases where parts of the animal are literally torn from the body because they are not acting in harmony with stronger regions of the individual. The trail of starfishes can be traced over the sides of aquaria by the foot fragments they have left behind, torn off because these feet were pulling in the wrong way. Such fragments of starfishes die although the animals themselves grow new feet to replace the old.

The sea-anemone, an animal which may reach a diameter of more than three inches and is frequently taller than it is thick, has a mouth surrounded by food-catching tentacles at one end and a broadly expanded foot for movement and attachment at the other. When such an animal is crawling over a glass plate or a smooth rock, parts of the foot may be torn off and left behind because they are unable to let go of the smooth surface soon enough to keep up with the rest of the animal. Such fragments round up and within a short time may grow into whole, new, small anemones. Meantime the holes from which they were torn have also healed. The most composed city-dwelling man would be amazed if in walking barefooted to the beach on a warm summer's day, his feet were so poorly co-ordinated with the rest of his body that toes, or bits of his heel came off in the warm, sticky asphalt; and consider his reaction on returning after the wounds had healed to find a row of doll-like children developed from the missing fragments!

It is to animals with such relatively slack systems that an animal community is to be compared rather than to the closely organized bee, or dog, or man; though the community is much more poorly organized than are the simplest animals and should be thought of as a quasi-organism rather than as a full-fledged one.

In human society we are accustomed to the idea of community organization. A village is composed of a number of people who are more or less grouped into families. These individuals and families are woven into a unit not only because they live in the same locality and so are forced to meet the same sort of problems as to food supply, protection from storms and from cold; they are also connected by numerous other bonds including those of kinship, of occupation and perhaps of tradition. All such forces knit the community into a working unit which at times may be remarkably effective. At best the whole community organization is loose; individuals may come and go; whole families may depart or die out and be replaced by alien stock; but the village retains a definite unity with a more or less distinct individuality which may persist for decades.

In such a community as a village, men are associated not only with each other but also with other animals. If in the country, horses and cows are present; cats and dogs are to be found everywhere; they feed on surplus food and provide in their turn companionship and amusement for man; they add to the dirt of his household and spread bacteria and other parasites. Flies rear their young in the offal from larger animals and associate themselves with man even at his meals; mosquitoes breed in water reservoirs and feed on man and other animals. Birds are attracted by the shrubs and trees planted by man or to the openings he makes in the surrounding forest; rats and mice are also attracted. Snakes come in to feed upon these. Insects feed upon the growing gardens or orchards and are in turn eaten by other insects; and finally some animals exist without close relations to the human community except that they occupy the same general space.

Unexpected interlocking of interests occurs between different animals in such a community;

one such was pointed out by Charles Darwin long ago. Succinctly stated it is that the more maiden ladies in an English farming community, the more clover seed will be produced per acre. The reasoning is: the more old maids, the more cats; the more cats, the fewer mice; the fewer meadow mice, the more bumble bees; clover is pollinated by bumble bees, hence the more bumble bees, the better the pollination and the more clover seed.

The balance of life in a community is never complete; always there is change. If a progressive chamber of commerce attracts a new factory, the village stream may be dammed and breeding places be made for myriads of mosquitoes; if some of these are the malaria bearing *Anopheles*, malaria may become common and the village will suffer from the resulting chills and fevers. Meantime the range of fishes, mussels and water insects has been expanded; boating and bathing facilities have increased and the whole community is directly or indirectly affected.

Similarly a mild winter which does not kill off the usual number of insects that feed upon plants may result in such orchard and garden depredations that more than the usual amount of human food will have to be imported. Meantime the insects themselves are furnishing an unusually abundant food supply for the birds and other insect-eating animals so that fewer than usual will starve. Even though no other checking force were to act, the increase of insect feeding forms would in time bring the insect pests under approximate control. This would no sooner be established than another shift in weather, perhaps a cold winter, would upset the whole balance again.

The effects produced by insects upon the basic food plants show that plants as well as animals are to be considered in such communities. This means that life processes in a given community are so interrelated that any development which affects one important set of plants or animals in the community, sooner or later, affects all.

One of the best descriptions of the working of this web-of-life in a non-human community is that given by the late S. A. Forbes of the Illinois Natural History Survey in his description of the inter-dependencies of life in a small lake. It is relatively easy, though sufficiently exciting to be called sport, given the right body of water and the proper season and bait, to lift a large-mouthed black bass out of the water; but if one should undertake to unravel all the tangle of interrelations from which the fish had been so unceremoniously removed, he would see the complicated system of mutual relations which bind the community into the loosely organized unit that it is.

In the food of the black bass are to be found fishes of different species at different ages of the individual which represent all the important orders of fishes; insects in considerable numbers, especially the various water bugs and larvae of may-flies, crayfishes, fresh water shrimps and a smaller crustaceans of many species and of several orders.

On looking at the food of the fishes which the black bass eats, it is found that one of these lives on mud, algae and small crustacea; another takes nearly every animal substance in the water, including mollusks and decomposing organic matter. The crayfishes are nearly omnivorous; while of their relatives, some eat still smaller crustaceans, some eat algae, and others live on protozoans. At only the second step in what we may call a food-web, we find the black bass related to every class of animals, to many plants and to decaying animal and plant materials in the mud of the lake bottom.

Turning to the competitors of the black bass, which are extremely numerous; all the young lake fishes except the suckers feed at first almost wholly on small crustaceans, so that the newly hatched black bass finds himself launched into a scramble for food with almost all the other fishes of the lake and, in fact, not only with the other fishes but with the insects and larger crustaceans as well. Mollusks are not in such direct competition, but they do compete since they feed upon the minute organisms which the smaller crustaceans themselves use as food.

In their turn the small bass become food for other fishes as well as for turtles, water snakes, wading and diving birds, large beetles, dragon-fly nymphs and giant water bugs; even the lowly fresh water hydra feed upon the small black bass at every opportunity.

An illustration of more remote and unexpected rivalries is found in the relation of the black bass to the green plant called bladderwort which fills acres of the ponds of northern Illinois. Small bladders, several hundreds to the plant, grow on its leaves and give the basis for its common name. They serve as tiny traps for the capture of minute animals. The plant has no roots ordinarily and lives largely on the animals taken in its bladders. Ten of these sacs, taken at random, yielded 93 different species of small crustaceans and insect larvae. Hence the bladderwort competes with fishes for food and, by consuming large amounts of this food, helps keep down the number of black bass in an otherwise favorable lake; and it has an especial advantage, since, when the animal food becomes scarce, it may grow roots and live as do other plants. Here again we find good evidence that plants cannot be excluded from the community life which we are describing.

When poisonous materials, such as come from many factories, find their way into a lake, the greater the volume of animal and plant life, the greater the chance of survival of each individual. If the poison is not too great in amount, or too deadly, the myriads of animals either directly or through their secretions and waste products, absorb or otherwise fix the toxic materials so as to cleanse the water. At the worst, if there are many, each receives a smaller dose of the poison than if there were but few, and many will be able to survive the lighter dosage that would perish if exposed in small numbers to the full strength of the poisonous materials. In such cleansing of the waters, conducted in an entirely subconscious manner, all the animals and plants are associated. In this the black bass aids the fishes which to-morrow it will take as food, just as the latter help prevent their arch enemy from being poisoned by automatically fixing a part of the poison themselves.

A different phase of the story is shown by the history of life in prairie lakes which are appendages of river systems and form in oxbow cut-offs or bayous, or in other regions where the normal deposition of materials has been retarded. Normally they are connected with each other during the rainy season. The amount and variation of animal life in them depends chiefly on the frequency, extent and duration of the overflows. They illustrate how a flexible animal community adjusts itself to widely and rapidly fluctuating conditions.

Whenever the waters of a river remain long outside its banks, the breeding grounds of fishes and other animals are correspondingly extended. The slow and stagnant waters of such an overflow, frequently enriched by sewage to a limited extent, furnish the best possible place for the growth of myriads of algae and of the one-celled animals called Protozoa. This development allows a similarly great increase in the numbers of small crustaceans. These animals reproduce asexually and increase with tremendous rapidity under favorable conditions. The sudden development of food resources allows a corresponding increase in the rapidly breeding fishes which feed upon them; and at last the game fishes, which derive their food mainly from other fishes, also increase in numbers, both on account of the greater extent of the breeding grounds and because of the greater food supply which keeps those that hatch from starvation.

The multiplication of each of these food classes acts as a check on the one preceding it. The development of Protozoa and algae is arrested and sent below normal by the swarm of minute crustaceans; the latter are met and checked by the vast swarm of minnows, which in turn are checked in their increase by the rise in numbers of predaceous fishes and by fish-eating birds attracted by the good fishing. In this way a gradual readjustment of the numbers of animals in each of the food classes will occur; but usually, long before a new balance is reached, a new disturbance in the water level results from the recession of the flood waters to their more usual channels.

As the lakes grow smaller and the teeming life they enclose is daily restricted within narrower and narrower bounds, a fearful slaughter ensues. The predaceous fishes thrive for a time, since their food is more easily caught; but finally they too are thinned out by the lack of food and space.

Year after year and century after century in such lakes, there is a continuous ebb and flow in the amount of animal and plant life present, but with all and in the long run, a fairly definite balance is maintained. Over a term of years the rate of reproduction about equals the death rate. Any individual may find itself in danger of being eaten at any moment between hatching and maturity. Fully mature individuals are as rare as human centenarians; yet a species is only rarely exterminated and each maintains itself at the average number for which we have reason to think there is sufficient food and shelter available year after year. Two ideas explain the order that is evolved in such communities. First, there is the background of common interests and of unconscious co-operation among all the elements of the community, the nature of which will be discussed later. Second, there is the struggle for existence and the elimination usually of the less fortunate but, at times, of the less fit animals.

Such water communities as those culminating in the black bass represent islets of older, lower life in the midst of the higher, more recent life of the surrounding region. Will the relationships described from such a relatively simple community hold for the more complex relations existing among land animals? This question will be examined in the following chapters.

The study of such communities, their interrelations with other communities as well as the inter-actions between members of the same community and the relations of the communities or of their individual members with their complete environment constitute the content of modern ecology. Popularly speaking, ecology is the scientific study of the home life of animals and plants; the growth and development of this phase of biology has been one of the outstanding developments of the present century.

CHAPTER II

ANIMAL HABITATS

WE ARE beginning to recognize the mutual interdependence of widely separated human communities. The golden apple of Paris or the shot of an inconspicuous and otherwise unknown Serbian may set the armies of the world in motion. In the last instance equally unknown Americans, Australians, African negroes and Russian peasants who never heard of Serbia are still, after almost two decades, in the process of readjustment from the effects of that shot.

Similarly, interconnections can be demonstrated among non-human animal communities that are widely distributed; an unusually prolonged, snowy winter in northern Canada may send the northern birds of prey southward to feed upon the mice and small birds over-wintering in the northern United States, or a migrating horde of Egyptian locusts may devastate the African countryside for hundreds of miles and destroy the normal food supply of myriads of unsuspecting local insects. I am not interested here in giving the numerous cases which show that the plant and animal communities of the world form an interlocking system; that the web-of-life is woven on a geographic as well as on a local scale; it will be more interesting instead to examine the organization of animal communities of the land on the basis of the places in which they live.

In human or non-human communities one of the first and most striking methods of sub-division into smaller units is on the basis of the dwelling place, or as it is more commonly called, the habitat of the community; the habitat includes all the environmental factors which center about the dwelling place except the competition between the animals themselves. In general, animals distribute themselves as though they recognize three main types of habitats: the aquatic, the terrestial and the parasitic.

Land animals divide themselves fairly definitely into those of the tropical rain-forest, the tropical grasslands, the deserts and semi-deserts, temperature deciduous forests, temperature evergreen forests, temperature grasslands, the arctic tundra, alpine regions, and lands of eternal snow and ice. These different major habitats are variously subdivided; in each except the last there may be swampy areas which possess a set of animals decidedly different from those to be found in the surrounding country.

The distinction between swampy life and the more general life of the region is particularly marked in arid regions. Thus on the Bear River flats near Great Salt Lake in Utah, the surrounding sage-brush country shelters a sparse population of desert lizards, snakes, insects and birds, with a few mammals including the coyote. Nearby in the swampy lands eleven species of ducks nest and some fifteen thousand ducklings come to maturity each year. Bitterns, great blue herons, egrets, snowy herons, and other similar marsh birds, yellow-headed and red-winged blackbirds and marsh wrens make their nests here in abundance. Finding nests during the breeding season is not arduous; the greater difficulty is to avoid stepping on the eggs or the nestlings while tramping through the short marsh grass or breaking through the canes.

Later, water birds gather in great flocks for the mid-summer moult and the autumn feeding. I have seen a flock of male pin-tail ducks there in June that literally darkened the sky when flushed, as my father says wild pigeons in Indiana once did. Later in the season shoveller ducks have been seen on the lake in a bank two miles long and a quarter of a mile wide, busily feeding on the brine shrimps and the salt marsh maggots that thrive in the briny waters of Great Salt Lake.

One cannot tramp these marshes near the close of the breeding season without being impressed with the prodigality of nature. The thousands of birds in the air and on the ground show that the birds are locally extremely successful, yet everywhere one sees dead nestlings, broken eggs, nests that have been flooded, others deserted for no obvious cause with the clutch of eggs only partially completed; while all around are evidences of a rate of avian infant mortality that is appalling. There can be no question but that the physical conditions within the habitat do set off different animal communities for within easy walking distance of this prodigality, one comes out on the desert paucity of an almost entirely distinct community.

The major animal habitats just listed occur on a world wide scale and while the habitat conditions are similar in different parts of the world, and the physiological requirements which the animals make of their surroundings are also similar, it does not follow that the animal life is the same in the different world areas which present essentially similar habitats. This is particularly well illustrated by the conditions found in the tropical rain-forests, the "jungles" of popular writings.

These extend in a wide belt in the rainy regions around the equator. They present a strikingly similar picture of luxuriant plant growth which extends high above the forest floor. While the forest canopy is bathed in fierce tropical sunlight, the floor below is in deep shadow broken only by the intense flecks of sunlight that filter through the scant openings in the leafy roof. Above, tropical gales may blow; the temperature changes rapidly from noon heat to midnight chill, for the night is the winter of the tropics; the humidity of the air also varies widely. At the forest floor, throughout the rainy tropics of the world, the wind is absent and only slight breaths of air relieve the forest stagnation; the temperature in constantly shaded regions may change less than two degrees in a whole week and the humidity is similarly constant. Only in caves, deep in the soil or in the shadowy depths of the water do the environmental conditions become more constant.

But the animals living under these conditions in the forests of South America belong to different species, families, and even to different orders from those of the physically similar forests of Africa and Asia. For example, in America the mammals of the tropical forest floor are mainly guinea pig-like rodents with claws, which are replaced in Africa by the hooved antelopes. The hairy anteaters of the South American forest have their counterpart in the scaly anteaters of Africa, which while similar in feeding habits, belong to a different order. The okapis, the elephants and the apes of the African forests are absent in South America, while the tapirs of the latter region live in the forests of Malay but are absent from the other tropical forests of the old world.

The continental differences in ground mammals are fully as marked among arboreal forms. The South American monkeys have prehensile tails, their nostrils open outwards and they lack cheek pouches. The old world monkeys, on the other hand, lack a prehensile tail, they have cheek pouches and their nostrils open downwards close together. The two possess other structural differences which divide them into two distinct taxonomic series. The monkeys of the African and the Asiatic forests are less distinct but they belong to different families; and the forests of tropical Australia are inhabited by animals such as the tree kangaroos and other marsupials which are not to be found elsewhere. These animals that occupy similar niches in the tropical rain-forests of the world are physiologically equivalent despite their differences in structure and classification. Physiologically they reflect their environment while their anatomy shows that they have arisen from diverse stocks.

The animals of the northern forest are more similar on both the American and the Eurasian land masses than are those of the tropics. In both Canada and Siberia, lynxes, wolves, foxes, bears, martens, gluttons, weasels, minks and badgers may be found. It is true that differences occur. The American puma is replaced by the Siberian tiger; the wildcat of Europe is distinct from that of America. The skunk is absent from Europe while we lack the Siberian wild dog and the European wild hog. However, in the main the animal life of these northern forests is much more nearly similar all around the world under similar conditions, than is that of the tropics.

The greater similarity of animal life in similar regions at the north of the different land masses as compared with the tropics does not mean that the habitats there are more similar. Rather, the indications are that the similarities are due to the fact that the two areas have been separated for a shorter time and less effectively than have the tropical forests. There is good evidence that in relatively recent times, geologically speaking, close connections existed between Siberia and Alaska across the Behring Straits. Close land connections between the different tropical lands of the world, if indeed they ever existed, have been much more remote in geological history.

In other words, these cases demonstrate that similarity in animal habitats does not necessarily mean that there will be a similarity in the animals living in those habitats. There are historical factors to be considered which concern the opportunities animals have had to occupy the particular space. Obviously insurmountable barriers of water or mountains or deserts may block the path of migration of animals well fitted to occupy a given habitat, or more subtle barriers of climate may accomplish the same result. Further, suitable species may have arisen too recently to have had time to reach all the habitats they are fitted to occupy to advantage, or on the other hand, other species may be dying out from lack of racial vigor sufficient to maintain themselves even in territory in which they formerly lived in strength.

In some instances mere chance occupancy by one species may prevent another later arrival with similar habitat requirements from being able to obtain a foothold. An example of this sort is furnished by the distribution of crayfishes in Pennsylvania. Two species with similar ecological requirements formerly occupied different river systems which later joined into one. At the old water shed where the ranges of the two species now come together without an environmental obstacle there is only an exceedingly narrow zone of overlap. The niches required by the one are already fully occupied by the other and since they are approximately equal in vigor and abilities, neither species is able to invade the territory occupied by the other.

The relations existing between animal habitats and the animals dwelling therein which have been shown to exist for different continents also hold, though less exactly, in habitats in different regions of the same land mass, and may hold even in similar habitats that lie adjacent to each other. In Illinois, the pocket gopher, which lives almost entirely underground, occurs to the south of the Kankakee river and is again found in Wisconsin, but in wholly similar habitats lying between, even in those just north of the Kankakee river, the animal is absent. The reasons for such erratic distribution are not known but are apparently related to the barriers furnished by the rivers of the region which have not as yet been crossed by the gopher.

