

# **The Ecological Web**

More on the Distribution and  
Abundance of Animals

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and  
L. C. Birch

1984

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# The Theory of Environment

## 1.0 The Scope of Ecology

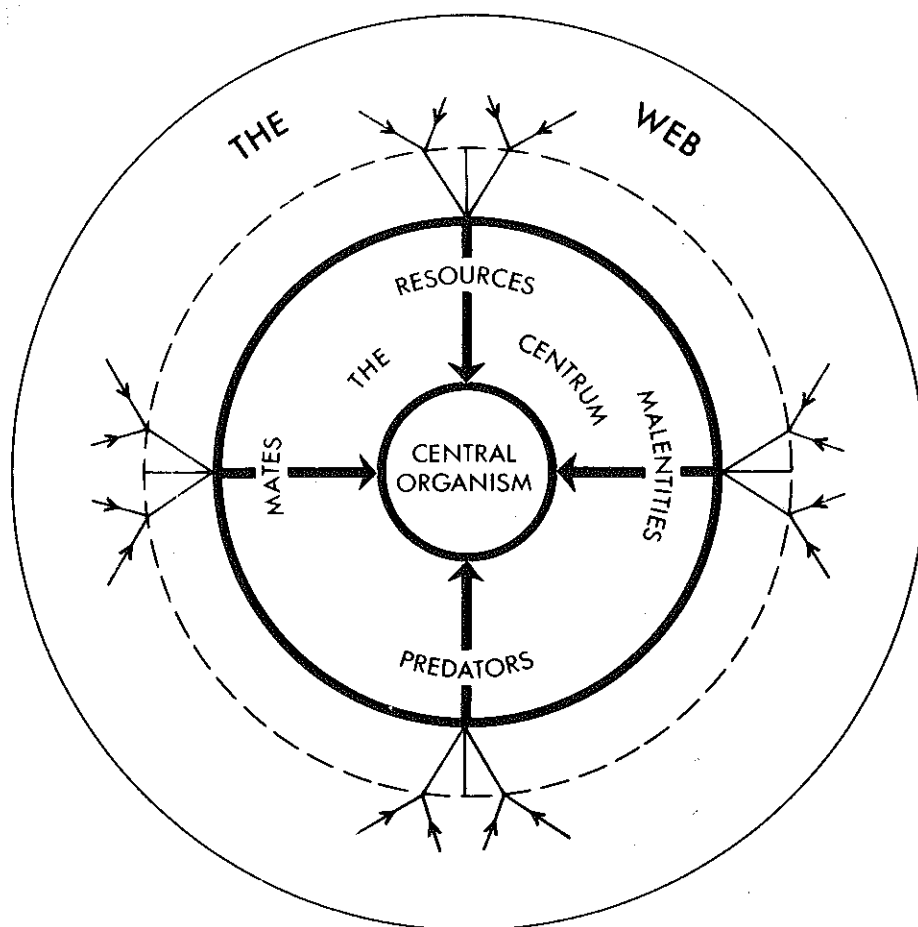
In this book "ecology" means the study of the distribution and abundance of particular species of animals or, in certain contexts, the knowledge that might come from such studies. We build on the theory of environment that was outlined in Andrewartha and Birch (1954); that is, we seek to explain the distribution and abundance of species by studying the environments of individuals in natural populations.

The theory of environment depends on a definition (an axiom) that says that *the environment of an animal consists of everything that might influence its chance to survive and reproduce*. The expectation of life and the fecundity of the individual are reflected in the birth rate and death rate of the population, which is reflected in the distribution and abundance of the species. The theory is outlined by three propositions given in section 1.1. A little detail is supplied in section 1.3; and the detail is completed, with examples, in chapters 2-7.

## 1.1 Three Propositions That Outline the Theory of Environment

*The first proposition:* Any environment is made up of a *centrum* of directly acting components and a *web* of indirectly acting components (fig. 1.01).

Any animal's chance to survive and reproduce depends on the probability that certain "things" will impinge on its body, influencing its physiological condition and thereby its chance to survive and reproduce. Changes in physiological condition might be reflected as changes in behavior, growth, or expectation of life. "Things" is used broadly to imply any accumulation or configuration of matter or energy. "Impinge" is also used broadly: thus a fox (a predator) may impinge on a rabbit by eating it; leaves of a grass (food) may impinge on the rabbit by providing nourishment. The fox and the grass are said to be "directly acting" components in the environment because each is the immediate cause of a characteristic change in the rabbit's condition. That is, no intermediate link can be discerned between the environment (fox) and the animal (rabbit). So to say that the fox is a directly acting component in the environment of the rabbit means that the fox is likely to be the proximate cause of the rabbit's death. When a component of environment makes its influence felt through an intermediate link or links it is said to be acting indirectly, so its place is in the web. Note that physical contact, even aggressive



**Fig. 1.01** The environment comprises everything that might influence the animal's chance to survive and reproduce. Only those "things" that are the proximate causes of changes in the physiology or behavior of the animal are placed in the centrum and recognized as "directly acting" components of environment. Everything else acts indirectly, that is, through an intermediary or a chain of intermediaries that ultimately influences the activity of one or other of the components in the centrum. All these indirectly acting components are placed in the web.

physical contact, is not a sufficient criterion for "directly acting". If by overt physical aggression one animal preempts the food that was coveted by another (of the same or different species), shortage of food (not aggression) will be recognized as the proximate cause of the second animal's disability. The aggressive animal will be said to have exerted its influence indirectly through food, and it will properly be placed in the web of the environment of the victim.