Animal habitats which are obviously units in themselves, such as the forests, can be divided readily enough into sub-habitats. In forests the most obvious of these are arranged in different levels usually called strata and the animals living at these various levels may be spoken of as forming stratal sub-communities. In the tropical rain-forests where stratification is best developed at least eight different strata can easily be recognized by a naturalist. In Panama these have been found to be divided as follows:

8. The air above the forest.

7. The trees, 125 feet or more in height, that extend above the main forest roof.

6. The upper forest canopy.

5. The lower tree tops, 40–60 feet high.

4. The small trees, 20–30 feet high.

3. The higher shrubs, 10 feet high.

2. The forest floor.

1. The subterranean stratum.

This is an excellent statement of the facts that a zoologist observes and careful work would doubtless show that some of the animals living within the tropical rain-forest are limited to these different levels of the forest, but in general in Panama the majority of the animals themselves appear to recognize only the following:

6. The air above the forest which can be occupied only by flying animals such as birds, bats, and insects.

5. The tree tops which have a distinct bird population.

4. The mid-forest, again distinguished by its birds.

Many animals do not recognize the distinction between these two strata and are known as the animals of the mid and upper forest. Thus the monkeys and sloths, forest lizards, birds and insects range through the mid and upper forest strata but are only rarely seen, if at all, in the lower levels.

3. The lower forest stratum. Through this stratum flit the low flying insects and birds; prominent among them are the great *Morpho* butterflies and several species of humming birds. Into this stratum mount many animals more commonly found on the ground, such as the *Anolis* lizards mistakenly called chameleons; while everywhere ants are found similar to those of the forest floor rather than to those of the upper forest.

2. On the forest floor are to be found turtles, ground dwelling snakes, lizards that cannot climb, and the non-climbing, non-burrowing mammals such as the peccary and the tapir.

1. Burrowing forms of the subterranean stratum include earthworms, and many termites and, in the dry season at least, the interesting worm-like arthropod, *Peripatus*.

To many animals dwelling in the tropical rainforest even this simplified stratification has little or no meaning. Some, such as *Nasua*, a relative of our raccoon, range indifferently from the forest floor to the tree-tops; others, like the armadillo belong to the underground and the ground strata.

Insects also may or may not recognize the existence of these strata. Even in one group, the termites, there are forms that are limited to one level and others that burrow in the ground and range to the tree-tops. Here as in all phases of human and non-human sociology the general principles stand out plainly, but there are many exceptions.

Within one and the same stratum, animals recognize different sorts of regions as making distinct habitats. In the tropical rain-forest again, one of the most obvious distinctions in the dry season is the nearness to water. Land isopods, land crabs, the long-legged spiders known as harvestmen, frogs and toads, crocodiles, some lizards and turtles, to mention no more, are limited to the moister regions, while others, equally representative, are found generally or exclusively on dryer ground.

But not all moist or dry regions of the forest floor have a similar set of animal inhabitants. The animals themselves distinguish between different sorts of soil or between different plants that in turn are limited by the soil conditions. In Panama during the dry season, it is useless to try to collect *Peripatus* regardless of soil or moisture conditions, unless in the immediate vicinity of a decaying log or stump which is well along its way back to humus.

These much restricted habitats are spoken of as habitat niches and they may be indeed tiny; during the tropical dry season, mosquito larvae are to be found in the forest in the tiny amounts of water held in leaves that chance to be upturned and cup-shaped. Or again there exists a large number of so-called mining insects that obtain their food during their larval life by burrowing between the upper and lower surfaces of leaves, and there are many other animals whose small habitats are limited to such detailed niches as those furnished by the stamens of flowers.

The animals limited to micro-niches must themselves be tiny, and in general the larger the animal the larger the niche occupied, but large animals may occupy small niches for considerable periods of time. Thus, in hibernation a bear may be restricted to a small niche in his forest habitat; or during the dry season in the Panama rain-forest, an alligator-like *Jacare* may spend his time in a shallow pool scarcely larger than he is long.

Such relationships are exceptional and, in general, the relation between size of available habitat and size of animals is such that, even in the same species, those with the larger amount of space at their disposal tend to grow to larger size. The belief is widespread that fishes grow larger in large lakes than in small ones and, despite exceptions, there is much truth in the belief. In Wisconsin lakes, for example, the size attained by yellow perch appears to be directly related to the size of the body of water in which they live. Similarly with larger mammals, those on small islands, are smaller when fully grown than are their relatives on the nearby mainland where their ranges are less restricted. In many cases the dwarfing in the smaller ranges is definitely related to the decreased amount of food available but other factors such as the accumulations of wastes, are certainly effective. There is evidence that active animals limited to a narrow habitat may be so stimulated by repeated contacts with the habitat margin or with other animals enclosed in the same narrow island space that dwarfing results from such over-stimulation.

In summary of this section it may be stated that a habitat niche is a special habitat in which a given animal lives; or, more generally stated, it is an area, large or small, in which the principal relations of the habitat conditions and the living forms related to them, are uniform. Groups of similar niches may be united into a more general habitat; in the excessively dry regions, rock desert, sandy desert, gravelly desert, alkali desert and arid regions with fertile soil, all are thought of as forming the more generalized habitat we call a desert. Such deserts may be considered together with the desert-like polar regions as forming a yet more extensive habitat. There the rainfall is also low and continued cold is an additional life handicap. This indicates either that animal habitats and the animal communities that inhabit them can be analyzed into simple terms or on the other hand, that the simple units can be united into fairly complex regions or communities which still have common elements.

CHAPTER III

COMMUNITY ANALYSIS

COMMUNITIES of land animals are more complex than are those of the waters. The facts concerning their organization are not easily come by since man, the investigating animal in these cases, cannot readily appreciate to the full the interplay of forces that operate to organize non-human communities. With all of the smaller animals the mere matter of difference in size prevents us from being able to realize completely the effects of relatively minor changes in humidity or temperature; while our relations with elephants, for example, prepares us somewhat to understand the effects of being exposed to more powerful animals, we have only experiences in inter-human relations upon which to base judgment of the effect of being exposed to animals of equal or of infinitely greater mental ability.

Perhaps we can best appreciate the difficulties under which modern students of the organization of animal communities have to work by attempting to see how much of the activities of a human community we could understand if our information were limited to that which is available for human students of the community relations of non-human animals.

Everyone has a considerable amount of information concerning the needs, the inter-relations and the tolerations of man. Even with this interesting animal species, I suspect that many of the things we think we know are not true, but our personal and collective store of knowledge about man and his relations to the animals about him is greater than that for any other animal. Against this background of knowledge we can test the limitations of our best methods of investigating the inter-relations of other animals. The question we are asking is: how much would we know about human affairs if our information were limited to that which modern methods of studying animal communities would reveal?

The number of animal species is appalling and no one person can be expected to be able to recognize all that are to be found in an ordinary animal community in nature. In the Chicago area, for example, there are more species of beetles, or of flies, or of ants, bees and wasps, or of butterflies and moths, than there are of flowering plants, and most of the different species are more difficult to recognize than are even the various sorts of grasses. There are more species in the Chicago area in the four limited groups just mentioned than there are individuals on the University of Chicago quadrangles but their components scarcely make a good beginning in a species census of the region.

The oldest and crudest type of community study is to collect, identify and list the names of the different species found living in a given habitat. This is not an easy task yet it yields about the same amount of information to the average student that a list of the names of people in a University would give to an outsider. When the species present in an animal community are numerous and diverse, the collections in the field must of necessity be carried on by field workers who would recognize at sight few, if any, of the species concerned. These collectors conscientiously select habitats that seem to them to be typical and make more or less complete, drag-net collections which are sorted and sent off to specialists in the various groups who are able to name the different specimens submitted to them.

The field worker then assembles these identifications and matches them with his field notes where each specimen is represented by a number in place of a name and so acquires named lists of the animals that were taken from the different localities. Such collections are often made during a limited period of time, frequently in regions with which the field collector is only slightly acquainted.

Suppose a super-man unacquainted with the location loosely known as the university district in Chicago were to attempt such a survey of the human material that makes up the university community. For the purposes of this comparison he may use individual people to represent the different species with which the animal or field worker would be dealing. Presumably the first procedure in this hypothetical survey of the University of Chicago community would be to look over the ground somewhat superficially so as to get a general impression of the whole. Immediately afterwards stations for observation and collection would be set up in supposedly representative parts of the community both in the open air of the university quadrangles and in various buildings.

In order to find how the university community is related to those around it, stations would also be established in the surrounding residential district, in the neighboring parks, and perhaps in the more crowded shopping districts at a greater distance. In addition to collecting in these regular stations, the investigator would also cruise about the whole community and its environs and make more or less casual observations or collections in regions or of specimens that seemed to him to be interesting or otherwise important.

The main part of the collecting would be done, however, at the regularly constituted stations, at more or less regular collecting intervals and with some sort of standardized collecting apparatus. As time limitations were imposed by other responsibilities and as the magnitude of the task became apparent, we might expect to find certain stations neglected and others dropped altogether from the collecting rounds.

The collections so gained would consist mainly of different sorts of white men with a scattering record of other races and of other animals such as dogs, cats, monkeys, and other domestic or laboratory animals, a few wild birds and many more cockroaches, silverfishes and the like, with occasionally, perhaps, some insects more intimately associated with man. These collections would be suitably tagged and pickled, roughly classified into easily recognized groups and sent to the appropriate specialists, who in due time and after appropriate tactful stimulation, would report the scientific name of each. After comparison with field notes and after a study of the usually lamentably meager published records of habits and relations of the different sorts of animals concerned and the compilation of habitat lists with a brief discussion of the most obvious relationships, the results might appear as a preliminary survey of the University of Chicago.

Translated into such a situation, many of the limitations inherent in this method of studying the organization of an animal community become plainly evident. If the collections have been frequent enough and have been made in the cold weather as well as in summer, at night as well as in the day, the lists will probably include all the different types of individuals to be found regularly near or in the University together with a sprinkling of regular or casual visitors from other parts of Chicago, or indeed from other parts of the world.

The extent to which such lists would begin to indicate the true organization of the community would depend on the wisdom with which the habitat niches were chosen for study and the attention paid to the relative numbers of the different sorts of animals collected and also upon the general thoroughness of the survey. Even such a preliminary study would show that the community in question is dominated by white men but the interrelations of the different sorts of white men would probably not be apparent.

If to such a study one adds a survey of the environment, including a careful inspection of the physical surroundings, the orientation, construction and size of the buildings and their relation to the unbuilt areas and if there is the further addition of an instrumental survey of the temperature, humidity, carbon dioxide, illumination, etc., some of the results that would be expected may be summarized as follows:

With moderate temperatures many of the animals (people) under discussion would be found in the open air for a great proportion of the time, while with low temperatures or with very high ones, more of their time is spent in sheltered regions. This result would be somewhat puzzling to interpret because of the humidity complications; in fact even a careful researcher with such data before him might conclude that the migration from the cold outside air in winter was as much a reaction to the lower humidity to be found indoors as to the higher temperatures. A student of light intensity might conclude, with some justice, that the reactions to the open air were due, at least in part, to reactions to light, and that there is some inter-relationship between the light responses and the prevailing temperatures.

The data made available by such a survey would undoubtedly convince some that there is a significant correlation at least during the colder months, between the behavior of the white men in this community and the amount of carbon dioxide in the rooms. One might easily conclude that under the complex of environmental conditions associated with cold weather, the animals in question move into the classrooms due to a positive reaction to carbon dioxide and that they become negative to this gas after about an hour's exposure and give an avoiding reaction.

The carbon dioxide data might mislead one in another direction. In comparing the concentration of carbon dioxide in different rooms of the university buildings, we should probably find that there is a greater concentration of this important gas in certain poorly ventilated but well populated university class rooms and lunchrooms than in the university chapel and on such data one might well conclude that people, particularly young people, aggregate in these popular classes or meeting places because they react positively to the amount of carbon dioxide to be found there. Similarly, illumination experts would discover that the university community occupies a region of higher illumination, due to the less dense smoke pall, than that which covers the animal communities of Chicago's "loop district" and might easily draw unwarranted conclusions from this fact.

While such excellent analyses of the physical elements in the environment yield interesting and valuable data, their interpretation is not always evident. Our inside information concerning the motives that underly the actions of the university people, allows us to see immediately the need for checking such field data as we have been discussing with information gained from other sources. One such source available is the use of appropriate laboratory experimentation; another is the use of more refined methods of collecting data in the field.

One of the more careful methods of field study in common use is the selection of areas of standard size which are frequently square and are therefore called quadrats. If quadrat studies are to be made, the experience used in the preceding survey should be drawn upon in the location of the quadrats. Unfortunately in practice the investigator frequently does not know the names of many of the animals with which he is dealing and a certain length of time must elapse before the identifiers can report. This handicap combined with time limitations of the investigator, further combined with the fact that the studies must frequently be carried on far from the usual laboratory or even the usual area of residence often causes the student to use his general impressions gained from field experience in selecting areas for special study. Under these conditions he locates the quadrats first and regrets his selection later. The question of the size of quadrat to be used in careful study must be answered as well as its location. In this connection it is recognized, of course, that the reason for turning to the study of these sample plots is that it is impossible to go over the entire community with similar thoroughness.

Many of the conclusions that will be reached from the study of a university community will depend on the location of the standard quadrats. Suppose we are impressed by the number of animals that collect at periodic intervals during the morning before the entrance of the most used lecture hall and locate one of our quadrats there. The conclusions drawn from these periodic morning aggregations might be that this part of the community is dominated by a decidedly collegiate type of person who nevertheless is quite methodical in his habits. Turning to our real knowledge of the subject we know that their real importance in the community is less than would be indicated by a painstaking study of this and similar habitats and that they are not notably methodical in habits.

The more I consider the problem of the proper location of these sample quadrats in a community one knows as well as he does his own place of business, the more I am impressed with the care needed in the location of such areas for the study of non-human animal life and for the use of data so collected in making generalizations. Is a football field characteristic? Certainly a survey which omitted this locality would be incomplete but its significance would be missed if the collections failed to catch the crowds present for a few hours on a few days in the autumn. Are deans' offices typical, or students' lounging rooms, or fraternity houses? Shall a quadrat include the university chapel or the cashier's office? Which laboratory shall we select, if any? Shall dormitories, dining halls and libraries be represented? If so and if we find ourselves pressed for time in making careful quadrat counts, which shall be neglected or eliminated? By the location of a sufficient number of quadrats and by the study of the specimens to be found there during the entire twenty-four hours of the day and for all the seasons of the year, we can learn much of the organization of a human community such as we are considering.

Having selected the quadrats with all the skill and knowledge available, we must next decide how we are going to study them. We may visit each in turn with field glasses and notebooks and take down records of the numbers and behavior of those organisms which we happen to recognize at sight and make rough notes concerning the behavior of others which we cannot so recognize and name. We may set traps that will catch certain sorts of specimens that enter the quadrats without killing them and after appropriately labeling them we can turn them loose for further study by observation or by trapping. By so doing we may learn in the course of time of the distribution of a given individual during his normal round of activities. Or we may have to limit ourselves to trapping all the individuals possible and labeling them for future study. With certain other of our quadrats, we may proceed by plumping down a large box over the whole quadrat or a selected part of it and by means of a small opening introduce ether until all the contained organisms are dead. These may then be pickled as coming from quadrat "A" on date "B" under weather conditions "C."

If the quadrats are located sufficiently near a field or base laboratory, we may collect as many individuals as we can from a given quadrat and carry them to our laboratory, there to observe their behavior or to test their reactions under laboratory conditions. Such animals can also be subjected to toleration tests to determine the limits of their resistance to the different elements of their environment such as determining the heat or cold that will just kill them, the amount of humidity they can stand, the length of food or water starvation periods before death, and so on. All these experiments will be carried on in carefully cleaned laboratory rooms and containers as well as under conditions roughly approaching those normally found in nature.

Whether by these quadrat methods or by some other means of quantitative sampling, we can readily collect an impressive amount of mathematical data. These must be tested by statistical methods to determine the coefficient of correlation in distribution in order to find whether we have unearthed a real relationship. At about this stage in the analysis of the ecological relations within the university or community, it may be necessary to use other collecting methods. For this purpose we may devise nets of known size and mesh and test their efficiency in collecting by dragging them through a measured amount of space in which we have released a hundred freshmen or other easily recognized members of the college community. With tree-dwelling animals, if they are present, we may spread a canvas of known size and beat or shake the tree in as nearly a standard manner as is possible under the circumstances. Or we may use all our ingenuity in collecting in a given area for, say, thirty minutes and keep careful count of all the specimens taken; later these may be compared with the results from similar periods of collecting in other regions.

We may turn to random marking or banding individuals we think we can recognize and then record their location at intervals. By such a method in the study of the university community we might find that a well-set-up, fine-looking individual X, is apparently to be taken everywhere, now in the physics building, now at a faculty meeting, in the faculty club, in a dean's office, at a football game, alumni dinners, senate meetings; that he has tea with some regularity with the president; and we might conclude that we had discovered one of the important men of the community and we might be correct, for the data might concern an important academic figure. On the other hand, a bespectacled recluse taken only rarely and then in limited habitat niches might easily be still more important, more so even then twenty X's or hundreds of other members of the community present in significant numbers.[1] Such a one might be a distinguished

[1] In nature, the bobcat is rarely seen ever by trained hunters yet one of these in a region is of more importance than are hundreds of mice.

scholar furnishing the research leads that will justify the existence of many unproductive research laboratories; or he might be the modest donor of the millions needed to increase faculty salaries to the point where these important members of any university community would no longer of necessity live meagerly.

In such ecological analyses in nature the effort of the investigator is directed toward sifting out the important constituents from the less important or inconsequential ones. All the trapping, quantitative and qualitative collecting, and them arking of individuals for the more careful study which we have been supposing to be made in a university community might be carried on for some years without yielding many records of important scholars usually away from the immediate community, whose spoken or written ideas alter the community organization profoundly. We might have caught an occasional conscientious trustee, or a composed benefactor, and failed utterly to sense that the activities of the men concerned with the stock market may affect the immediate fate of our community more than any or all of the individuals we have collected.

It is needless to labor the comparison further. Suppose instead that we have in hand not the crude, though carefully collected data from the quantitative study of quadrats, but the president's report of the numbers and kinds of individuals that make up this particular community. With such data, we can accurately determine a part of the relationships existing between different members and groups of the university, but even such relatively complete statistics do not allow a correct evaluation of the forces that regulate the community, or an accurate analysis of the effectiveness of the community organization. Even with all available knowledge, who will be bold enough to predict future trends of university attendance or of curriculum emphasis? Yet what ecologist would not be thrilled to be able to prepare a data sheet for any non-human animal community which would be half as complete as the inadequate annual report of a conscientious university president?

Each and all of the methods suggested above have been made to yield information of value concerning the constituents and organization of animal communities but by comparing them with the possible results of a similarly limited study of a human community, their inadequacy is immediately apparent. One can readily see the greater insight into community life that would be gained by living as a member of a community, meantime studying it thoroughly. Under such conditions, one can soon begin to pick out the important men and movements and to separate them from those that are merely active or numerous. One may find that university policies and events are controlled by forces far removed from a given campus, just as an unfavorable summer in Canada may so affect our migrating birds that millions of insects are left alive that would otherwise furnish food for the horde of spring and fall birds of passage.

In brief, one cannot really understand the workings of so relatively simple a thing as a university community without an intimate, and sympathetic, though critical knowledge of the many complexities arising from the different sorts of contacts between its senile, mature and juvenile elements and between these and the other communities which they touch.

This method of personal acquaintance with the life of animals was the ideal of the older naturalists, Fabre, John Burroughs and Thompson-Seton, to name only three. By this method, one learns not alone from notebook entries, why the individual X mentioned above, engages in his varied activities but still more because of his understanding of the reactions to be expected from X as an individual.

If correctly applied, this method will use all the data collected by quadrat and other methods of study, all the results of controlled experiments and will interpret these in the light of personal knowledge too securely held to need notebook confirmation. Ideally such workers "measure that which can be measured and count that which can be counted, but remember always that the figures obtained are purely relative" and are to be interpreted in the light of all other knowledge of community organization that can be gained.

From such considerations, one is driven to the conclusion that we cannot understand the working of an animal community until we have lived in it or in one similar for years, insofar as that is humanly possible, studying it meanwhile by night as well as by day, in winter as well as in summer, individually as well as by communities, and the community as well as the individuals that compose it. We must attempt to get first hand knowledge of all the forces acting and even then we may be led astray, for how can a man know all the forces that control the behavior of a bumble-bee?

CHAPTER IV

THE ORGANIZATION OF LAND COMMUNITIES

THE white man found an almost unbroken forest of deciduous trees occupying much of the eastern part of what is now the United States. American beech and hard maple were present in largest numbers and were plainly the characteristic trees of this thousand mile long forest of hard wood trees. Included in favorable locations were trees of various sorts; oaks, tulip trees, black walnuts, sassafras and others on the uplands, while in the lowlands were elms, sycamores and cottonwood (poplar) trees. The under-forest was scanty. In regions near natural openings around ponds, or in places cleared by forest fires or by the falling of trees in storms, berry briars grew in abundance for a time before they were choked out by the regenerating forest. Elsewhere the lower forest held a scanty growth of spicewood and pawpaw bushes and a few other shade-tolerating shrubs. In the spring, the forest floor was carpeted by flowers which pushed up through the thick leaf mould between the time of the melting of snows and the opening of the forest leaves; pepper and salt, trilliums, dutchman's breeches and particularly hepaticas were especially abundant. Later in the summer when the forest was in full leaf, there were few herbs to be found growing through the heavy covering of dead and decaying leaves.

We know much concerning the animal population of this almost departed forest, but there were many relationships, knowledge of which can only be pieced together. Earthworms were the characteristic animals of the soil. Ants and a variety of beetles and their larvae, together with a multitude of other insects, lived in the decaying wood and helped hasten its transformation into forest mould. Many other animals including bears, and gray foxes, burrowed underground for their dens and white-footed mice flourished in tunnels just below or through the leaves in summer and through the snow in winter.

Over this old forest floor ranged the Virginia deer and the wapiti or elk; the bison, later so closely associated with the western plains, originally had a Pennsylvanian race that ranged through much of this forest. Timber wolves, panthers and wild-cats were also present, and beaver and muskrats congregated about the waterways. Squirrels were the characteristic animals of the trees, and bats, forest birds such as woodpeckers, owls and hawks, and insects represented the flying arboreal animals. Life along the forest margins was richer than in the depths; rabbits, groundhogs, skunks, chipmunks, mice and raccoons were particularly abundant near the natural breaks in the forest.

With the coming of the white man in numbers, the fluctuating balance of life which had developed under the age-long hunting of the Indians was gradually broken. Some of the inter-relations that had existed are revealed by the fact that as the pioneer white settlers in Illinois killed off the wolves and wild-cats, the number of deer and of several smaller mammals showed a decided increase. The observed increase in the number of deer may have been a part of one of the unexplained cycles in abundance which will be discussed more fully in Chapter VII; the increases in other animals cannot have been entirely due to such cycles.

Later as the country became more closely settled, the deer and other mammals were mostly crowded out. Many were killed by hunters; more were never born on account of the clearing of the breeding places. At present only a small remnant of this formerly abundant mammalian community exists, but of this remnant the tiny animals such as the white-footed mice appear to be present in greater abundance than they were a century ago. It is worth repeating that with the decrease in the larger carnivores that fed on squirrels and on deer, the latter became more abundant; with further decrease in the number of powerful predators, the smaller competing predatory forms, notably the foxes, raccoons and skunks, increased in numbers.

In fertile areas the advance of the white man has meant the practical disappearance of the forest and of its accompanying plant and animal life. Unfortunately this disappearance came before many of the more complicated problems of the organization of animal communities could be studied and, obviously, the solving of such problems can be undertaken still more imperfectly at the present time than a century or more ago. Such studies are being carried on in the available splinters of the former forest and in the much less broken Canadian woods. Among the forest fragments that have been much studied are two small tracts that lie near the state university of Illinois. These include a bit of low-lying woodland with its characteristic growth of elm and maple trees and a neighboring parcel on higher ground with maple and red oak as dominants.

In such forest communities, the trees are the dominant living things. Subject to the greater power of climate and soil, both of which they modify, they control the habitat in that they meet the full impact of the physical environment, wind, rain and sun and so modify the effects of these that the reactions of the plants and animals associated with the trees are profoundly affected; frequently these associates could not tolerate conditions within the environment were it not for the modifications produced by the dominant trees. Under the shelter of the forest trees there has been built a community which not only shows marked interactions between the different subsidiary constituents, but some of these attack the trees at all times and in periods of unusual stress may help destroy these dominant elements that make the community possible.

Some of the relationships among the animals living in these bits of Illinois woodland are illustrated in Fig. 1. The most important animals of the permanent nucleus of strongly influential animals are shown in the center. The symbols placed around these give at a glance the relative numbers of the three invertebrate animals present in greatest numbers at different seasons of the year. These symbols are placed end to end—with the least abundant next to the base line so that in determining the relative numbers present

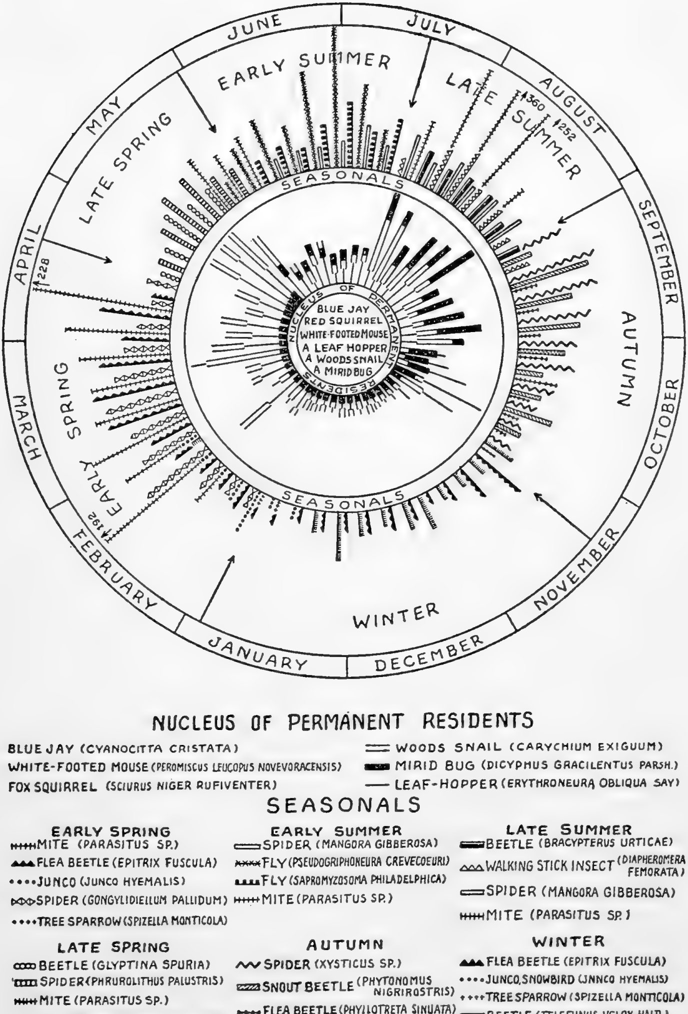

FIG. 1. An animal clock of the seasons in an Illinois Woodland. (After V. G. Smith.)

it is necessary to include the distance covered by all the symbols in order to find the value of the most abundant form which is represented by the outer part of the line. Thus in winter and spring a few true bugs of the family Miridae, more leaf hoppers and still more snails were to be found, but in late summer the leaf hoppers were fewest in number and the mirid bugs were most numerous. All these forms were present throughout the year, although they varied in numbers, and from time to time assumed different degrees of relative importance. Similar fluctuations of the important vertebrates are not recorded.

The outer circle represents the animals that were strongly influential for more or less limited seasons of the year. The scale of importance here reads from the base line except for a few inter-seasonal records. These seasonal animals approach or surpass the permanent residents in degree of influence during the period of their greatest activity, but have practically no influence at other seasons. From this chart it can be seen that the whole community may be regarded as being made up of a series of seasonal subdivisions of which, in the present instance, six can be recognized; those of winter, late winter and early spring, late spring, early summer, late summer, and autumn. In other communities there may be more or fewer seasonal subdivisions and their time limits may differ.

The data given in Fig. 1 for animals other than birds and mammals are for the strata of the forest on or near the forest floor. This diagram largely disregards the food and shelter interactions within the community but is based primarily upon the numbers of animals taken at weekly collecting trips throughout the year. The data so collected must be interpreted with many of the reservations suggested in the preceding chapter. Results so gained cannot be an accurate picture of the organization of an animal community; they do present the numerical structure as found during the period of study and the data indicate the type of organization that probably exists.

Although the data diagrammed in Fig. 1 will repay careful study; it is not needed to comprehend the main point presented, which is that around a permanent nucleus of important, influential members of such a community, there exists a series of seasonal sub-communities frequently called societies, whose importance waxes and wanes with the season. Such a diagram does not give much more of a picture of the true organization of an animal community than does a president's report that shows the number of faculty members, and of the different sorts of students present at different seasons of the year. It must be remembered, however, that even with college communities such data are considered to be sufficiently important to be published annually and frequently are broadcast widely in an attempt to give some definite information concerning the structure of such a human community.

The same sort of picture but with a different background and with some interesting implications has been revealed by recent studies in the aspen parkland of southern Canada. This aspen forest extends in a great crescent a thousand miles long, from northern Minnesota northward through Manitoba and Saskatchewan, west through Alberta to the Rocky Mts. and then south along their eastern foothills to western Montana. At its widest, this crescent extends north and south for 150 miles. To the north of this parkland lies the great transcontinental evergreen forest and to the south lies the great plains; it is the connecting link, the zone of transition, between the two.

The aspen is the dominant tree of this woodland. In places the box elder, the American elm, the burr oak and the balsam poplar also occur. The aspen trees are advancing southward invading the prairie all along their southern front, while to the north the evergreens are filtering in, replacing the aspens locally.

Grasses are the dominant plants of the prairie; within the memory of men still living, these were held in check by the activities of the bison. These formerly abundant animals not only kept the grasses well cropped but also prevented the invasion of the prairie by aspen pioneers. An early observer records: "The grass would be rather long were it not for the buffalo. Buffalo have ravaged this small grove; nothing remains but the large elms and oaks whose bark has been polished to the height of the buffalo by their perpetual rubbing. Brush and grass are not to be seen in this little woodland which on the whole is a delightful spot."

The bison, elk and antelope are gone and their place is taken by domestic cattle. The buffalo wolves are also gone; foxes are decreased in numbers. Coyotes increased at first with the decrease of their more powerful competitors but are being reduced as the result of a bounty having been placed on their heads. With the decrease of their enemies, Richardson's ground squirrel and the badger, which feeds largely upon this squirrel, also increased in numbers only to go into decline after an intensive killing campaign was inaugurated. Of all such large or medium-sized mammals, only the jack rabbit is now holding its own or increasing in numbers.

At the present time Drummond's vole, often called a meadow mouse, is the most abundant and the most influential animal, man and his beasts aside. It has been found to be impractical to attempt an estimate of the numbers of these voles present per acre but every square foot of prairie is crossed by their runways. They feed entirely on plants, and hence are true "key-industry" animals in that they convert the grasses into meat which is then a source of food for hawks, coyotes, weasels and the great horned owl. Where in the boyhood of my father the mighty and picturesque bison roamed in countless numbers, so many that men could smell them at a distance, today the retiring, apparently insignificant meadow mouse is the most important wild animal left!

The crow, the introduced partridges, the leopard frogs, meadowlarks, insects in general and particularly ants and invertebrates as a group may be considered to be important prairie animals. Of these, the invertebrates reach a total population of about 6,000,000 per acre upon the prairie in March at a time when the larger animals are still hibernating. As these emerge and become active, the numbers of insects decrease until in June there are only about a million per acre; then with more favorable conditions their numbers increase, only to diminish again during the late summer droughts until at the beginning of winter there are only about a million invertebrates to the acre.

Along the sloughs and water courses are communities, characterized by willows, which have a somewhat different composition. The bird life shows the effect of the presence of water; warblers are abundant and the red-winged black-bird and bronzed grackle occur along with more truly aquatic birds. Here leopard frogs breed in tremendous numbers and from these centers they migrate onto the surrounding prairie in sufficient numbers to become of considerable, though not of first rank importance. One estimate showed about 200 per acre over the area being studied. They are entirely carnivorous as adults and eat mainly the prairie insects and snails.

The curve of insect abundance along these moister regions is like that of the higher prairie. The spring maximum of 9,500,000 is higher; the June minimum of a million per acre is the same as before. This rises to a summer maximum of 2,500,000 and falls off to an autumn minimum of a half million per acre. Leaf-feeding beetles, snails and gall-forming insects are notable additions to the community. Those who have personally visited this region will remember also the presence of the mosquito hordes which breed in the sloughs and infest their neighborhood.

In the aspen forests where the aspen trees dominate the community and where formerly the American elk, the bison, deer and bear were common animals, today the most influential animal of the community is a mere beetle of the genus *Saperda*. To the lay mind even a meadow mouse would seem important as compared with one of these beetles. Their importance depends upon their numbers and upon the fact that they feed upon the dominant aspens and in turn are fed upon by woodpeckers.

The bird population in these woods is much greater than in the open country both in species and in numbers of individuals. The insect population is decidedly less than in the neighboring communities; the maximum for the year is only 4,500,000 and the fall minimum is a mere quarter of a million per acre. Individually most of these insects are of no importance; even as species only a few reach even relatively slight importance in the general community organization, but as a whole they form one of the main sources of food for the bird population and for many small mammals and are of further importance because of the damage they do to plant life.

The forest margin, the edge where the aspen forest meets the prairie, forms a separate community. There the aspens are still the most important plants but their associated plants differ from those of the mature woodland and the influential animals are also different. Along the forest margin the most important animal is the snowshoe rabbit. Some idea of the extent of its influence may be seen from the fact that in a square of 25 meters 39 per cent of the aspens had been ringed and killed by rabbits and all of the associated hazelnut, rose and chokeberry bushes were dead as a result of rabbit attacks. Obviously the rabbits are a strong influence in retarding the invasion into the prairie of the aspens and their associated shrubs.

The rabbit breeds in the forest margin. Many are killed, especially in winter by coyotes, owls, hawks and weasels as well as by men, both red and white. Coyotes and weasels and skunks are more characteristic in many ways of the open prairie but they breed in the forest margin. The birds also include characteristic species that feed in the open. The invertebrate life is less here than in the prairie or in the woodland proper but in the autumn there is a great migration particularly of insects from the open country to the protection of the forest-margin bushes. The migrants take shelter under leaves and grasses and burrow into the soil and are joined in this migration by insects that spend the growing season on the upper levels of the forest margin trees and shrubs.

Some of the important relationships within these communities are suggested by the diagrams given in Fig. 2, which outline some of the interactions between and within the communities of the aspen parkland. The arrows point from the aggressor to the plant or animal which is eaten. This chart helps us to understand the way in which distinct communities are united into a larger web-of-life since we can see here that there are inter-community activities that tend to unify the whole. The food-web interactions within a single community are also illustrated.