The probability that a rabbit will be eaten by a fox may depend on the number of foxes that are hunting rabbits in that place and on the number of obstacles that may impede the hunt (e.g., a fox may be more successful in digging out the nestlings in a friable sandy soil than in a hard rocky soil sec. 12.432). To express

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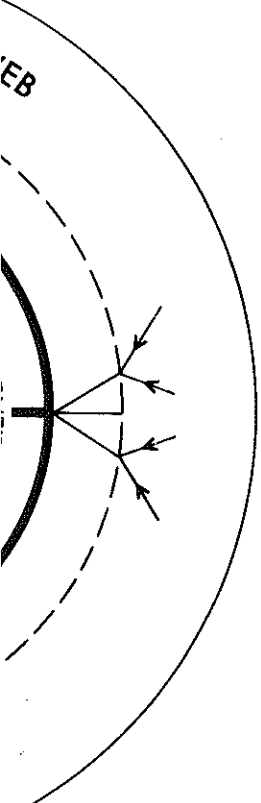
This proposition centrum is based "function" of the centrum the animal's chance of the parental population of the animal

*The third proposition* (figs. 2.01-2.06). residue) or inorganic

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this idea, not only with respect to predators but quite generally for all components of environment, we speak of the "activity" of the component. In the present instance the "activity" of predation might be represented by a factor for the abundance of foxes multiplied by a factor for their success in hunting. So it becomes necessary to study the ecology of the fox in order to fulfill our study of the ecology of the rabbit. Let us imagine that the fox supports itself by eating a certain sort of bird during the season when rabbits are hard to get; and the bird eats certain insects that eat certain grasses and other herbaceous plants that are likely to be more widespread and abundant after copious rain has fallen at the right season. The rain, the plants, the insects, and the birds all have their place in the centrum of one or other of the organisms in this chain, but insofar as they influence the rabbit's chance to survive and reproduce they do so indirectly, through their influence on the distribution and abundance of foxes. The fox belongs in the centrum of the rabbit's environment, but all the other organisms and the rain belong in the web. The web is made up of many such chains (chap 2).

*The second proposition:* the centrum of the environment of any animal comprises four divisions (or "compartments"); each division houses a characteristic set of components that we call resources, mates, malentities, and predators.

This proposition is developed in section 1.31. Briefly the partitioning of the centrum is based on the function of the component in the environment. The "function" of the component is defined by (1) the influence of the component on the animal's chance to survive and reproduce and (2) the influence that the density of the parental population has on the activity of the same component in the environments of the animals of the filial population.

*The third proposition:* The web comprises a number of systems of branching chains (figs. 2.01-2.06). A link in the chain may be a living organism (or its artifact or residue) or inorganic matter or energy (chap. 2).

Any living organism that is in the web or contributes an artifact or residue to the web will have an environment of its own. Consequently, to investigate its contribution to the activity in the web requires only that it be put into its own centrum and that the standard ecological inquiry be broadened accordingly. For a link that is not a living organism or does not have such an origin, the inquiry might lead into almost any branch of science.

The web in our theory of environment is essentially the same idea that Darwin (1859, 73) developed when he wrote about "the web of complex relations". The food chains that are familiar to students of communities may be counted in Darwin's "web" and in the web of our theory too. But our theory differs from Darwin's web because we emphasize the difference between directly acting and indirectly acting components of environment, and we recognize nonliving components of environment in both centrum and web.

We conceive of the web as a number of branching chains. In practice they are uncovered as each one is traced away from its particular component in the centrum. But the action flows in the opposite direction, inward toward the centrum and through the centrum to the primary animal whose ecology is being studied. Because the web includes everything that might influence the activity of the centrum, it is

convenient to have one word that can be applied quite generally to any component of the web. We use "modifier", in the sense that a component in the web might modify another component in the web or a component in the centrum.

It is the purpose of population ecology to focus the ecological action on one particular species at a time. This is what distinguishes population ecology from community ecology, which is more concerned to identify the ecological action in the community at large. We believe it is this difference that makes population ecology the sharper tool when it comes to pursuing such practical goals as pest control, wildlife management and conservation.

Because population ecology focuses on one species at a time, the questions that arise in population ecology are different from those of community ecology. Population ecology is not primarily concerned, for example, with species diversity, community stability, energy pathways through different trophic levels, ecological succession, and "trophic complexity".