Like the communities in fragments of Illinois woodlands which were discussed earlier in the chapter, the animal communities of the aspen parklands consist of a permanent nucleus of perennially important animals, mostly vertebrates, to which are added others, mainly birds and insects that are present or active only during the summer season. In these parkland communities the seasonal sub-communities are characterized by birds that pass through in their spring and fall migrations, or are summer or winter residents,

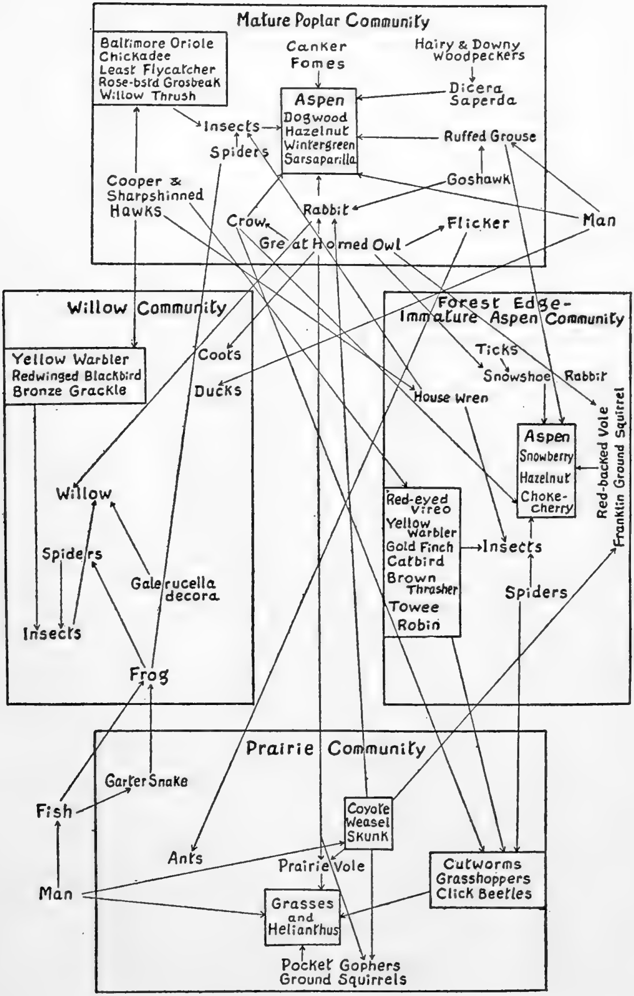

FIG. 2. Food-web relationships in the aspen parkland of Canada. (After R. H. Bird.)

rather than by changing numbers of invertebrates, even though the latter have striking seasonal significance.

The composition of these communities indicates that before the white man's influence became so marked, the important, frequently the predominant, influence in the community was held by the larger mammals. In many cases this influence was strong enough to control the distribution of the dominant plants, in part at least. With the coming of the white man, these passed away and their place was taken either by man and his domestic associates or by smaller, less conspicuous mammals and by insects. In these more northern communities, the rôle of the insects does not seem, even today, to be as important as that assigned to them after careful study of their place in the Illinois communities. This shift in importance may be due to the fact that the Illinois countryside is more completely man-controlled and that man has been able to control the insect population less readily than that of the mammals; or it may be that the warmer climate enhances the importance of insects and of other "cold-blooded" invertebrates. We know that in the tropics, insects and insect-borne diseases are of sufficient importance to keep even the white man and his domestic animals from extensive and otherwise attractive regions.

CHAPTER V

THE EVOLUTION OF ANIMAL COMMUNITIES

If, as has been suggested earlier in this discussion, animal communities show similarities to organisms, then we should expect to be able to discover differences in the communities that occupy the same habitat as time passes; in other words there should be some sort of community evolution which would run from pioneer communities in which the habitat is being penetrated for the first time by animal life, to mature communities, usually called climax communities, in which community life has become stable. Such evolutions should take place fairly rapidly. Beyond these there should be the changes brought on by the slow shifting of climates such as have produced a desert in southwestern United States in an area where forests once grew and where fossil trees are still to be found.

In nature even fairly rapid community evolution is usually too slow to be observed in the life of a single individual; fortunately all are not so. For example there are the changes which take place in a protozoan infusion that runs its course rapidly enough so that the entire progress up to the climax stage can be followed within a few months.

It is a common laboratory practice to set up such protozoan cultures in the brownish "hay tea" made by boiling common hay in water. The hay may then be filtered out and the "tea" allowed to cool. If such an infusion is allowed to stand open to the air, first bacteria will collect and grow and later air-borne cysts of Protozoa will fall into the liquid and populate the medium. In such a non-seeded culture, the development or evolution proceeds slowly. Its speed can be quickened by seeding the newly cooled infusion with a variety of organisms including bacteria and a number of different sorts of Protozoa. Tests have shown that the numbers of kinds seeded have little if any effect upon the order of their development in the ageing culture.

The liquid of the newly made infusions is transparent though colored, but within forty-eight hours it becomes plainly cloudy due to the development of countless bacteria which at this time are equally distributed through the medium. During this period the acidity of the liquid rises rapidly due to the fact that the bacteria cause fermentation which produces acid. The acidity reaches a maximum at the end of about three days and a slow trend toward alkalinity follows; at this time a jelly-like "zooglea" begins to be formed at the surface and gradually increases in thickness until fragments fall to the bottom. As soon as the bacteria have become numerous and their action on the hay "tea" has put a part of it in a form available for animal life, there occurs a great growth of Protozoa, which have been shown time and again to run through approximately the following course first reported by Woodruff of Yale: the description of one of his typical series of cultures will furnish the basis for the following account.

The first animals to appear in numbers are the flagellated protozoans known as monads (Fig. 3). These may come in as early as the second day of the life of the culture and reach a maximum on the third to ninth day, after which they decline rapidly in numbers and frequently become extinct so far as active forms at the surface are concerned although they may live on in reduced numbers for two months. In every case these monads are the first to appear and the first to reach a maximum. This is explained by the fact that these forms feed directly on the bacteria and also upon the food products which the bacteria release into the surrounding medium. The monads are also the first organisms to decline in numbers and practically to disappear. Their decrease is probably due in part to the rapid decline in numbers of the bacteria present as fed upon by the monads

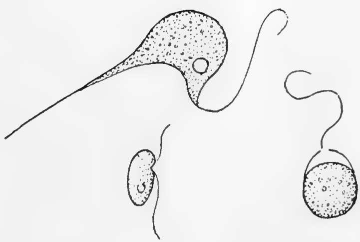

FIG. 3. Monads.

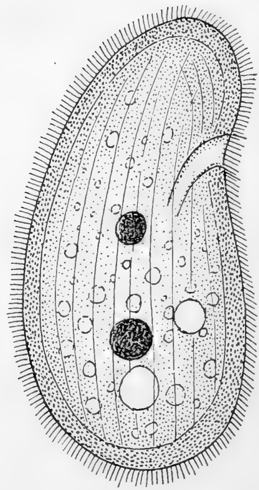

FIG. 4. Colpoda.

and to the rising generation of *Colpoda* (Fig. 4). The fact that they appear at a time of high acidity is probably incidental.

Infusorians known as *Colpoda* are the second organisms to appear in numbers. In the series we are following they are present in maximum numbers on the sixth to the eighteenth day; their extinction is usually rapid and occurs from the fifteenth to the thirtieth day of the life of the culture. They are followed by certain of the

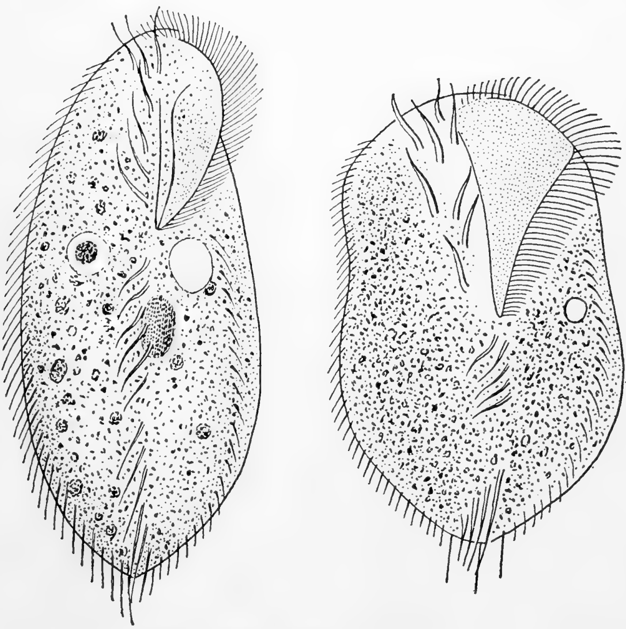

FIG. 5. Hypotrich infusorians.

infusorians that have strongly developed cilia on their lower sides and are known as hypotrichs on this account (Fig. 5). These are the third set of organisms to develop in considerable num-

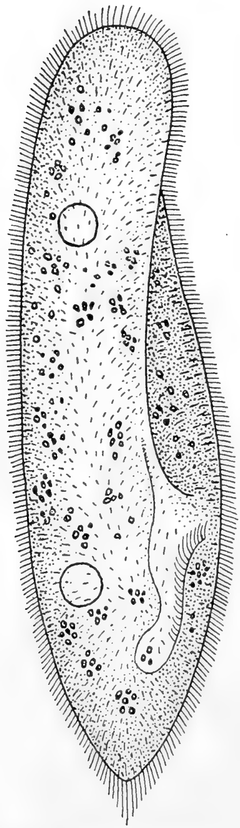

Fig. 6. Paramecium.

bers; sometimes they reach their maximum abundance before the *Colpoda* but they usually remain much longer. They are normally present in greatest numbers after the monads have passed their maximum. During this period the medium is usually becoming more alkaline but this fact may have nothing to do with the changes in animal life which we are following.

The hypotrichs are succeeded by another infusorian, the common *Paramecium* (Fig. 6). These usually attain their greatest numbers at the surface after the hypotrichs have passed their maximum. They may appear early, as early as the third day, but usually come in much later; their usual maximum comes about the seventeenth to the twentieth day. If the culture becomes infested by their small but voracious enemy, *Didinium*, they may go into rapid decline; in cultures without this *Paramecuim*-eating animal, they live on for sixty-five days or more.

Paramecia are present in cultures along with a stalked form called *Vorticella* (Fig. 7). This animal appears irregularly in the cultures from about the second to the eighteenth day and reaches its maximum in from sixteen to fifty-nine days. The *Vorticella* have been known to become extinct in sixty-seven days but in other cultures they persist as long as counts are taken. Clearly they belong to the more mature life of the cultures.

Finally there are the *Amoeba* (Fig. 8) which do not develop in all cultures even if they are seeded

Fig. 7. Vorticella.

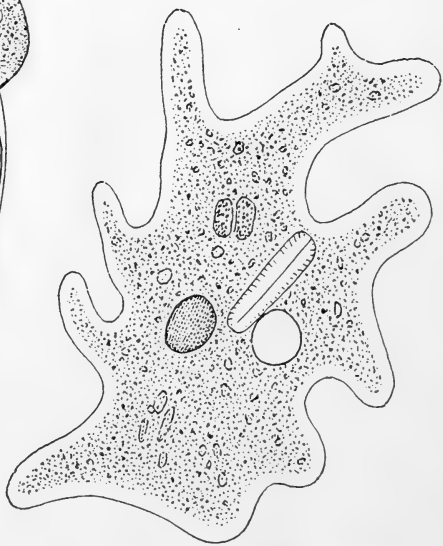

Fig. 8. Amoeba.

into them at the beginning. Their appearance is erratic; they may come in fairly early or not until the fortieth day. They usually pass to a maximum soon after they appear, and become extinct in from eighteen to eighty-seven days. At the surface of the cultures they run their cycle after the Paramecia have completed theirs and before the *Vorticella* are through.

The following summary of this sequence of protozoans in hay infusions gives the essential facts:

Order of first appearance	*Order of maximum populations*	*Order of disappearance from the surface*
1. Monad	Monad	Monad
2. Colpoda	Colpoda	Colpoda
3. Hypotrichs	Hypotrichs	Hypotrichs
4. Paramecium	Paramecium	Amoeba
5. Vorticella	Amoeba	Paramecium
6. Amoeba	Vorticella	Vorticella

Relatively few protozoans are to be found at any time at the center of the cultures. Aside from *Amoeba*, the animals we have been considering are essentially surface forms. After standing for some months the culture becomes almost balanced, that is, it reaches a climax condition where life is fairly stable. Green filamentous algae appear at the bottom and at the end of three years almost all these animals mentioned may be found in small numbers, chiefly at the bottom among the algae. Often, however, all of these protozoans disappear completely from the cultures as active forms, and only rotifers and small crustaceans are left. These manycelled animals do not usually enter the cultures during the early period which we have been following but when they do come in, they persist for months. If a small amount of bread or a few grains of cracked wheat are added to one of these old dormant cultures, the fresh food will cause the whole cycle to start up again and run through approximately the same course which it originally followed.

There is evidence that the cycle is caused in part by the excretions which the protozoans themselves give off as well as by the food which they consume. Paramecia, for example, normally follow the hypotrichs in the succession series; they reproduce fully as rapidly in media contaminated with hypotrich excreta as they do in uncontaminated media but they reproduce more slowly in the presence of their own excretions. On the other hand, hypotrichs are retarded in their rate of reproduction by their own and by *Paramecium* contamination.

With protozoan cultures it appears to be true that these animals by living in their environment tend to make it unsuited for their prolonged existence; however, they make changes which prepare the way for the coming of other animal life. The evolution of an animal community through different stages in the same habitat is usually spoken of as forming an ecological succession. There are many other small habitats in which succession of communities can readily be traced within a few months or years. One good example is the animal community inhabiting a fallen tree. Animals such as the wood boring beetles attack and feed upon the solid wood. They open tunnels through its structure by means of which other animals or water or fungus spores can enter. The feeding of these animals, the freezing of the water and the growth of the fungus spores all help to disrupt the woody structure until as it softens, the first pioneers can no longer remain. The wood is too soft and decayed for their food; they must either die or migrate and their place in the decaying log is taken by other forms that do feed upon the softened wood. Finally through the activities of these animals, of bacteria and other plants, and of weathering processes, the once solid log is reduced to a mere mound of much decayed humus occupied by a few ants and earthworms, a totally different community from that of the newly fallen log.

The same sort of evolution of plant and animal communities can be observed in nature on a much grander scale than in a protozoa infusion or in the decay of a log on the forest floor. The forest communities themselves show such successions.

One of the best studies of these is in the Indiana dune region at the south end of Lake Michigan. Many of us have followed various stages of this development during our lifetime but the whole series of events there takes too long to be covered by a single human life and our awareness of these processes had not developed until nearly the end of the last century, consequently the succession has not been watched from beginning to end as have those just described, but our certainty that it has taken place in some such manner as will now be sketched is almost as great as though we had actually been present to observe the whole process.

The high bluffs on the western side of Lake Michigan north of Chicago are eroded by wave action and a shore drift results, particularly in storms. The load of sand thus obtained is gradually shifted southward to be piled up by the waves at the south end. There as the sand dries, it is picked up by the wind and carried back until the force of the wind is broken and the load of sand is deposited to form a dune. Many other things besides the sand itself are cast up by these same lake waves which have a part to play in the development of the dune region.

After an off-shore wind for a day or so, when the wind changes, the waves deposit on the shore not only sand but also animals of many different sorts. If the storm is severe a great collection of shells of small lake snails or finger-nail clams may be cast up together with an occasional crayfish and many small and some larger fishes. In spring and summer countless insects will be found in the same drift line with these water-dwelling animals. Normally these insects live in the trees or grasslands along the lake, from whence they were caught up by a land breeze and carried out over the water into which they dropped when exhausted. They were then cast up by the onshore drive of the waves. With them may be fragments of birds and at times an occasional larger animal. I have seen in this drift line a collection of beetles that extended for miles in a row, from one to three feet wide and with hundreds of beetles to the square foot. At the time of the fall migration of monarch butterflies, I have seen similarly a brownish tinge in this drift line that could be distinguished a quarter of a mile ahead caused by the brownish color of the cast-up butterflies. This insect drift furnishes season after season and year after year a fair sample of the insects that are flying on the nearby communities.

Some of the animals of the drift have survived their watery immersion and are still alive; others are dead. Not all of the animals in this drift have been cast up by the waves. Flesh-flies and beetles soon find the fishes and lay their eggs thereon. Some find enough such fishes to make them their regular breeding habitat. Many other animals, spiders, predaceous insects and even toads, snakes and white-footed mice of the fore-dunes find their food among the drift. Truly the drift line is the lunch counter of the fore-dunes.

In summer the drift is cast up near the water's edge along the damp sand of the fore beach; in winter it may be carried further back and the winter's storm drift consisting of tree trunks and broken bits of ships and other timbers are carried far back and left high and dry on the upper beach. There they serve as shelter for many of the predaceous animals that feed on the summer drift and for food as well as for shelter for the wood-eating termites frequently called "white ants."

Between the damp lower beach and the tree-drift of the storm beach there is usually a level extent of sand almost unoccupied by plants, but in which animals are busy. There, in favorable places, the tiger beetles make their burrows; many other animals of the fore beach burrow more or less. Gradually the animals transform the dead bodies of the animal drift into humus and scatter this through, as well as over the surface of the sand. On the whole this beach region is controlled in the winter by the lake waves with their waterborne sand, while in the summer the wind-carried sand-blast is a controlling feature.

Even in the face of this adverse environment, pioneer plants invade the shifting sand. These include the sand-binding grasses. If these grasses gain a foothold, they tend to break the force of the wind and to cause a deposition of sand around their roots. Similarly the birds may bring seeds of the sand cherries which frequently start to grow just back of the winter or storm beach and again form the basis for a growing dune. In these more stable dunes, the burrowing spiders (*Geolycosa*) and the digger wasps continue their burrowing, with the resulting mixing of humus with the sand.

Around moist places in the fore-dune system, seeds of the cottonwood trees may germinate. These trees as they grow form a most potent means of collecting sand. Like the sand-binding grasses and the sand cherries, they too are able to grow without being smothered by the sand that accumulates about them. Frequently only the upper branches of a tall tree extend above the level of the sand; the rest is all buried. In this way great dunes are built up which normally extend parallel with the lake shore. With the increasing stability of these dunes, the animal population becomes more varied and abundant. There are more spiders, digging wasps, tiger beetles, grasshoppers, snout beetles and flies of various sorts. The trees themselves are attacked by insect borers and by leaf feeding forms. All these plants and animals add more humus to the sand; as before, this is mixed through the upper layers by the activity of the burrowing insects. The grasses bind the dune increasingly more firmly and conditions gradually are made more favorable for the growth of bunch-grass and for the seedlings of a scrub pine.

These pines develop until they come to dominate a characteristic community in which other plants are able to invade the dunes successfully, notably the junipers. Spring flowers make their appearance and the accompanying insect life becomes still more abundant. The six-lined lizard, and turtle from the nearby ponds, bury their eggs in the sand; blue racer snakes place theirs under rotting logs. White-footed mice, ground squirrels and rabbits breed here; common grouse nest on the ground and woodpeckers make their nests in the trees. The pines are attacked by a multitude of borers. Their needles form a thick mulch over the sand and in a relatively short time the soil has been built up sufficiently for an invasion of black oaks.