## 1.2 The Origin and Growth of the Theory of Environment

Despite the fundamental differences between the goals and methods of ecology and evolution, both sciences depend on the concept of environment, or the struggle for existence, as developed by Darwin. When we first put forward our theory of environment (Andrewartha and Birch 1954) we leaned heavily on Darwin. The three brief passages from *The Origin of Species* that we quote below show that "food", "weather" and "other animals" were seen by Darwin as parts of the "web of complex relations" that shaped the struggle for existence; we borrowed these three components of environment from Darwin and added a fourth of our own contriving, which we called "a place in which to live". Darwin wrote:

I use the term Struggle for Existence in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny. Two canine animals, in time of dearth, may truly be said to struggle with each other which shall get food and live. But a plant on the edge of a desert is said to struggle for life against drought, though more properly it may be said to be dependent on the moisture. (Darwin 1859, 62).

A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with individuals of distinct species, or with the physical conditions of life. (Darwin 1859, 63).

In looking at Nature it is most necessary to keep the foregoing considerations always in mind—never to forget that every single organic being around us may be said to be striving to the utmost to increase its numbers; that each lives by a struggle at some period of its life; that heavy destruction inevitably falls either on the young or the old during each generation or at recurrent intervals. (Darwin 1859, 66).

From these passages we see that the struggle for existence is not only against what we might call "natural enemies" but also against the environment. In *The Origin of Species* Darwin defined the environment as "the sum of the external conditions of an animal's chance to live". We think of the environment as the sum of the conditions that constitute the environment. The "average" animal must avoid the error of focusing on the environment as a whole, associated with the environment.

This definition of the environment is not a population because it is not "fecundity" that is the environment. It is by sampling the population that we get the "average" individual. The specific birth-rate of the population, these statistics, extend to the environment, to survive and reproduce. Statistics for the population are the environment.

We frequently hear that the environment represents the population when there is risk of extinction. All those others that are the environment.

In 1954 we revised our theory of environment, which was anthropocentric; we were seeking an environment that influenced the animal. The environment looked "functional" analysis approached it more.

The first step to a new theory of environment was taken by Browning (1962), who called the environment "hazards"—allowing for the environment too narrow and "a new environment" extended the scope of the environment. The idea is essentially the same as the distinction between the environment that we now have and the environment in which she used to live. The theory, shared by Darwin and in doing so shared by Darwin, but especially by Darwin.

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(Darwin 1859, 66).

From these passages it is clear that Darwin saw the *individual* "struggling" against what we now call its "environment" in an effort to survive and to leave progeny. In Andrewartha and Birch (1954), again following Darwin's lead, we defined the environment of an animal as everything that might influence the animal's chance to survive and reproduce. We use the same definition in this book. We think of the mean of the environments that are experienced by the individuals that constitute the population. So we speak of "the animal" in the singular, meaning the "average" animal that has experienced the average environment. In this way we avoid the error of circularity when analyzing a whole class of important reactions associated with overcrowding.

This definition relates to a hypothetical animal that is said to represent the population because the values for such statistics as "expectation of life" or "fecundity" that are attributed to it are, by definition, the same that would be gotten by sampling the population. Expectation of life and "expected fecundity" for the "average" individual are calculated from "age-specific death-rate" and "age-specific birth-rate" as estimated by sampling the population. In theory, we sum these statistics, expressed as probabilities, when we speak of the animal's "chance to survive and reproduce". We take for granted their relevance to the corresponding statistics for the population.

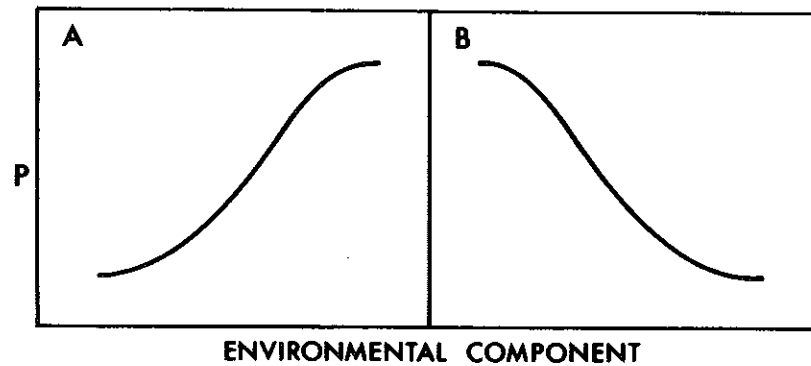
We frequently have occasion to refer to this hypothetical "average" animal which represents the population. When no ambiguity threatens we call it "the animal"; when there is risk of ambiguity we call it the "primary animal" to distinguish it from all those others that are in the web.

In 1954 we reviewed the current concepts of environment and found them anthropocentric; we criticized this approach as too "descriptive". By contrast we were seeking an analysis that would depend more on how the environment influenced the animal's chance to survive and reproduce and less on what the environment looked like in the eyes of a man. We said we were seeking a "functional" analysis of environment. This is still our aim; we hope to have approached it more closely in this book.

The first step toward a more functional concept of environment was taken by Browning (1962, 1963, 90) who defined two new components—"resources" and "hazards"—allowing him to discard two of the original ones: "food" because it was too narrow and "a place in which to live" because it was too diffuse. We have extended the scope of hazards a little and now call this component "malentities" but the idea is essentially the same. Maelzer (1965) drew attention to the important distinction between the directly acting and indirectly acting components of environment that we now call the centrum and the web. Niven (1980) in a seminal paper in which she used the concepts of mathematical logic to define the basic principles of the theory, sharpened the boundaries between the four divisions of the centrum. And in doing so she greatly clarified our thinking about all components of environment, but especially those that popularly constitute "the weather".

Insofar as "progress" contains an original idea, it stems, as all originality must, from the fundamental epistemological process of deciding what shall be called "alike" and what "unlike". There is the story from the history of mathematics, perhaps apocryphal but nevertheless instructive, that Dantzig (1947, 101) told about Pythagoras.

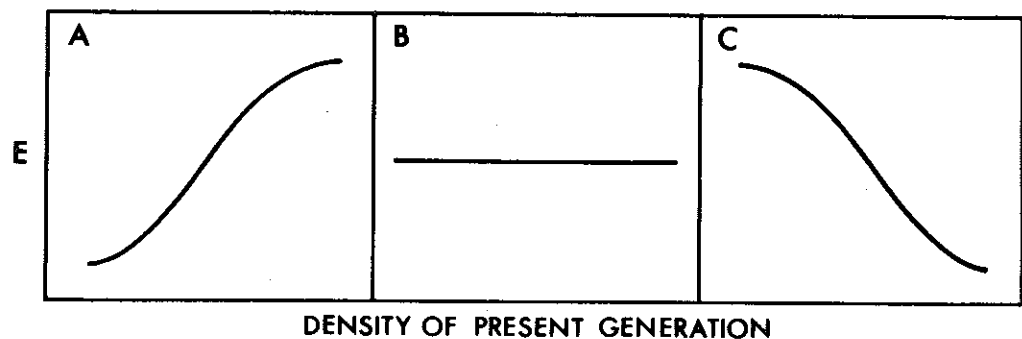




**Fig. 1.02** The influence of the environmental component on the probability that the animal will survive and reproduce (P) is positive in A and negative in B. In each cell of the diagram the activity or abundance of the environmental component increases to the right.

question permits three alternatives because there are important components of environment that do not react to the density of the population (fig. 1.03B). For example, the amount of fruit produced by a fruit tree is independent of the number of fruit flies that ate the fruit in the previous generation. Or the supply of cow dung in one generation is independent of the number of dung beetles that fed on the dung in the previous generation. The reaction is said to be zero when the component does not react to the density of the population. It is said to be positive when the curve slopes upwards from left to right (figs. 1.02A, 1.03A) and negative when the curve is downward from left to right (figs. 1.02B, 1.03C).

Six interactions can be described by different combinations of the two reactions in figure 1.02 with the three reactions in figure 1.03. If the zero reaction as shown in figure 1.03B is confounded with the negative reaction as shown in figure 1.03C we get a 2 by 2 interaction table as shown in table 1.01. The 2 by 2 table is more convenient than the 2 by 3 table, and very little information is lost—but see section 6.2. Each cell of table 1.01 defines a directly acting component of environment. The centrum of any environment comprises these four components and only these four components—no other situation is logical.



**Fig. 1.03** The influence of the density of the present generation on the activity of the environmental component (E), as it is experienced by future generations, is positive in A, zero in B, and negative in C. Components that conform to curves A and C are called interactive; those that conform to B are called noninteractive.





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renamed it malentities. Malentities are to be distinguished from predators as described in section 1.42.

Colloquial English distinguishes between carnivore and herbivore, predator and parasite, and so on, but it has no word to denote generally any organism whose food includes any other sort of living organism. Yet this general meaning is important in ecology. Any organism—animal, plant, or microbe—whose food includes any other living organism, be it animal, plant, or microbe, belongs in the bottom left cell of table 1.01. We have put such organisms there and called them "predators", thereby greatly expanding the colloquial meaning of this word to include herbivores, carnivores, parasites, and pathogens.

We say that the fox is a *predator* in the environment of the rabbit; but to be precise we should say that *predation* by the fox reduces the rabbit's chance to survive and reproduce. For convenience we shall always use the concrete noun to name the component of environment, with the understanding that the concrete noun implies the *action* that would be more properly named by an abstract noun—thus predator (fox) implying predation, food (grass) implying the nutrition that comes from eating grass, heat (absorbed from a hot medium or hot body in the medium) implying the heating of the animal, with the consequent change in temperature leading to changes in physiology or behavior that influence the animal's chance to survive and reproduce.