The oaks succeed each other, first black, then white and finally the red oaks. Each has its characteristic set of accompanying plants and to some extent, a characteristic set of animals, but the larger animals and particularly the birds, tend to range throughout. As the sand becomes more firmly bound and more thoroughly mixed with humus, the plant growth becomes thicker, and the resulting leaf mulch tends to hold the soil moisture while the growing density of the tree crowns lessens light and so lessens the amount of evaporation. These processes go on, with each community gradually making conditions that it can no longer tolerate and so preparing the way for the coming of another; at last the climax forest of this region, the beech and maple, begins to grow on a sandy sub-soil that has accumulated humus from the numberless plants and animals that have lived on and over it since it was originally cast up along the bare lake shore. The beeches and maples and their associates gradually replace the majority of the oaks and the type of community develops which once dominated the eastern section of the United States. Unlike its predecessors in this succession which we have been tracing, this community is immune to the effects which it produces and so becomes virtually permanent, changing only with a change in climate.

At times the lake winds may rip off the plant cover in a weak or particularly exposed spot and start what is graphically called a "blow-out." These are more frequent in the fore-dune region but may occur elsewhere in the dune complex. When one is formed, its recapture covers many of the stages and shows the majority of the processes that have been outlined for the dune succession as a whole until finally it too becomes completely captured by the climax vegetation.

Professor Cowles of Chicago, a pioneer student of dune vegetation, found that plants appear to be unable to stop the movement of a rapidly shifting dune. Such a travelling dune is first checked by a decrease in wind energy due to increasing distance from the lake or to the growth of barrier dunes which may form across the mouth of a widening blow-out. Such barriers are formed about pioneer vegetation just as in the growth of the original fore-dunes.

Throughout the whole process the animals and plants form a series of units which exhibits the loose co-operation characteristic of any community. After the plants come into the succession on the fore-dunes, they are the dominant force either living or physical. The animals aid in preparing the soil for their coming and in enriching it so that still others can tolerate dune conditions.

They are instrumental in the distribution of seeds as in the case of the sand cherry; in pollination of many of the flowers and in the destruction of plants which in other environments may dominate the community life. Thus the cottonwoods have more insect enemies when they grow late in the dune succession than when they are in the exposed fore-dunes.

As the climate changes, the climax communities change; comparatively recently, just following the last ice age, the climax forest in the Chicago region was a conifer one such as exists today in the Canadian forests. With the gradual change in climate, this forest community could no longer maintain itself except in favored spots, such as have allowed the relic grove of white pines near Oregon, Illinois, to persist; gradually this old conifer forest gave way before the advancing beech and maple community.

Such slow climatic changes are as characteristic of community evolution, as are the more rapid changes toward the existing climax in the case of successions such as those of the dunes. If as persistent spirits we could hover over the Chicago area as Hardy in *The Dynasts* imagines the ethereal spirits watch the creeping of the human armies in the Napoleonic struggle in Europe, so in centuries of time we would doubtless see a gradual shifting of the plainly marked plant communities carrying with them their less readily recognized animal associates.

From the considerations given in the last chapter, we know that the shiftings are checked and at times are stopped for centuries by the activities of animals, as the bison held the western plains in a short grass condition and helped keep the trees from invading the margins of the grass-lands where otherwise they could have grown successfully. Similarly other animals by scattering seeds or by breaking the sod mat of the grasses may aid in the establishment of advancing pioneers of an invading plant community.

CHAPTER VI

UNBALANCE IN NATURE

UNDER constant laboratory conditions the number of constituents in a simple laboratory community should come to a constant level. Ordinarily such a combination of conditions is difficult to realize even in modern laboratories with their various devices for environmental control. In the case of protozoan infusions, the population of any given species or of all species taken together begins with only a few representatives, rises to a climax and falls off to a few active forms or to none at all. The decrease in population in such infusions is apparently due to an exhaustion of the food supply, or to an increase in the amounts of excretory products present, or to both acting together.

When these two causes of decline are eliminated, the population should come to the maximum level at which it can be maintained and should continue indefinitely at that level. This condition has been reached in laboratory populations of the flour beetle (*Tribolium*) which thrives in cultures of common wheat flour. The beetles

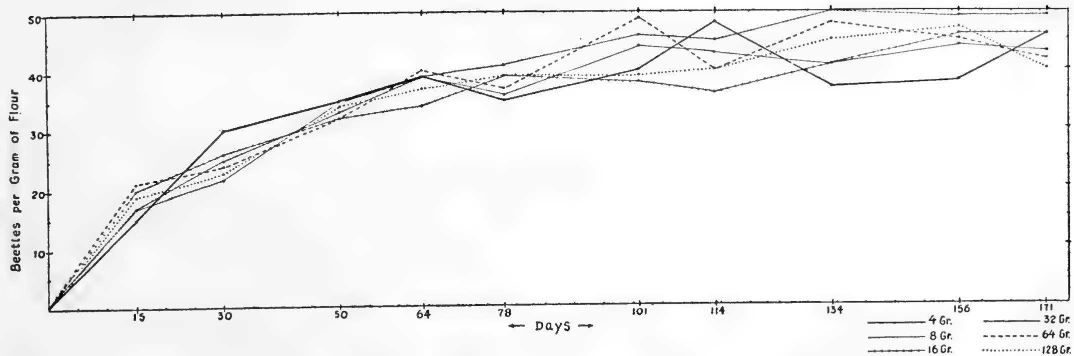

FIG. 9. Regardless of the size of their floury environment, these *Tribolium* beetles tend to have the same number present per gram of flour after about one hundred days. (Data from Chapman.)

can be screened out of the flour from time to time; even the eggs and grub-like larvae can be recovered uninjured from the screenings and be transferred to fresh flour. They are thus supplied with fresh food in an environment that is uncontaminated by the waste products of the population of beetles which have been occupying the flour. The course of the growth of such a community under laboratory conditions is shown in Fig. 9 which records the increase of different initial populations to an approximate balance at the same number of beetles per gram of flour regardless either of the initial population or of the number of grams of flour used.

When such beetles were reared in whole wheat flour at twenty-seven degrees Centigrade with an initial "seeding" of one pair of beetles for each four grams of flour, the population became practically constant at about forty-four individuals per gram of flour after one hundred days and remained so for the next fifty days. With different sorts of flour, the beetles come to have a constant number per gram of flour which varied apparently according to the food value of the flour used. The exact series of reactions which lead to the establishment of this population balance have not yet been analyzed but there are many indications that there is a certain amount of cannibalism practised which has a definite relation to the degree of crowding.

In nature the problem which faces animal communities is never so simple. Many more factors are continually fluctuating; temperature values change in daily, yearly and in longer cycles. Periods of relatively mild winters are followed by years when the winters are unusually cold; similarly there are cycles of drought that may be seasonal or may run over periods of several years. The exact number of factors in the physical environment that show similar daily, seasonal or longer cycles, would be difficult to list. These may all affect the numbers of animals that may be found living in a given habitat at any given time. The problem which the animals have to face is further complicated by the fact that the numbers of plants or even of animals present also affect the numbers that the habitat can support both of their own and of related species. Some of these interlocking and fluctuating relationships in community life have been pointed out in the opening chapter in connection with the animal life of lakes; population cycles among many land animals are even more striking.

One of the best studied cases of apparent unbalance in nature is that of the lemming populations of the arctic regions. Lemmings are small animals related to rats and mice; they are about six inches long when fully grown, but about half this length is tail. The arctic tundra in Lapland, Greenland, North America and Siberia is fairly alive with these animals. In many places the moss-covered ground is riddled with lemming holes and the lemmings are among the most joyous features of the tundra. With the activity of rabbits they pop in and out of their holes keeping the while a sharp outlook for their arch-enemy, the snowy owl. They are key-industry animals of the tundra and are at the base of the food pyramid not only for the snowy owl but also for arctic wolves and arctic foxes; and even the polar bear when ashore, hunts and feeds on these tiny lemmings.

Lemmings do not remain at a steady level of population year after year; quite the opposite. Their periodic increases in abundance have been so conspicuous that they have been known to many men for centuries. As a result of such increases they become too numerous to obtain food in their native habitat and accordingly act as do many other animals, man included, when faced with threatened starvation; they migrate.

Lyell, friend of Charles Darwin, recorded such migrations approximately as follows: Once or twice in a quarter of a century[1] they appear in

[1] More recent studies show that "lemming years" come every third or fourth autumn.

vast numbers, advancing along the ground and 'devouring every green thing.' In Lapland, innumerable bands march from Kolen, through Northland and Finmark, to the Western Ocean, which they immediately enter; and after swimming about for some time, perish. Other bands take their route through Swedish Lapland to the Bothnian Gulf, where they are drowned in the same manner. They are followed in their journey by bears, wolves, and foxes which prey upon them incessantly. They generally move in lines which are about three feet from each other and exactly parallel, going straight forward over precipices or through rivers and lakes; when they meet with stacks of hay or corn, they gnaw their way through instead of passing around them. One observer remarked: "There is no sense in this."

The lemmings march chiefly at night and may cover a hundred miles before reaching the sea into which they plunge in such numbers that their drowned bodies form drifts on the nearby shores. Such migrations are caused primarily by over-population and are a symptom of maximum numbers which migration and epidemics reduce until the following year relatively few individuals are left.

Records show that ordinary "lemming years" occur about 3.5 years apart but there is evidence that years of extraordinary abundance show remarkable synchrony in such widely separated regions as Canada, Greenland and southern Norway. When lemmings are abundant, the animals feeding upon them have much food and consequently increase in numbers. Elton, a British naturalist much interested in these cycles of animal life, has studied the records of the Hudson Bay Company and finds that the times when many arctic fox skins have been taken by the Hudson Bay trappers follow the years of great lemming abundance.

The field mouse, *Microtus*, is another key-industry animal of the tundra. It is a somewhat close relative of the lemming and has a similar cycle of abundance. When these mice are at the peak of their population fluctuation, they attack the vegetation in such numbers that larger animals like the caribou are forced to move to other feeding grounds and even men are affected, for the mice devour young crowberry shoots and thus prevent the Eskimos from collecting their annual crop of crowberries.

The seed and bud-eating ptarmigan of the tundra are protected by the increase in numbers of the lemmings and field mice because their normal enemies are feasting on more easily caught food, and thus they too tend to increase when these small rodents are plentiful. Foxes, owls and hawks find their food more plentiful and they too increase in numbers. Then just as the point of greatest abundance is reached comes the "crash" in the cycle. The lemmings and the mice die off and disappear as if by magic leaving an increased population of predatory foxes, hawks, and owls to shift as best they can in the face of a diminishing food supply. They too migrate. The snowy owl comes down into New England and New York by the thousands at such times and causes great loss of life among the native small birds and rodents. These predatory migrants usually perish in their turn, for in the case of the owls at least, the evidence is that they do not return north and they cannot successfully breed in the southern regions which they penetrate.

It is well known that there is a sun spot cycle of about 11 years. This affects the temperature of the earth's surface, which is higher when there are fewer sun spots. Atmospheric pressures and rainfall of different parts of the earth also vary with the sun spots. The tracks of the regular cyclonic storms in North America shift with more or less regularity and this shift appears to be correlated with the sun spot cycle. The changes in level of Lake Victoria in Africa show a high correlation with the sun spot cycle.

It is interesting to note, however, that many of the observed biological cycles do not run with an eleven-year period. The lemming-mouse-ptarmigan-fox cycle is less than four years in average length. A study of the size of rings of growth in the fossil trees of southwestern United States and of living forest trees in Germany do apparently indicate an eleven-year cycle but otherwise the most commonly indicated biological cycle is one of some nine or ten years. Such cycles have been found in the population numbers of grouse and rabbits in Wisconsin, in grouse and other non-migratory birds, rabbits and coyotes of Alberta, Canada; in hares, muskrats, grouse, lynxes, foxes, martins, wolves, minks and goshawks of Canada in general.

An astonishing feature of all this lies not only in the fact that the same cycle occurs in so many different animals which are not closely related in an evolutionary sense although they are related ecologically by food webs or habitat relationships, but also that the same period occurs in the far northwestern part of Canada and south well into the United States. The increase or decrease of population appears to begin in northern Canada and works its way slowly southward and eastward; it reaches southern Canada in about three years but in each region the period of somewhat less than ten years is constant for that particular region. Similar cycles are found in records of the salmon fisheries of New Brunswick (9.6 year period), in the growth of the giant sequoia trees of California and in a rabbit-destroying disease in Canada.

This 9 + years cycle has not been much studied in meteorological records. Apparently it is not related to sun spots. It is a little longer than the lunar cycle of 8.85 years and almost half of another lunar cycle of 18.6 years. It is interesting to note that the most distinct cycle of rainfall and of the value of farm products in the United States between 1837 and 1930 showed a period of 18.6 years. Parenthetically, during this time there have been six marked financial depressions separated by average periods of 18.4 years. These financial depressions accompany the agricultural depressions which, however, they may precede or follow, and it is interesting to note that droughts, financial panics and decreased productivity of American farms have a cycle which is twice the length of that shown by population fluctuations of rabbits, grouse, foxes, salmon and sequoia trees.

When we turn from considering the fact that there are cyclic fluctuations in numbers of animals, to attempt to determine the causes of such fluctuations, we are in an entirely different world. The situation resembles the shift from the uniformity of evidence that there are cycles in human business to the dissension concerning the causes of these cycles. The causes of cycles in numbers of animals appear to be divided into three groups: biological, climatic and astronomical. Among the biological causes we must suspect variations in food, in reproductive rate, in parasites, both bacteria and animal, but particularly in the food.

Regarding variation in food production, I have already indicated that this may play an important rôle. There is some evidence that the rate of reproduction varies in a somewhat cyclic manner, beyond the annual cycle; thus the snowshoe rabbit of Canada tends to produce larger litters when food is plentiful and smaller ones when conditions are severe. The importance of parasites has probably been under-emphasized. The layman particularly is happily unaware of the enormous numbers of animal parasites which infest most forms of wild life, plants included. Thus there is evidence that the growth of the forests of Germany is influenced as much by their insect pests as by temperature and rainfall. An even greater rôle in determining population numbers among animals is played by bacterial parasites. Apparently these undergo fluctuations in virulence such that in the case of the most recent rabbit cycle in Minnesota, the "crash" when the animals suddenly died off in great numbers, was due to the appearance of a particularly virulent form of bacteria, which came when the number of immune rabbits was low.

Among the climatic factors, variations in temperature, rainfall and humidity are obviously important. The amount of sunlight received, including the amount of ultra-violet, is also important and this is subject to cyclic changes. With mammals, knowledge of the presence of cycles of abundance is least in regard to those of the tropics and greatest concerning the sub-arctic regions. In the former, the climatic conditions are most constant; in the latter, the most varied. There are strong indications that cycles are more likely to occur on the margins of available habitats rather than in more favorable regions; this holds whether the margin is due to coldness or to drought. Under such conditions a small fluctuation in climate may produce a catastrophe for the animals present.

There is much good evidence that in fishes at least, the numbers of animals present depend on the length of time since there has been a good spawning year. Fishes frequently produce unbelievable numbers of eggs; a single female codfish may produce from one to five million eggs in a single year. When there is a favorable opportunity for these to develop, such fishes are abundant. With codfish, the numbers of young of the year found off the coast of Sweden is correlated with a high average temperature in the spring months and this correlation is probably due to the fact that the higher temperatures in spring allow a rich development of the minute animals and plants upon which the cod-fry feed.

An almost random sample of the way a fish population depends on successful breeding years is given in the case of lake-herring in Finnish lakes. These fishes congregate to spawn in October and November. The fertilized eggs sink to the bottom and remain there over the winter. The stock of herring in 1930 in these lakes consisted almost entirely of fishes hatched within the last four years, that is of the last four year classes. Since 1905 there have been good year classes in nine different years with a mean interval of two and five-tenths years and with three years as the most common interval between good year classes. In bad years the newly hatched fishes are driven ashore by windy weather. With favorable conditions, an excellent year class may result from a decimated stock.

There is considerable support for the view that the chief causes of climatic variations on the earth are solar variations, lunar variations and other astronomical causes. Of the solar forces among others, we know of variations in sun spots, in sun prominences, in the amount of heat reaching the earth's surface, in electro-magnetic and perhaps other phenomena. The lunar forces are known to control tides, and variations in the depth of tides and in upheavals of cold water are supposed to affect the atmospheric pressure and so modify winds, cyclonic storms, rains and temperature. Variations in both solar and lunar activities are probably affected by yet more remote astronomical changes the nature of which has not yet been determined. It is an interesting conclusion to which we are drawn, namely, that in order to understand the organization of an animal community and its fluctuations in numbers, men must first understand the organization of the universe.

CHAPTER VII

AGGREGATIONS OF ANIMALS

WITHIN the ecological animal communities of the forest or prairie, ocean, lake or stream, there occur collections of animals, frequently in large numbers, which make up more or less organized units within the larger community. Frequently these are closely knit into compact societies such as those of the ants, bees, wasps, or termites; frequently also they are much less organized, such as loosely bound flocks of birds or straggling schools of fishes; and still more frequently they are even less closely knit together than are any of these. Such aggregations of animals, whether closely or loosely organized, serve as intermediate units between individual animals and the larger ecological community whose structure and organization have been discussed in the earlier chapters of this book.

Many of the same forces can be recognized in these aggregations of animals that are effective in the larger community, but here they act in a simpler way under less complex conditions. The interplay of life is full but on a smaller scale which is less confusing to observe. Here, for example, the animals themselves become the principal element in their own immediate environment; this is more truly the case for those individuals in the center of dense aggregations where they are literally surrounded by their fellows.

There can be no doubt concerning the importance of these animal aggregations in nature; the frequency of their occurrence precludes that. In favorable places along the sea shore every available habitat is crowded with animals as tightly packed as they can penetrate a soft substratum or hold on to a solid one. The surface waters of the ocean may be discolored for miles by starfish eggs or by shoals of tiny mollusks or crustaceans and a pailful of water dipped at random in favorable seasons may contain more jelly-like sea walnuts than water. Fresh waters are notoriously poorer in animal life than is the sea and yet even there suitable ponds are paved with the pebble-like clusters of salamander eggs in the breeding season, in the same way that suitable stream habitats are crowded with fish eggs. In a small stream in the Indiana dunes I once studied for over five months a series of aggregations of water isopods, each animal of which was smaller than a honey bee, but the whole mass can best be pictured by comparing it to full swarms from twenty or more well populated beehives which have settled near together.