This convention makes for easier reading by avoiding a surfeit of abstract nouns. It also gets us off the horns of another dilemma that arises when one natural entity is or gives rise to more than one component in the environment of the same animal (sec. 2.32 figs. 2.01–2.06). For example, the sheep tick *Ixodes ricinus* lives near the surface of the ground under the matted vegetation that is grazed by sheep (see summary of Milne's work in Andrewartha and Birch 1954, sec. 13.32). Once a year during its life of three years the tick may crawl up a grass stem and climb onto a passing sheep. For several days the tick clings to the sheep, engorging with blood, while the sheep wanders, perhaps a long way from where the tick was picked up. In due course the tick drops off and seeks its usual shelter under the vegetation. The sheep is both food and an agent for dispersal in the environment of the tick. The context in which we use the concrete noun "sheep" will tell whether we are implying the action of nutrition or the action of dispersal.

Another example. In inland Australia immature scale insects, *Saissetia oleae*, living on orange trees, thrive when heat absorbed from a warm medium raises their body temperature moderately, say to 20–25°C; they die when heat from a hot medium raises their body temperature extremely, say to 35–40°C. Heat absorbed from a warm medium is classified into the top right cell of table 1.01 and called a resource; heat absorbed from a hot medium is classified into the bottom right cell of table 1.01 and called a malentity. Again, there need be no ambiguity because the context will tell whether we are dealing with heating that maintains the body within the temperature range that favors healthy metabolism or raises the body temperature to a fatally high range (sec. 2.32).

Many of the "things" that we shall have to consider and allot to their proper places in the centrum bear names that are familiar to us humans as components in our own environment—food, weather, and disease to mention only a few. This is not surprising because, ecologically at least, the human animal is much more like

other animals than many philosophers, theologians, or politicians would have us believe (Birch and Cobb 1981, chap. 4). But remember that in our theory of environment these words have special meanings that are different from the anthropocentric meanings of colloquial English. For example, contemplating oxygen in our own environment and realizing the fatal consequences of an acute shortage, we might be tempted to say that oxygen is very important to us. Yet in the general run of ecological texts and papers oxygen scarcely gets a mention: it is of little interest to ecologists because the supply of it is usually so reliable in the places where aerobic animals live. For many species the same is true of food and water. In general it can be said that beneficial components (fig. 1.02A) whose activity is not likely to fall below the optimum and harmful components (fig. 1.02B) whose activity is not likely to rise above a negligible threshold are unimportant. It is the highly variable ones that attract all our attention, especially those whose activity is likely to exceed such limits, or those that might be artificially manipulated so that their activity exceeds a critical limit.

### 1.32 The Web

The concept of the web is necessary because the activities of the components in the centrum have to be explained. In other words, we must study the ecologies of the organisms that are seen to be important in the centrum; and we must also seek to understand the "events" that determine the activity of the important nonliving components of the environment. This program must not be planned indiscriminately. On the contrary, we must follow our hunches in the search for "key" components, not only in the centrum but also in the web. The web and centrum are equally essential to the model. Indeed, the limelight is more often than not focused on some part of the web, as it is in the ecology of *Thrips imaginis*.

According to Davidson and Andrewartha (1948a,b) and Andrewartha (1970, 27), *T. imaginis* lives and breeds exclusively in certain flowers; a diet of pollen is essential for the growth of nymphs and the production of eggs by adults (sec. 10.12). Also, no doubt as an adaptation to a life-style based on exploiting short-lived flowers, the thrips are highly dispersive; they readily exploit the turbulence of surface breezes to go seeking new flowers as the old ones senesce. This dispersiveness pays big dividends when suitable flowers are abundant and densely distributed, but it entails a severe risk of premature death when flowers are few and sparsely distributed. Armed with this sort of knowledge of the physiology and behavior of thrips, Davidson and Andrewartha postulated that fluctuations in the population of *T. imaginis* were caused by fluctuations in their supply of food, which in turn were related to certain aspects of the weather that were thought to be important in the ecology of the plants that provided food for the thrips. They formulated an equation of the form:

$$y = a + b_1x_1 + b_2x_2 + b_3x_3 + b_4x_4,$$

where  $y$  stands for the number of thrips;  $x_1, \dots, x_4$  are quantities calculated from standard meteorological records of temperature, rainfall, and evaporation and  $b_1, \dots, b_4$  are constants, calculated from the empirical data; they measure the independent association between  $x_1, \dots, x_4$  and  $y$ .

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Two of the independent variates  $x_2$  and  $x_3$ , might have had a direct influence on both plants and thrips, but the other two might have had a direct influence on the plants alone.

The equation accounted for 78% of the variance in the thrips' populations. So there seemed good reason for accepting the hypothesis that the thrips' chance to survive and reproduce depended largely on fluctuations in their supply of food, which in turn depended largely on fluctuations in certain aspects of the weather.

In this example certain aspects of weather (temperature, rainfall, and evaporation) influencing heat and water in the environments of certain plants turned out to be important components in the environment of *T. imaginis*. A prior knowledge of the natural history, physiology, and behavior of *T. imaginis* and some knowledge of the biology of the plants led Davidson and Andrewartha to recognize the importance of these components; and empirical testing confirmed the hypothesis. When the theory of environment, with its concepts of centrum and web, is used in this way we think it may often lead accurately and economically to the solution of ecological problems.