On the land the story is similar; dancing aggregations of midges which appear like animated particles are well known to all country folk. Flocks of birds, herds of deer, hordes of lemmings and even concentrations of snakes are all well known.

The colonies of social insects have received particular attention. Near Chicago there is a mound-building ant which forms mounds from ten inches high and a foot in diameter to those three feet high and over seven feet in greatest length. The tunnels of such nests extend farther below the surface than the mounds pile up above it. These mounds are not scattered indiscriminately about but are themselves concentrated in two main localities. The largest of these contains 400 nests in a patch of oak woodland that covers only one-ninth of a square mile. 1200 colonies of another species of ant have been counted on a single acre of Manitoba prairie.

Many of these colonies contain great numbers of individuals; the eastern relative of the mound-building ant of the Chicago area has been calculated to average 10,000 individuals in a colony; its European relatives have from 30,000 to 100,000 ants and tropical colonies of termites have been estimated to contain 3,000,000 termite inhabitants, to say nothing of the numerous and frequently curiously modified insects that live with them in the same colony.

Such collections of animals must be considered in analyzing the larger communities of which they are parts. They also have significance in that they furnish transition stages between the loose community organization of which we have been speaking in previous chapters and the more closely knit social life which men and other highly social animals exemplify.

These aggregations of animals may be chance collections piled up by the waves as are those in the animal drift along Lake Michigan's shore line; as such they may be almost lacking in organization other than that of habitat and food web and the like which characterize the general ecological communities; or they may be actively brought together by the reactions of the animals to light, heat or food or to some other stimulus which serves to collect them in large numbers in a restricted area where conditions are favorable; or finally, they may collect as a result of positive reactions to each other, a sort of social drive which may be inherited along with body color or length of legs and if so is usually regarded as an expression of instinctive or in-born behavior.

The collections which show the greatest group organization belong in the last class.

Animals that collect in numbers in limited regions on account of their response to physical forces of the environment may do so because their own physiological processes in the presence of some stimulus such as light, cause them to make certain forced movements which result in aggregations forming as near the source of the stimulus (light) as the animals can get. This type of reaction is commonly called a tropism; in behaving so the animals orient and move as if they were giving a reflex action of the entire body. One of the best examples of this sort of behavior in nature is furnished by the minute freely swimming larvae of the *Arenicola* worm of our New England coasts.

The eggs are laid in a jelly-like mass at the mouth of a burrow on a sandy tide flat. The newly hatched larvae are positive in their reaction to light and move to the surface where they collect in great masses unless scattered by waves or tides. In the laboratory, their reaction can be controlled by pencils of light, and a careful study of their behavior shows that these minute swimming worms turn directly toward the light when it strikes one of their two eye spots and that they continue to swim toward it in a long spiral.

If another and stronger light is thrown on such a worm at right angles to its former course, it will turn immediately and swim directly towards the new source. There is no trial reaction in this process which seems to be as precise a mechanism as one would expect to find in as complicated an organism as a free-swimming worm.

Another, and indeed more common method of forming these aggregations, is shown by such animals as land isopods which, if the surroundings are dry, tend to collect in the more moist regions. These are found not by direct orientation and moving in a straight line to a nearby damp spot but by a sort of random movement which can but remind the observer of the human method of trial and error. Eventually this behavior results in the selection of the least stimulating spot which for these land isopods is usually the dampest place found in their wanderings.

When there is no difference in dampness in different parts of their environment and when it is not so dry that the isopods are so stimulated that they find it impossible to come to rest, then they tend to wander about until one of them stops for some reason unknown to a non-isopod and then in time all the rest collect on or near this quiet animal. After many have collected, some disturbance may cause the whole group to break up and wander off only to come together again later; or, if the disturbance is not too strong, the animals may be stimulated enough to move a tiny distance and then settle more closely together than they were before. After such a collection is formed, mere inertia may prevent its being disrupted by stimuli which would set less quiet individuals off into rapid motion. In such collections as these, and many others that might be named, the animals seem to be substituting each other for missing elements in their normal environment.

As the social appetite grows, animals may move about until by directed movement, more frequently, by trial and error, they find other members of their species with which they can aggregate. In the case of the common fresh-water fish known as the black catfish or black bullhead, the adult male or female stands guard over the eggs and the newly hatched fishes. After the adult fish has abandoned the young school, they still continue to aggregate into dense masses which mill about continually during the day but break up at night to come together again with early dawn. Field and laboratory studies show that these fishes will move towards any object they can see of about the same size and color as themselves.

When two such fishes move together on sighting each other, they move their sensitive barbels (which are tentacle-like processes that grow out from around the mouth) over each other and appear to get a definite chemical stimulus to which they react. If they have moved towards a black paraffin model of a catfish minnow, on touching it with the barbels, they move away apparently recognizing that the model is not the real thing. Their touch-chemical sense is not very sensitive for they apparently cannot distinguish other species from their own. They attempt to to push against a second fish whether of their own or of another species; if both are catfishes a mutual pushing results which, if many are present, leads to a dense group formation. If the second fish belongs to some other species, it moves away and leaves the catfish again alone. There is some evidence too, that even blinded catfishes can recognize the passing of another fish by the vibrations which it sets up and that they will turn and follow such vibrations.

With these catfishes, the groups at the outset are family affairs, but this condition soon changes, first usually, by the withdrawal of the female, then by the withdrawal of the male; with the young catfish groups, the daily separation and reforming of the aggregations brings in representatives of other family groups in the vicinity.

Unlike ants, these young catfishes readily accept strange minnows of their own species into their group even though they may be markedly different in size. This means that they form an open society as contrasted with the social organization of the ant family.

With ants the recognition of other members of the family-colony is usually by a contact-odor sense. Many ants are totally blind and even those with eyes frequently live in totally dark places. For all such it appears that theirs is a world of odor-shapes and spaces, just as ours is a world of color forms. Ants will attack and kill another that lacks the colony odor to which they are accustomed. The ants appear to learn which odor to accept, for observations have shown that if newly emerged, so-called callow ants are placed together, though they come from different species as well as from different colonies, and if for the first few days of their adult life, each is made to touch every other member of the artificially mixed colony with her antennae at least once a day, then this group will form a new unit and will attack outsiders that lack the nest odor to which they have become accustomed.

Relatively unorganized aggregations occur in nature most frequently as over-wintering collections; thus snakes collect in the autumn in favorable rocky hillsides and hibernate in numbers in the same locality where the greater heat of the rocks may be a factor in causing them to collect. Lady-bird beetles similarly collect in great numbers in favorable places and may occupy the same location year after year even though, to man, nearby unoccupied niches seem equally desirable. In general, as winter approaches there is a movement into the less exposed niches. Insects of the upper forest move down to the forest floor and insects and many other animals of the open field or forest margin move into the more protected woodland niches.

Many of the highly social ants and bees collect into dense clusters as winter comes on. The mound-building ants of the Chicago region almost completely desert the upper, exposed parts of their nests and collect in the lower passages just above the water line. Here they gather in great masses that may fill the branching passage in the hard clay so compactly that water cannot enter when the spring thaw raises the general water level of the soil.

In many cases no apparent benefit results from the collection of the animals in a restricted space in nature. They do benefit by living in the most favorable portion of their available habitat. When these favorable areas are limited in extent, then there is some advantage in being so constituted that the available space can be shared by others, perhaps by many others. Here we come upon one of the first steps towards the development of a closer social structure than the very general one that pervades all ecological communities; and we may call it the social level of toleration, mere toleration for the presence of other animals within the same limited space.

Another widely spread type of collection of animals in nature occurs with many species during the breeding season. Then animals which are ordinarily solitary, such as frogs, move into favorably located bodies of water where they collect in large numbers which are well advertised, to human ears at least, by the spring chorus of the males. The formation of such breeding aggregations is widespread in nature. Worms, insects, fishes, snakes, birds and mammals as well as less familiar animals are known to collect so.

In dry regions, even near Chicago in dry summers, many moisture-requiring animals aggregate together either in some damp spot or in a niche when the group may conserve the bodily moisture of its constituents. Such collections frequently show what is called "summer sleep" or aestivation, as opposed to the "winter sleep" or hibernation with which we are more familiar.

One of the most interesting of the aggregations of animals is that which occurs in the coming together of many species in the evening to form over-night aggregations, the members of which pass the night close together in a condition closely resembling sleep. The formation of such sleeping collections is more common than is generally supposed. We are well acquainted with the habit men have of collecting in groups in some sheltered place to pass the night; travelers arrange for shelter and in many lands the peasants return to the common village to sleep after their work in the fields. In a somewhat similar way the so-called solitary wasps may collect to the number of some hundreds in one locality. As high as a thousand such have been counted in a restricted locality and marked wasps have been known to return to the same spot to spend successive nights for at least two weeks. Males of certain solitary digger bees have the same habit.

Swarming locusts of several species are known to spend the night in dense masses both as wingless nymphs and later when they become fully adult, although the night clusters of the flying adults are not nearly so dense as are those of the nymphs. These aggregations frequently form conspicuous black patches which stand out against the vegetation. Butterflies representing both the least and the most highly specialized families of that order have the same habit. With all these insects, the collections formed over-night tend to remain together on the following morning until the day becomes warm. On dull, cool days, the groups may be found together in a state of lethargy well into the day.

Many birds form such nightly collections. Crows, robins, martins, blackbirds and chimney swifts are notable examples. Several different species may share the same roost for the night. The birds may roost so closely together that they actually pile upon each other; certainly on many occasions they tend to occupy much less than the total available and apparently equally desirable space.

Bats also come together in similar close-packed roosts. Hundreds may hang themselves to rafters or rocks so close together that their bodies are touching. With many birds the common roosts end with the breeding season or, if continued, they are not occupied by the breeding birds. With some, including robins, there is evidence that even during the breeding period, the males come together for their community roosts. The bats have the sexes segregated, at least during the period when the females are carrying or caring for their young.

At the low level of social development of many of these aggregations, the appearance of a social appetite is an intermittent phenomenon which may be awakened by the physiological changes that lead to the breeding season or by climatic changes that induce hibernation or aestivation. In many cases these exhibitions of a more than usually strong social appetite may be given only in yearly cycles. Some of the breeding aggregations of marine worms show monthly or, better, lunar rhythms, and the outbreaks of social appetites that lead to slumber aggregations, are awakened by the daily approach of nightfall. Such inconstant social appetites resemble in this respect the spasmodic appearance of sexual or food appetites. In more closely knit and better developed social communities, the action of the social appetite is more steady and therefore less spectacular than in its initial stages.

These aggregations of animals may be knit into co-operative units by various sorts of stimuli. One of the simplest methods is that of contact integration whereby a stimulus received by one animal causes it to start to move; its movement is sensed by a closely pressed neighbor and so the stimulus to motion is passed throughout the entire group. With earthworms, ants and other animals the integration by touch is aided by chemical stimulation which can be perceived only or mainly when the animals are in contact with the material that gives the chemical stimulus. With ants, for example, it is impossible to separate purely touch from purely chemical stimulation since the two are closely bound together and with earthworms, there is doubt whether they can perceive chemical stimulation of many sorts unless they are in contact with the stimulating agent.

Sight plays an important rôle in the integration of many aggregations which range from herds of mammals, flocks of birds and schools of fishes to the breeding collections of many frogs, where the males will attempt to clasp any moving object of about a frog's size which they can see. Similarly the well-established flashing in unison of fireflies appears to be set off by the synchronous flashing of some pace-setting individual.

Many of the activities of animal groups are regulated by low frequency vibrations which are perceived through the substratum while other groups are bound into working units by sounds carried through the air. Beebe has found that there is a close correlation between the development of vocal powers of tropical birds and the habitats in which they live. Relatively solitary birds that live in the open country where the view is undisturbed tend to have negligible voices and react to their fellows by sight, while those of the nearby jungle, where vision is distinctly limited, have remarkable vocal powers, with loud staccato calls or insistent rhythms. With many animals, including such widely separated forms as pigeons and men, the social integration depends primarily on the use of voice as a means of social control.

In this connection, however, a note of caution must be introduced. Animals may produce sounds which are distinctly audible to man without their having social or other importance to the animal that produces them. Thus it has been generally thought that the spring chorus of male frogs helps orient wandering frogs and brings them to a suitable breeding place. With some frogs, careful stalking of "singing" individuals through muddy swamps at night has been rewarded by finding that female frogs were also stalking the croaking male; in other cases there seems to be no connection between the extensive and far-carrying croaking of the frogs and migration to the breeding ponds. Such sounds appear frequently to have only a generalized value in that they stimulate the frogs to a pitch of excitement which results in breeding activities rather than directing migration to a given pond or of directly benefiting an individual croaker.

Many of the sounds made by apparently social animals may be an effect and not a cause at all. They may serve only as a reflex expression of a physiological state given in chorus because many individuals are in the same state of stimulation. Such an interpretation is indicated by watching grasshoppers "singing" on a summer's day. The chorus may be composed of hundreds of voices, yet there is no sign of any moving together or apart as a result of the noise produced. The sounds are made, in this instance, by the grasshoppers drawing the long hind legs over the horny upper-wing; this fiddling may be kept up for hours on a warm summer's day. Both the adult grasshoppers and the wingless nymphs as well, fiddle away endlessly. Yet the latter have no wings, and are producing no sounds, so that the social significance of the whole group performance is open to question.

CHAPTER VIII

PHYSIOLOGICAL EFFECTS PRODUCED BY AGGREGATIONS

Collections of animals into apparently unorganized crowds have been recorded for years, particularly in connection with breeding activities of otherwise solitary animals or with their hibernation. At times of drought great numbers of animals collect about favorable water holes, or they may collect in regions where food is plentiful or where shelter is abundant. Similarly for years it has been well known that many animals collect into closely organized flocks or herds which are able to protect themselves by the results of their social activities, either by structures they build together, as in the case of beaver dams, or by the protection furnished by multiplicity of eyes or of voices to give warning of danger, or of beaks, claws, teeth and hooves, to furnish active protection from enemies.

Little or no connection was thought to exist between the two sorts of aggregations because, breeding season aside, crowding has been demonstrated again and again to have ill effects on crowded animals. Thus snails and many other animals grow more slowly and produce stunted individuals if crowded. Fruit flies and common hens reproduce less rapidly if crowded than if given plenty of space, and many animals including Protozoa, certain beetles, small crustaceans, mice, rabbits and men have a higher death rate under crowded conditions. The warning from these accumulated experiences is needed; but the work of the last decade and a half has demonstrated that this is not the whole effect of crowding; some of this newer evidence furnishes the subject matter for this chapter.

Many different animals have been found in the laboratory to use less oxygen per individual if they are present in small numbers than if isolated. Goldfishes do not form schools but when four of these are placed together in about a liter of water, they consume less oxygen per fish than if the same four are isolated and each put into the same amount of water. These relations hold whether the fishes are in quiet or in flowing water. Similarly groups of serpent starfishes in the early stages of such experiments, groups of water fleas, isopods and frog tadpoles have the same sort of effect upon the rate of oxygen consumption of the individuals that compose the groups. It is as though the group exercises some sort of soothing effect upon the members that compose it. All these records are for animals which are not generally regarded as being social.

The case of the serpent starfishes is illuminating. When similar lots of these marine animals are placed so that half are grouped and the other half are isolated, each individual being exposed to the same quantity of water, the grouped animals use less oxygen in the early stages of the experiment than do the isolated ones. As time goes on and the animals are kept without food, the isolated animals come to have a higher rate of oxygen consumption and finally mutilate themselves by fragmenting their arms sooner than do the grouped individuals. In the early stages of such an experiment, the starfishes are using less oxygen if grouped and in the later stages they use more. The rate of oxygen consumption falls with the process of starvation both for the isolated and the grouped starfishes but more rapidly for the former which first lose the ability to keep themselves intact. After a period of starvation the grouped starfishes are definitely in better condition than if they were isolated. Such conditions hold when the animals are not in the breeding season. During the time of breeding activities it is impossible to predict the relations between oxygen consumption and grouping, the more so since one cannot tell the sexes apart by simple inspection.

Similarly with the water fleas widely known as *Daphnia*, the grouped animals consume less oxygen than do similar isolated individuals. On analysis it appears that the lower rate of use of oxygen by these water fleas is due to the accumulation of carbon dioxide which acts as a depressing agent and so lessens the consumption of oxygen. Under certain conditions such a state of depression turns out to be of benefit to the grouped animals. If they are exposed to fairly severe concentrations of various salts, the grouped individuals will survive longer than if they are isolated. Chemical analyses show that with salts, the grouped Daphnias do not remove the salts from solution but that their increased resistance is due to the fact that they do not respire so rapidly as do their isolated fellows; hence they are making smaller demands on their environment and so are able to live longer under adverse conditions.

On the other hand, if the concentrations of salt solutions were made very low so that the most vigorous animals could become adjusted to their presence while the less vigorous ones are unable to so acclimate themselves, then the isolated animals with the higher rate of general metabolism lived longer.

Grouped fishes in the presence of a poisonous material such as colloidal silver are able to remove the toxic silver from the suspension and survive, when isolated fishes are unable to do so, and perish. Chemical analyses show that the grouped fishes protect themselves because of the adsorption of the silver on the slime which they secrete. Such group survival is most clearly shown when the volume and the concentration of the harmful colloidal silver is the same for the grouped that it is for each of the isolated fishes. Under these conditions the group gives off more slime than can a single isolated fish, hence more of the toxic substance can be removed.

Animals in nature may be called upon to encounter exactly such a set up. In a given pond, the entire fish population whether it consists of one or of many would be exposed to the same total amount of toxic material if any were present. In the presence of many fishes, each one would receive a dosage of the poison which might be insufficient to cause its death, while if only one were exposed to the whole amount of poison, death might certainly result. A similar clearing up of poisons by groups of animals has been demonstrated for many other kinds of animals and appears to be a widespread phenomenon in nature.

Unlike animals are able to protect each other in this respect apparently as effectively as similar forms. Water in which fresh-water mussels have lived and into which they have secreted slime will protect fishes and other animals from the harmful action of some poison as effectively as will the presence of other fishes.

The physiological effects of groups of fishes even in non-schooling species do not end with respiration and survival effects. Experiments have shown that four goldfishes will learn a simple maze more rapidly than will isolated fishes. The experiment is run in this way. A series of small glass-sided aquaria are set up each of which contains a heavy wire partition in the form of a cone with the apex replaced by a sliding door. The door is large enough for more than one fish to swim through side by side. The fishes are placed in the larger part of the aquarium with the cone-shaped partition pointing toward the forward and smaller end where the fishes are to be fed. The fishes are trained to come through the door in the funnel and be fed when a red light is turned on.

In some experiments eight fishes were placed in such an aquarium, four were placed in two others, two were put into four more and eight more similar ones were isolated into eight additional tanks of the same size. In all cases where this experiment has been tried, the isolated fishes learn to come through the opening more slowly on the average than do the grouped fishes; the twos react more slowly than do the fours but there is no essential difference between the larger groups tested. In all cases, once the fishes have learned this simple maze, they react more steadily if a small group is present than if the individuals are isolated. These are, so far as I know, the first experiments to be reported upon the effect of class size upon the rate of learning in a school of fishes and they show quite clearly that in non-aggregating goldfishes, up to a given number at least, the group learns more rapidly than does a single animal.

While this result is uniformly obtained with a set-up such as has just been described, it does not follow that the same results are to be expected from all sorts of experiments upon the effect of numbers of fishes present upon the rate of learning. In our earlier experiments on this subject, mud minnows were trained to jump out of water about a half inch in order to obtain a bit of worm held there under a red light. If four fishes were present the number of responses was much reduced, in fact, at times, no jumping would occur. The isolated fishes readily learned this problem and would continue to jump even when the wire loop held only tasteless filter paper in place of the usual worm.

The group behaved thus: just as a fish would be moving up preparatory to jumping for the food, another fish, or more than one would approach, all making the same preliminary motions which if they had been alone would have led to a jump for food. When they came near together, however, they turned their attention to each other rather than to the food and pushed or gave other indications of a combat and so did not jump. Jumping under these conditions rarely occurred unless the fish chanced to be relatively alone. It is apparent that even with fishes, the effects of numbers present on the rate of learning depends in part on the problem set and there is good reason for thinking that it also depends on the sort of fishes that is being tested.

There is good evidence also that groups of these fishes eat more than would the same individuals if they were isolated. These effects are apparently the result of a certain more or less nebulous sort of group solidarity which reaches a much higher state of development in the schooling species. Incidentally it is worth recording that with the black catfishes that form close aggregations when they are young, the grouped fishes consume more oxygen per individual than do the isolated animals. Under these conditions the outer catfishes are continually pushing in toward the center of the group and consequently use up more oxygen in the course of their greater activity. Again it is evident that the type of the response obtained depends in part on the behavior of the different species of fishes under the stimulus furnished by being grouped together.

Many pond and aquarium fishes grow best in relatively stagnant water. If such fishes are subjected to daily changes of water so that their relatively large aquaria are almost constantly full of relatively uncontaminated water, the fishes do not grow as rapidly as when they are put into water in which freshwater mussels have lived for at least 24 hours. It is known that such mussels give off slime into the water and that this slime has some food value for associated fishes but the fact remains that after such mussel-conditioned water has been filtered to remove the slime it still has greater growth promoting power than has plain well water also allowed to stand in similar vessels for 24 hours and similarly filtered. It is known that the mussels change the chemical content of the water and that they affect the bacteria present. It is also known, however, that fish will not grow in this mussel-conditioned water if they are not fed and that they will starve to death in practically the same time as if placed in unconditioned water.

Similarly salamander tadpoles will grow more rapidly in such conditioned water than in raw, unconditioned water and both fishes and tadpoles will regenerate tails that have been cut off more rapidly if several fishes or tadpoles are present together than if they are isolated in the same volume of water. Evidently in these last cases the exudates from the cut tails condition the water so that the wounds heal more rapidly and growth takes place faster than if one animal must do the whole conditioning by itself.

As has already been stated it is easy to demonstrate that crowding, especially overcrowding, decreases the rate of growth of crowded animals. Even in this field more recent experiments have shown that the common fruit-flies, much used in experiments on heredity, grow larger in small culture vials when present in numbers of from eight to sixteen than at other population densities either smaller or larger. This is usually explained by suggesting that with too few flies present, harmful sorts of yeasts and bacteria which are usually present in the culture media are not kept under control; but with about eight to sixteen flies in the cultures, the number is about right to control these "weeds" without exhausting the food supply or without unduly increasing the concentrations of excretions to a degree that would be harmful. As the population increases beyond the optimum, both these latter factors act to retard growth.

With these same fruit-flies, other investigators have found that adult flies will live longer in one-ounce bottles with a standard amount of food, if from 35 to 55 are present than if either more or fewer than that number are used. This again shows that there is an optimum population for survival which is well above the minimum population and well below the maximum population possible. Again despite the well known harmful effects of crowding on the rate of reproduction, with the one-celled protozoans and with certain larger animals as well, we now know that the rate of reproduction is greater per individual under certain conditions if more than a single animal is present in the case of the asexually reproducing protozoans or if more than one pair is present with certain sexually reproducing beetles. In both cases the numbers of animals present must stand in the proper relation to the size of the environment if the rate of reproduction is to be stimulated by optimal crowding.

The common *Paramecium* (Fig. 6) is a protozoan that can readily be seen with the unaided eye; it reproduces asexually. If similar individuals are isolated or are placed in groups of two or more in a small drop of culture medium, the isolated individuals will divide more rapidly from the start of the experiment than will the two or more Paramecia crowded together in the same small drop. With larger amounts of medium, say approximately one or two cubic centimeters, the early division rate of each animal is greater if more than a single individual is present.

These animals change the medium in some manner not yet understood so that single individuals isolated into the conditioned medium will divide faster in the early stages of the culture than will wholly similar individuals isolated in wholly similar media which have not previously contained other individuals, provided, of course, that the volume used is sufficiently large.

Similarly with the flour beetle *Tribolium* (See Chapt. VI) which flourishes in ordinary flour, independent experiments in three laboratories have shown that two pairs of beetles introduced into 32 grams of flour reproduce more rapidly in the first 11 and 25 days of the life of the new population, than does a single pair on the one hand or a greater number of pairs on the other. In some experiments 16 pairs and even 32 pairs were found to reproduce at a higher rate per female during the first 11 days of the culture than did the female of a single pair isolated into the same size of environment. The rate of reproduction in such populations is shown in Fig. 10.

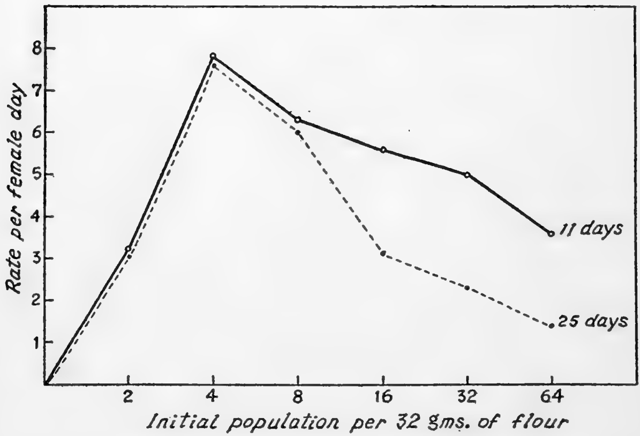

Fig. 10. *Tribolium* beetle populations increase more rapidly at first if more than one pair is present in 32 grams of flour. "Rate per female day," shown on the vertical axis, really means rate of population increase per female beetle per day. (From Allee, *Animal Aggregations.*)

Later, with increasing age of the culture, the rate of population increase decreases with the higher concentrations of beetles until finally the populations in the different cultures become approximately stationary, as was shown in the preceding discussion. The factors involved in this interesting demonstration that the minimum population density is not the most favorable for rapid rate of reproduction in early stages of population growth, still await discovery. The problem is being investigated in at least one laboratory at the present time.

Another type of group protection deserves comment. In the cases given above, the group was able to protect the various individuals of which it was composed by removing some harmful substance or by so distributing the poisonous material that no single individual received a full death-dealing dose. Group protection may also be given when the lack of necessary elements in the environment is causing death. This condition is found when marine animals are put into fresh water. Ordinarily they are accustomed to living in sea water with a salt concentration of about 3.5 per cent. Many die rapidly when transferred to fresh water.

Two different types of simple animals known as flatworms have been shown to survive longer if many are present than if but few individuals are placed together in the fresh water. These experiments have been carried on by different investigators on both sides of the Atlantic. In one lot of these experiments the amount of salts

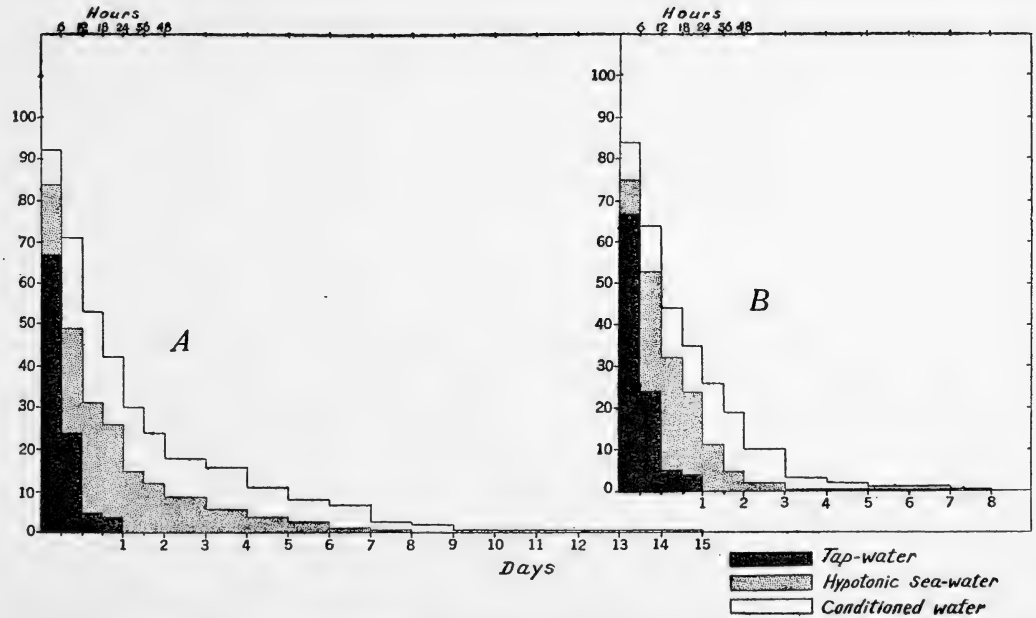

FIG. 11. Marine *Procerodes* flatworms live longer if isolated into conditioned fresh water in which other animals have lived than if isolated into extremely dilute sea water with similar salt content. (From Allee, *Animal Aggregations.*)

present was carefully checked and controlled. Individual worms were isolated into separate dishes containing various sorts of water and their survival time was determined. Results from such a test are graphically shown in Fig. 11.

In this figure, the solid black columns give the length of survival of marine flatworms isolated into ordinary tap water. The total height at any part of the figure shows the survival of similar worms placed in the same amount of tap or pond water in which other animals had lived, died and disintegrated, or which had been otherwise conditioned by association with living animals. The stippled part of the diagram which lies between the solid black and the open squares, gives the survival of similar worms in very dilute sea water which had the same amount of salt as did the conditioned water. The height of the figure at any point shows the percentage of worms living at that time; the horizontal line gives time in days except that the first 36 hours are divided into 12-hour periods.

The protective, conditioned water could be made in various ways. One of the most effective was to prepare a sort of worm soup from the marine flatworms themselves and to place this in a collodion bag in distilled water until the salts diffused out. Similar extracts of other marine or even of fresh water animals gave almost as good results; even the culture medium in which Paramecia had lived proved to be generally effective. It is sufficient to record here that the experiments showed that the conditioned water does definitely protect the worms exposed in it so that they live longer than if they were placed directly into untreated fresh water. Just how the animals conditioned the water to secure this beneficial result is not known. It is known that the protection furnished by these conditioned solutions is about the same as that furnished by a sugar solution that exerts an osmotic pressure of about five atmospheres; yet the medium itself exerts no osmotic pressure.

The flatworms tested in America are called *Procerodes*. They live near the low-tide regions under stones which may be washed by fresh water if heavy rains fall at times of ebb tides. They live in small natural clusters although each individual worm is distinctly separate. Such clusters cover the stone's surface to an extent equal to the size of a half-dollar or less. In the laboratory they collect in great numbers about the edges of stones where they come into contact with the bottom of the aquarium. Whatever other significance these aggregations possess, they do have the possibility of giving their members greater survival in the occasional times of stress brought on by a flood of fresh water at low tide.

Many other beneficial effects of crowding could be given. Massed spermatozoa live longer and retain their ability to fertilize eggs longer than if they are relatively isolated. Bacteria, if present in numbers, are frequently able to live and multiply in the face of adverse conditions which kill off isolated cells. Thus *Bacillus coli* of a strain sensitive to gentian violet will grow in mass cultures in the presence of the harmful dye. Inoculations of thirty cells will survive and flourish under conditions which kill off single individuals or smaller groups. The evidence shows that thirty such bacteria living together are able to accomplish more work than can thirty similar, isolated cells and this excess ability of the bacteria when growing near each other has been attributed to the communal activity of the bacteria.

The facts presented in the present hasty survey of some of the values that arise from aggregations indicate that such groups of organisms have the possibility of becoming what is commonly called "social." To be sure, they must possess other attributes. The mere existence of an aggregation implies that the collected animals have tolerance for the presence of others in the same limited area, and that they have reaction systems that allow them to aggregate or to remain together if passively collected. To develop social groups of higher order other qualities are needed, particularly the ability to establish close group integration. The facts show that not all animals whose groups show survival values are necessarily on the way toward becoming more closely social, but that animals, whatever their endowments, could not have developed the social habit had the incipient social stages lacked the type of survival values which has been repeatedly demonstrated for different animal groups and even for spermatozoa and bacteria.

CHAPTER IX

STRUCTURAL EFFECTS PRODUCED BY AGGREGATIONS

THE structure of animals is relatively hard to change. Environmental effects are more likely to be shown by animals as changes in behavior or in other physiological processes than as changes in bodily structure. In plants, on the other hand, such modifications readily appear as structural changes; for example, the growth-form of trees and shrubs depends in part on whether they grow in open or in crowded conditions. With sessile animals, similar growth-form changes occur as a result of crowding. The sea-mussel, *Mytilus*, has one shell-form if it grows in an isolated region and an entirely different one if it is crowded. Similarly many other marine animals, barnacles, ascidians, sea anemones and sponges are more slender and elongated if they grow in dense clusters than if they grow relatively alone.

Two of the most fundamental properties of living things are their organization along an axis and their sex. Not all organisms are sexual although most of them are, but almost all show some sort of an axial organization. In its simplest terms the main axis of an animal is that which runs from the head through the tail. Other axes may be present which are secondary to this primary axis. According to modern theories of heredity, each cell of a plant or animal receives similar chromosomes bearing similar genes, as the bearers of hereditary qualities are called. According to these theories, each cell from one end to the other contains the same sort of hereditary material. Something must work on this common heredity to cause one end to develop into a head and another into a tail.

In the marine plant, *Fucus*, one of the large marine algae, the determination of the axis is definitely under the control of environmental forces. Ordinarily when the eggs of this plant are uncrowded, the axis is determined by exposure to light and the end which is exposed to the action of light becomes the most rapidly growing, apical end. If, however, *Fucus* eggs are in darkness and are somewhat crowded together, that is if they are within 0.02 mm. of each other, then the part of the egg most nearly free, forms the apical end. Under these conditions the position of the egg with regard to its nearby neighbors determines which end will become free and which will be attached.

Other cases are known in which sex, a second fundamental property of organisms, is determined by crowding. It will not be feasible here to review all the known cases and the following brief account must suffice: *Bonellia* is a marine worm which lives in restricted regions in the Bay of Naples. The two sexes differ decidedly in appearance. The female is fairly large, three inches or so in length with a long, extensible proboscis at the anterior end. The males are minute flatworm-like animals about a millimeter in length and are totally different in appearance from the females. The female has a large body cavity with a well developed alimentary canal. The male lacks the proboscis and its reduced alimentary canal is without an external opening. It lives as a parasite within the uterus of the female.

The eggs develop into freely swimming larvae which at first are sexually indifferent. If these swimming larvae come into contact with a female, they settle upon the proboscis and start developing as males. After a few days in this position, they enter the alimentary canal of the female and continue their development for about two weeks, after which they make their way to their final position as parasites within the uterus of the female. The developing male takes no food during its life on the proboscis but lives on the yolk that has been stored in the egg. In the later stages of its life it has the parasitic habit. There is good evidence that the developing male receives some material from the proboscis of the female which starts it going in the male direction. The female does not need to be mature in order to exert this influence and even the female proboscis alone or extracts of it will have the same effect.

If the young, neuter larvae do not come into contact with a female, they remain indifferent for some ten to twelve days and then begin transformation in the female direction. This peculiar lability of sex in *Bonellia* has survival value for the species. The worm is not abundant even in the Bay of Naples, where it occurs in numbers in but a few places. If the sexes were unalterably determined at hatching in the usual 50–50 sex ratio, then the males must needs find a female before they could function and there would be considerably greater loss from isolation than now occurs. When the larvae first hatch, they are positive to light and swim away from the egg mass. There is evidence that they do not attach to their own mother although they may attach immediately to a neighboring female. If they fail to find a female during this free swimming stage, the chances of which are greater than if there were but 50 per cent females strictly determined at hatching, then they transform into females and are able to effect development of an indifferent larva into the male needed for fertilizing their eggs, if one comes near.

The outline of the development of sex in the American marine snail, *Crepidula*, is essentially similar. These almost sessile mollusks live in the shells inhabited by hermit crabs. If a young neuter animal settles near a larger one, whether the larger snail is male or female, the small neuter individual develops into a functional male. If later the larger individual is removed, the smaller animal reverts to an indifferent stage and then develops into a functional female. If the neuter animal settles in an unoccupied shell, it develops directly into a female. The causal factors are not so clear in this case as with *Bonellia* but the survival values of the case are practically identical.