In subsequent chapters, especially 2, 5, 6, and 7, we unfold many complexities of the web. This is not merely an intellectual pastime. The purpose is to establish guidelines that might help to direct an ecological inquiry (secs. 2.0, 2.1).

#### 1.4 The Sorts of Components That Might Be Found in Any Environment

The web is discussed in chapter 2. The four components of the centrum are discussed in chapters 36. Some introductory comments on resources, predators, and malentities follow in sections 1.41 and 1.42.

##### 1.41 Resources

A resource is defined by its position in the top right cell of the matrix diagram that is table 1.01. Food is the most familiar resource. The others are water, oxygen, heat, and tokens. Food and water contribute the chemicals from which the body is built; and food, with oxygen, provides energy. Heat, radiant or ambient, that is absorbed by the animal may help keep the body at a temperature that favors a healthy metabolism. What we call tokens are not usually recognized in colloquial speech as resources, but they clearly are such by our definition. We speak of a token when a caterpillar or a bird, having measured the length of day, changes its body chemistry to suit the season, preparing for diapause or migration as the case may be. In this instance the length of day is the token. It is in the centrum because it impinges directly on the animal (through the appropriate photoreceptors) and causes the animal to change its body chemistry. It is a resource because, by virtue of the animal's positive response to the token (fig. 1.02), and by virtue of the token's neutral response to the animal (fig. 1.03), the token fits into the top right cell of table 1.01.

The dictionary gives token the meaning "symbol" or "sign". We use "token" in the context that the token signals to the animal that it is time to prepare for the next season or day, or the next stage in the life cycle, the reproductive cycle, the cycle

of diurnal behavior, and so on. Light, especially the relative length of day and night, makes the most spectacular and most important tokens. In Andrewartha and Birch (1954, chap. 8) we discussed how light might synchronize life cycles with the seasons and synchronize the life cycles of individuals with each other, but we now see tokens a little more broadly than that.

#### 1.42 Predators and Malentities

Predators and malentities between them comprise everything that conforms to the negative reaction illustrated in figure 1.02B. But table 1.01 shows that the predator's reaction to animals is positive, whereas the malentity's reaction to animals is negative or zero (sec. 6.2). A malentity may kill the primary animal. If the malentity is an organism it may even eat the animal. But such behavior is not selective; the animal may be eaten incidentally along with some other sort of food that is sought. The primary animal does not feature as food and rarely, if at all, features in any other capacity in the environment of the malentity. Another characteristic of a predator that distinguishes it from a malentity is that it usually shows some adaptation that equips it for feeding on the primary organism.

Malentities were originally conceived as "unfortunate accidents". The typical malentity was considered to be an inanimate object, perhaps an artifact left behind by an animal. Browning (1963, 91) mentioned deep hoofprints left by a bullock walking across a marsh. The hoofprints fill with water and drown small insects (Collembola) that are trapped in them. There is no way that the death of the insects might benefit the bullock. "Malentities" is still used in the context of "unfortunate accident" but there may be a number of variations on this theme. Also, it is well to remember that the same natural object may occupy more than one place in the environment of the same animal (secs. 1.31, 2.32). For example, in section 6.2 we tell how the ant *Myrmica scabrinodis* is likely to aggressively evict *M. rubra* from any of its nests that are in open, sunny, well-drained sites. The aggression is direct and overt: the ants may bite legs off workers of *M. rubra* and eat soldiers. Members of the evicted species build nests in less-favored situations where they seem to be safe from attack. By their violence the aggressors, *M. scabrinodis*, are directly responsible for the death of their victims, and the more aggressors there are, the more victims there will be. Hence the reaction of *M. rubra* (the primary animal) to the aggressor (component of environment) is negative. On the other hand, the abundance of the aggressors does not increase as the numbers of its victims increase except insofar as they may have gained some food by eating a few soldiers. There is no suggestion that this reaction is described by the curve in figure 1.03A. The reaction is illustrated by figure 1.03B or possibly 1.03C; that is, it is zero or negative. It would be negative if a dense population of victims exhausted the aggression of the aggressor to the aggressor's disadvantage. But in no circumstance does the presence of *M. rubra* in either low or high numbers aid *M. scabrinodis*. *M. scabrinodis* unambiguously falls into the lower right cell of table 1.01 as a malentity.

In the environment of *M. rubra*, *M. scabrinodis* has a place in the centrum as a malentity by virtue of its direct attacks on the bodies of its victims. But its aggressive activities also drive the surviving *M. rubra* out of their favored sites. In less-favored sites the chance that *M. rubra* will survive and reproduce is less.

Hence the aggressive components of environment profits from its attacks, otherwise be considered an aggressor as male.

#### 1.5 The Implications of Behavior

In Andrewartha and Birch's theory, the study should begin with the physiology, and the behavior. Such knowledge of the environment where the animal lives is necessary. In addition, a hypothesis, a hypothesis of the environment, an appreciation of the environment with statistical methods, a hypothesis of the environment.

We would not be particular in empirical natural history, empirical study. The better the centrum and, the more sure guide to the environment, have served its purpose with the attempt to model should work in the environment, but the environment works, hope at each stage of the explanation for the environment.

#### 1.6 The Nature of the Environment

We have made it clear that the environment components are not isolated. Because of the environment, we shall try to use this term (see sec. 6.2): it is neither a component, it has been physically determined. For example, Andrewartha and Birch did with flour beetles, Myers did with rats, a population may be

Hence the aggressor has a place in the web of *M. rubra* as a modifier of all those components of environment that differ in the two sorts of sites. *M. scabrinodis* profits from its activities as a modifier because it gains favored sites that might otherwise be occupied by *M. rubra*. It is important not to confuse the roles of the aggressor as malentity and as modifier, since they are two quite different actions.

### 1.5 The Importance of Beginning with the Physiology and Behavior of the Animal

In Andrewartha and Birch (1954, 10, 557, 558) we said that an ecological study should begin with a general appreciation of the natural history, environmental physiology, and behavior of the animal so far as it is known or can be observed. Such knowledge, together with a naturalist's appreciation of the sorts of places where the animal normally lives, is sufficient foundation on which to build, tentatively, a hypothetical environment that can be tested step by step. A critical appreciation of the theory and practice of sampling and a working acquaintance with statistical methods and statistical inference are essential parts of ecological talent.

We would not change this advice today, except perhaps to be a little more particular in emphasizing the importance of beginning with a knowledge of the natural history, environmental physiology, and behavior of the animal chosen for study. The better the knowledge, the more surely it leads to key components in the centrum and, through them, to the web. If the theory of environment provides a sure guide to the important components in the animal's environment, the theory will have served its purpose. If here and there we seem to have been too preoccupied with the attempt to place a component of environment in its proper category, we would not want to give the impression that classification is an end in itself. The model should work better if we can be consistent in identifying the components of environment, but the chief aim remains to present a general model of how environment works, hoping that it might point to the most effective questions to be asked at each stage of an investigation (chap. 2) and perhaps to the most effective explanation for the empirical results (chap. 9).

### 1.6 The Natural Population

We have made it clear in sections 1.0 and 1.1 and elsewhere that the theory of environment concerns the distribution and abundance of animals in natural populations. Because population, in the ecological context, has only an elusive meaning, we shall try at this point to establish a meaning for "natural population" as we use this term (see also chap. 8). We begin by saying what a natural population is not: it is neither artificial nor abstract. "Artificial" implies that the animals have been physically deprived of some part of their natural experiences, as in an experiment. For example, consider the laboratory experiments summarized in Andrewartha and Birch (1954, 421), that Gause did with microbes or those that Park did with flour beetles or Birch with grain beetles, or the field experiments that Myers did with rabbits in enclosures (sec. 12.2). On the other hand, an abstract population may exist only in the mind, perhaps having been deduced as a mathe-



mathematical model from an imaginary premise. For example, consider the models that were put forward by Volterra and Lotka, and summarized in Andrewartha and Birch (1954, sec. 10.1). Or, more fruitfully, an abstract population may be conceived when a real population is contemplated but certain of its qualities are arbitrarily abstracted from it so that they can be ignored. Both the experiment and the abstraction make analysis simpler. (That is why we practice them). But simplicity may be dearly bought because the price is measured in departure from reality. This debt must be repaid before a realistic knowledge of the natural population can be claimed (chap. 9).

We approach a realistic meaning for "natural population" through an abstraction which we call a "local population". In southern Australia at any time during late winter or spring, a carcass of, say, a sheep lying in the open is likely to be occupied by large numbers of maggots of the blowfly *Lucilia sericata* and many other species of scavengers. When the maggots are fully grown they pupate either under the carcass or in some other sheltered place. In due course they emerge as adult flies. By this time the carcass may have been fully consumed, but in any case it is no longer any good for *Lucilia*, which requires a fresh carcass (Fuller 1934). An adult will fly away from a spent carcass and seek a fresh one to lay eggs on. Also dispersing from spent carcasses and joining in the search may be other *Lucilia*, several sorts of predators of *Lucilia*, and a number of species of scavengers that would share the carcass with *Lucilia*. Thinking in probabilities, as we must, it is clear that all the spent carcasses from which these animals might come and all the fresh carcasses that any one of these animals might find are linked, and none can be ignored without abstracting something from nature. In other words, our meaning for "natural population" must allow for the probability of interaction between these "local populations" centered on single carcasses. In other examples the local population may be less of an abstraction, as, for example, the black pineleaf scale *Nuculaspis californica*, where the population on a single pine tree constitutes a local population (sec. 11.1) or the "interaction groups" of carabid beetles studied by den Boer (sec. 8.41). With other species, especially those that disperse great distances, such as the bush fly *Musca vetustissima*, the local populations are much less obvious, and their boundaries may be drawn much less objectively than for the examples given above (Hughes 1981).