In nematode parasites of grasshoppers and other animals, if there are many parasites present in one host, all or the great majority tend to be males; when few are present, the majority are females. The causal relations here are not understood.

With water fleas, relatives of *Daphnia*, the whole group of which is commonly called Cladocera, the whole sexual history is different. These animals are most abundant in ponds which become dry in summer. Their life history runs as follows: A resistant winter egg hatches out in the spring into a female which is capable of reproducing without being fertilized by a male. She is a parthenogenetic female; her eggs will develop without fertilization. The young produced are all females and are parthenogenetic like their mother. This may go on for many generations and then an epidemic of sexuality appears, males and sexual females occur. The latter produce eggs which must be fertilized for development to take place. These are the so-called resistant or winter eggs, and after a period of quiescence which may last over the period that the pond is dry in summer or during the period that it is frozen in winter, this egg hatches into a parthenogenetic female and the cycle continues.

All the causes of the appearance of sexual forms are not yet clear but recent work has shown that the crowding of the parthenogenetic mothers tends to produce a high percentage of males at times when uncrowded sister cladocerans are continuing to reproduce parthenogenetically. The mechanism whereby crowding results in the production of males is not known with certainty but there is good evidence that the reduction of available food will have this effect. The suggestion that a high concentration of excretory products has the same effect also has value and, in fact, further researches may show that any condition that tends to reduce the rate of metabolism of the females at critical periods will increase the percentage of males produced. As we know from work reported in the last chapter, crowding these animals does have such an effect.

A somewhat less important change in body form is illustrated by the effect of crowding upon wing production in the plant lice commonly called aphids. These aphids are small, usually greenish bugs which push their beaks into juicy plant tissues and obtain their food by sucking the juices of their host plants. Their usual life cycle runs something as follows: In the autumn a sexual form appears and an over-wintering fertilized egg is formed which hatches out the following spring as a wingless female capable of producing young without fertilization, that is, like the cladoceran females, she is parthenogenetic. Her immediate offspring all tend strongly to be parthenogenetic females like herself. These reproduce very rapidly; the young settle near their mother and soon produce a crowded condition on the host plant which may lead to the withering of the plant. About this time winged, parthenogenetic females appear which can and do migrate to other neighboring host plants and start a new colony of wingless, parthenogenetic, female aphids. After one or more such transfers, males and sexual females appear as in the Cladocera and resistant eggs are formed which serve to carry the colony over such adverse conditions as the winter season and the like.

The cause of the appearance of truly sexual forms in these aphids is not yet fully known, but there is much good evidence that the appearance of winged forms may be influenced by decreased temperature and by decreased illumination but in some species at least, the production of wings follows over-crowding closer than it does any other environmental factor. Many investigators have reported wing production following crowding in different species of aphids. In one case 59 generations of *Aphis* were reared without any winged forms except in three cases when the aphids became crowded. This experiment lasted a full year. In the species used, decrease in temperature or in light intensity would not produce wings but in every case they apparently followed directly upon the crowding of the wingless mothers. At various times sub-cultures from the uncrowded experiments were allowed to become crowded and winged forms invariably resulted. Crowding appears to be proven to be a potent and perhaps the dominant factor in controlling wing development in this species of aphid. The survival value of this arrangement is immediately apparent when one remembers that the winged individuals are capable of migrating through the air to new host plants and hence can keep the colony alive by such transfers after conditions become crowded and the original host begins to fail.

Other bodily changes are produced in different animals as a result of crowding. The marine ascidian, *Salpa*, exists in two distinct forms, the asexual, solitary, cask-like form and the crowded sexual salpa chains whose individuals, apparently through crowding, have lost their barrel-like form. Crowded snails are not only smaller than non-crowded ones but if the crowding is extreme, other physical changes are produced as well. The male organs may be suppressed, the liver becomes smaller in proportion to the other organs and the shell proportions are so changed that experienced experts in the identification of snails recognized the dwarfed forms as sufficiently distinct to be placed in a distinct species from that of their uncrowded relatives.

The recent mass of careful work in the culture of the common fruit-fly, *Drosophila*, in the course of studies on its heredity, have shown that overcrowding is one of the three main causes of disturbance of expected ratios of different sorts of offspring. If the larvae of such carefully selected, pure-bred flies are over-crowded, differences appear not only in weight and length of the whole animal, which would be expected, but also in the proportions of body parts. The number of facets in the eyes, the number of hairs, the number of teeth in the "sex-comb" of the male, are all affected by crowding. There is some evidence that too small a population of flies produces some changes similar to those produced by population numbers above the optimum. In general it has been found that unless at about their optimum population, it is unsafe to draw quantitative conclusions concerning the effect either of hereditary or of other environmental factors.

From this evidence it is apparent that profound as well as superficial changes in bodily structures of animals as well as of plants may be produced by crowding. Taken together with the findings reported in the preceding chapter, we are prepared to support the contention of other research workers that: "In general there can be no question that this whole matter of influence of density of population in all senses, upon biological phenomena, deserves a great deal more attention than it has had. The indications all are that it is the most important and significance element in the biological as distinguished from the physical, environment of organisms."

CHAPTER X

THE HIGHER SOCIAL LEVELS

WE HAVE seen that all animals and plants live as members of more or less loosely integrated communities; that within these communities aggregations of animals occur, frequently of considerable numbers and at times fairly well organized as social units; and that such collections, even though unorganized, may exert profound influence upon the behavior and even upon the structure of the animals which compose them. There remains the question of the relation, if any, between such communities of animals and those which are regarded as being definitely social.

Here we come upon a considerable difficulty. What is meant by the term "social animals"? Deegener, of the University of Berlin, answers that societies are communities of similar or dissimilar animals which have a real value for the individuals composing them; in other words, any grouping that shows survival values, he would regard as being social. Alverdes, of the University of Halle, would limit societies to those groupings which are caused by the animals reacting to a definite social instinct; no social instinct, no society, would be his statement. Wheeler, of Harvard, in his earlier writings regards insect societies as the result of the extension of the time of affiliation of two or more generations; more recently he has defined societies as constituting more closely integrated and permanent systems than are mere associations and primarily dependent on the reactions of individuals to each other. Some students of social life are inclined to regard true societies as limited to those communities that show division-of-labor. I, myself, have been led by reviewing such facts as have been presented in this volume to the view that one of the first steps toward the development of definite social life is taken when groups of animals acquire definite toleration for the presence of other animals in a restricted space.

It appears that there are many different levels of social organization, any one of which can be taken as the beginning of true social life and anything less advanced in the social scale would then be regarded as being sub-social. If any of these different criteria is examined closely, it will be found that there are recognizable preliminary steps with more poorly developed social organization which appear to furnish evidence of social evolution. The principle of division-of-labor is a useful tool in describing certain levels of society but below these levels, as generally recognized, we have found in the community organizations discussed early in the present book, that there is a division of labor between plants as photosynthetic machines and the animals as consumers. With the animal constituents of the community, there are the key industry animals that feed upon raw plant food and make it available, in the form of their own flesh, for the consumption of others. With all sexual animals everywhere, there is a definite division-of-labor between the sexes, so that if this criterion alone were strictly applied, all such animals must be regarded as being definitely social.

Similarly, if we examine the frequent limitation of societies to those groupings which consists of a consociation of parents and offspring, we find that these begin with the partial parental care of eggs such as is given by certain male fishes that pick out and stand guard over a definite location in a brook; into this holding females may come and go, each contributing a share of the eggs, while the male stays by, guarding the eggs from enemies until such time as his drive towards breeding activities ceases, when he abandons the formerly carefully guarded eggs to their fate. Recognizable steps of increasing parental care can be traced from even more humble beginnings through different stages of increasing length and degree of protectiveness to their culmination in the extreme human cases where a doting father may provide trust funds for his children in attempted perpetuity.

With this criterion, or with any other suggested for limiting social life, there are difficulties in application. The young nestling birds and their parents, according to this definition, are members of a social group as long as they continue to live together; but if, as in the case of the cowbirds, the young are hatched and reared singly as social parasites in the nests of other species, then the compact flocks which such birds form by the collection of these nestlings which were reared in isolation from others of their species, would not be considered a social group although otherwise it presents all the characteristics of a closely integrated bird flock. The difficulties of precise definition are great for one who tries to delimit the more closely knit societies from their loosely organized forerunners.

One of the most easily applied tests of the degree of integration of a social group is the extent to which the animals co-operate with one another to accomplish a common end. There is good evidence that many of the beneficial effects of relatively unorganized aggregations of animals are the expression of a vague, unconscious mutual co-operation and that the principle of co-operation should rank as one of the major biological principles comparable with the better recognized Darwinian principle of the struggle for existence.

Let us trace briefly some of the steps in the development of group co-operation from its incipient stages such as were suggested in the earlier chapters to the conditions found in closely knit social organizations. In doing so, we shall of necessity see much of the development of the principle of leadership in animal societies. Such a development invites comparison with the evolution of co-ordination and of leadership in individual animals at different levels of their organization.

The generalized ecological animal communities have a more or less loose organization that is not definitely pointed in any direction. In such communities the process of "muddling through" is the only one that seems to apply. There is interaction between the different biotic elements in the community with each other and with the physical environment, with now the biota and now the physical elements in the ascendency. Such blind interactions are well illustrated in the early stages of the forest evolution on sand dunes. Now the animals and plants of the growing forest community may gain the ascendency over the shifting sand and a stabilized dune is formed which by the action of the wind, may escape from captivity and start moving across country, burying all in its path.

The organization of such a community reminds one of that of a simple animal such as an *Amoeba* (Fig. 8). These shapeless lumps of protoplasm, microscopic in size, move about now with one part in advance, now with another. They send out pseudopodia from one side or another which temporarily become the anterior end of the animal. The location of such pseudopodia depends, in large part at least, on the external stimuli that reach them. Many of the animal aggregations exhibit a degree of social organization roughly comparable with the physiological organization of an *Amoeba*.

A higher stage in physiological organization is reached when, as in the radially symmetrical jellyfishes, any part of the circumference can move ahead, or the animal can move as a whole in the direction of its aboral pole. Such animals have a set of so-called sense-organs about the margin of the jelly-like disc, each one of which lies at the end of a radius that is similar to any other sense-organ-bearing radius of the animal. These different sense-organs act to originate nervous impulses which cause the rhythmical pulsations by means of which the jellyfish moves. Any one of these marginal sense-organs may temporarily become dominant over all the others and so control the rate of rhythmic pulsations. The dominant organ is the one which is acting most rapidly at the time; it becomes the pace setter for the whole pulsating region of the animal's body. When it slows down, another of the potentially equal sense-organs with a higher rate of action becomes in turn the pace-setter and hence is the leader in the pulsations.

With animal aggregations a similar degree of development of leadership can be recognized. For example, there are aggregations of fire-flies that flash in unison. In one such lot which occupied a valley near Ithaca, N. Y., the observer was able to recognize the pace-setting center of flash origin for the fire-flies of the whole valley and by using his pocket flashlight, was able himself to assume control of the rate of flashing, as shown by his ability to speed the flash-rate above the normal period shown when the fire-flies were left to their own pace.

Similarly, the great aggregations of harvestmen often called daddy-long-legs, which may be found in the deep shadow of an overhanging brook-bank vibrate in unison their pea-sized bodies on their long thread-like legs. The initiation of the vibration appears to come from some part of the aggregation which is excited by the near approach of a stimulating object such as the finger of an inquisitive naturalist. Now one, now another part of the aggregation may assume the lead in setting up and maintaining the vibration rhythm. The stimulus to vibration in this instance is passed from body to body through the interlocking legs of the harvestmen.

With animals somewhat higher in the evolutionary scale than the *Amoeba* or jellyfishes, one end becomes set apart as the anterior region. This end meets the new and stimulating elements of the environment and comes to carry the greatest localization of sense-organs and of nervous tissue. In other words it becomes the head of the animal. For some reason the head develops at the end of the animal which has the highest rate of metabolism and as a consequence of its structure and physiological activity, it is the dominating region of the animal. With the evolution of a definite head, individual animals have developed definite and localized leadership for the rest of the body.

Similar localized leadership frequently occurs in groups of wild or of domesticated animals. In my boyhood, I remember the definite organization of our home-grown herd of dairy cattle which it was my duty to drive back the narrow Indiana farm lane to their woods pasture. If no bull was present the position of leader was held by the oldest cow of the lot and after her came the junior members in the order of their ages until at the rear the calves and young heifers that had not yet established their herd order were to be found. I remember with satisfaction the slow progress of a small black half-Jersey from the position of most hooked, least regarded member of the herd, to her rank as leader where she put cows half again her size into place by a shake of her head or at most a few prods of her sharp horns. Usually her authority was unquestioned.

Oddly enough some twenty years later I was to find the same sort of organization in the faculty meetings of a famous New England college. At the head of the group in a large, high-backed chair sat the president looking down the table to his dean seated in a chair not nearly so large and impressive. Around this table in order of seniority sat the professors in comfortable even though low-backed arm chairs. Back of them, again in order of seniority sat the associate and assistant professors but in hard bottomed Windsor chairs; while at the foot of the table in hard, uncomfortable "kitchen" chairs sat the instructors who were supposed to be present but were not to take part in the discussions unless asked to do so.

Such societies are called "open societies;" that is they will receive new members but they are obviously definitely organized. Similar organizations are common among animals; the leader may be an old female, as in the case of wild reindeer, or an old male as with the baboons. Herds of giraffes may be led by either a male or a female who accepts the post of danger, or directs group activities, or both.

In other animal groups leadership may be expressed by the arrogation of certain rights and privileges. This is very well illustrated in the organization of a flock of domestic hens. Such groups, again, are an open, not a closed society but the newly admitted members must fight for any privileged standing which is accorded them in the community. The ranking of the hens is indicated by their reactions when another member pecks or threatens to peck them. A given hen will submit to pecking by certain individuals without showing resentment, and will in turn treat others similarly without their making protest. Hens with such power are said to possess the "peck right" over those submitting to the pecking and the group is said to be organized according to the "peck order." The ranking is obtained by combat or by passive submission and newcomers can escape the bottom ranks only by fighting.

The "peck order" within a given flock may be a single series in which "A" pecks "B" which pecks "C" which pecks "D" and so on to "Z" which is pecked by all above. In other cases the order is complex. "A" may have the "peck right" over "B" and "B" over "C" and "C" over "D" which, oddly enough may have the right over "A" gained in some encounter when "A" was ill or otherwise below par. A revolt or a fight may upset or confirm the existing order. It is usual, however, for birds inferior in the "peck order" to fight less fiercely against those high above them than they do against those of approximately their own rank or lower. It is also generally true that a hen that stands high in the "peck order" is less likely to be vicious in her attacks on those below her than is a hen standing relatively low in this order.

Hens with chicks are more likely to revolt successfully against their positions in the flock organization than are those without or the same hen when her chicks are removed. A cock introduced into the flock stands at the apex of the "peck order." High position in the flock involves the right to peck without being pecked in return, to eat without being disturbed by those of lesser rank and bestows general independence from social interference. Other birds are said to show essentially similar flock organization.

In other bird flocks the leadership may be apparent rather than real, reminding us of certain human situations particularly those in the political field. Observations on some such flocks near Great Salt Lake suggested that the rôle of leader of the flock in flight is taken by the fastest flier who did not exercise real leadership as shown by the fact that the flock frequently turned leaving the apparent leader flying away by himself. At times it appeared that under such conditions the "leader" would turn and wing his way rapidly through the more slowly flying flock and again reach his former advanced position. Since the birds were similar and were not marked, one could not be sure of the facts. Recently, however, observations have been made upon Atlantic shore birds which corroborate the description just given.

Flocks of such birds flying in close formation frequently wheel in seeming unison as though each individual were simultaneously motivated by a common impulse rather than that he adjusted himself to the movements of his fellows or of one of them. In one specific case a mixed flock of shore birds made up mainly of dowitchers and blackbellied plovers included a single golden plover. When the mixed flock was flushed, the golden plover was found to be the fastest so that it was soon in the position of a leader out in front of the flock. The flock behind might wheel leaving the golden plover to itself; on sensing this it would turn, rise swiftly and dive forward on a place of leadership again. The dowitchers, slower in flight than the blackbellied plovers, usually straggled along the rear and were picked up in their flight as the flock wheeled since they would then be flying on a shorter sector than would the leaders. Often the stimulus to turn appears to arise not from the foremost bird but from one of the forward flanks.

In the most primitive animals that have developed an organization along a head to tail axis, the anterior end dominates the rest of the organism without the subordinate parts having much influence on the dominant region. In the higher mammals, particularly in man where the brain is well developed and is in close nervous connection with the other parts of the body, there is some approach to a physiological democracy as contrasted with the physiological autocracy of the more primitive animals with distinct heads. In these higher forms, the parts of the body, the viscera, the muscles, the endocrine glands acting through the blood stream, co-operate in determining the physiological condition of brain cortex and hence the content of awareness and the nervous impulses that may result.

Similarly within societies, as the connections between the different animals composing the group become more direct, as means of communication either by abstract signs, words in man, or by a flow of stimuli or of materials become more direct and rapid, and as the region of dominance becomes so developed that these impulses register rapidly, even so does the social control tend to become less autocratic and more democratic.

In *Amoeba* and other lower animals the communications are through protoplasms only, which have slight ability to transmit stimuli. The regions of dominance are little different, and then only temporarily so, from the subordinate regions and a state of physiological anarchy frequently exists, as in the sea anemones, where one part of the animal's body may work in direct opposition to another. This is similar to the social anarchy of the more loosely organized animal aggregations. At the other extreme, when a body becomes so highly organized that again the relative importance of each part is only slightly different from that of another and the whole is so closely bound by nervous system and by blood stream that anything that affects one part soon affects all, the organization of the individual may be compared with that in the highly organized bird flocks, or in colonies of ants, or in the best human societies in which the reactions seem to be group-controlled rather than controlled by any one individual.

Social organizations in which laws, not individuals, rule are the highest social development. In human societies, we say there is a respect for law and order. In bee or ant societies, we say they are controlled by "the spirit of the hive." Such social organizations have grown a long way from that existing in ecological communities where the struggle between different members is much more easily found than is evidence of their underlying co-operation. The highest organizations even tend to dispense with leadership; the individuals composing the group become entirely group-centered rather individually minded. There is neither individual authority nor obedience, for neither is needed in the face of complete co-operation for the common good.

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