The idea of a local population is a straightforward idea, but it poses the question, How many local populations make up a natural population? In an extensive area, where do we draw the line? An arbitrary boundary with local populations interacting across it is not permissible, because it would create an abstraction for just the same reason that a single population is an abstraction. The only alternative is to seek a natural ecological barrier or some other barrier to the exchange of genes between populations.

In southeastern Australia the distribution of the blowfly *Lucilia cuprina* extends over more than a million square kilometers, and there is no obvious ecological barrier except around the margins of the distribution. There are other populations in other parts of the continent and in other continents. It is impracticable to work with such a large unit, but there is no reason why it should not be the paradigm for our concept of a "natural population".

This concept of natural population is discussed in chapters 8 and 9. It is not surprising (Miller 1954) and on the sort of plane

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## 1.7 The Loc

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This concept of the multipartite natural population is developed further in chapters 8 and 9. It is an integral part of our theory of distribution and abundance. This is not surprising considering the patchiness of most terrains (see, e.g., Elton and Miller 1954) and the highly specific demands that animals characteristically make on the sort of place where they will live (Andrewartha and Birch 1954, chap. 12).

The meaning for the multipartite "natural population" that emerges from this analysis may be summarized:

- (1) It is the sum of a large number of interacting local populations.
- (2) It is not abstract.
- (3) It is not artificial.

There are two corollaries:

(i) As a consequence of (2) the natural population can be bounded only by natural ecological or genetic barriers. Consequently, in some species the only natural population that can be recognized is the whole species. In most if not all instances the smallest "natural" population will be too large to be sampled as a unit because it would be impracticable to take a sample that rigorously represented all the variability in the population. Of course ecologists are aware of this problem and know that their conclusions have to be qualified accordingly (sec. 8.4).

(ii) In the context of (3) we exclude experimental populations in the laboratory or field as natural populations but regard humans and all their works as part of nature. This means, for example, that the insect pests that owe their abundance to the great monocultures of commercial agriculture can be regarded as belonging to natural populations.

In seeking a meaning for "natural population" we have established a meaning for "local population" as well. This introduces a new idea, "the locality".

## 1.7 The Locality

The locality is conceived as an area that supports, or might support, a local population. The concept of locality is useful because it helps us to think about (a) the environmental risks experienced by the dispersive phase of the life cycle: a safe "landfall" is more likely when localities are abundant and densely distributed (sec. 8.4.11); (b) the stability in numbers of the natural population: a natural population that is distributed over many localities is likely to be more stable than one that is distributed over few localities (sec. 9.3); (c) the size of the natural population: a piece of country with many localities will support a larger population than the same area with few localities in it (sec. 9.2).

A locality might be obviously distinct from the countryside, as, for example, a carcass, a pond, or a tree. Or the boundaries might be distinct but the distinction may be so subtle that to perceive it calls for the esoteric art of the trained naturalist. We quote a passage from Ford (1945, 122) on this point:

We have three butterflies which are limited by geological considerations, being inhabitants only of chalk downs or limestone hills in south and central England, and they may reach the shore where such formations break in cliffs to the sea. These



are the Silver-spotted Skipper, *Hesperia comma*, the Chalkhill Blue, *Lysandra coridon*, and the Adonis Blue, *L. bellargus*... The two latter insects are further restricted by the distribution of their food plant, the Horseshoe Vetch, *Hippocrepis comosa*, and possibly by the occurrence of a sufficiency of ants to guard them. Yet any of the three species may be absent from a hillside which seems to possess all the qualification which they need, even though they may occur elsewhere in the immediate neighbourhood. This more subtle type of preference is one which entomologists constantly encounter, and a detailed analysis of it is much needed. A collector who is a careful observer is often able to examine a terrain and to decide, intuitively as it were, whether a given butterfly will be found there, and that rare being, the really accomplished naturalist will nearly always be right. Of course he reaches his conclusions by a synthesis, subconscious as well as conscious, of the varied characteristics of the spot weighed up with great experience; but this is a work of art rather than of science, and we would gladly know the components which make such predictions possible.

The boundaries of an area in which the animals might live might be perceptible, yet the area might be too large to be conveniently thought of or sampled as a locality. A suitable statistical convention must then be devised to define the boundaries (secs. 2.39, 8.41) but each case must be treated on its merits, according to the demands of the hypothesis and the nature of the animal.

## 2.0 Introduction

"Looking back", what the problems are rather than the problems in the light of the general environment is outlined. The same idea graphically (primary animal) is shown in the ecology

## 2.1 What Is an

According to the theory, the proximate cause of survival and reproduction is the environment, among the many modifiers may be one from a particular mechanism, pathways from other factors indicate the degree of steps away from the graphic representation.

So the environmental trace pathways from

Early in the investigation, the envirogram is not used to see the environmental representation. Each step is an experiment in the field, leading to a distribution in the field. of an explanation (the ecology of a particular distribution and abundance)