

ON TERRITORIAL BEHAVIOR AND OTHER FACTORS
INFLUENCING HABITAT DISTRIBUTION IN BIRDS

by

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INTRODUCTION

Howard (1920) suggested several roles for territorial behavior in birds, some of which involve the dispersal of the species over available habitats. Since this classic work, there have been a large number of sometimes conflicting statements regarding the relationship of territorial behavior to the habitat distribution of a species (e.g., Stewart and Aldrich, 1951; Kluyver and Tinbergen, 1953; Tinbergen, 1957; and Wynne-Edwards, 1962 have all argued that territorial behavior is involved in the dispersal of birds. Lack, 1954, and Johnston, 1961 have rejected this view, arguing instead that the behavior only isolates individuals or pairs.) Lack in particular has dealt with this problem and recently (1966, p. 136) has emphasized the absence of a clear understanding of it. The purpose of this paper is to present an interpretation of the different hypotheses considered by different authors, with the aim of clarifying and resolving the different points of view. The re-defined hypotheses will yield predictions which can be compared with field observations in order to ascertain the probable role of territorial behavior in determining the distribution of a given species.

The thesis will be organized into two major sections. The first will provide a theoretical statement of the general problem of habitat distribution. Hypotheses of the role of territorial behavior will be defined within the context of this theory of habitat distribution, and predictions derived from each. The problem of testing these predictions will be

discussed in general. The second section will provide sample studies which demonstrate the application of the theory.

PART I
THEORETICAL DEVELOPMENT

Introduction

In offering different hypotheses about the role of territorial behavior in habitat distribution, it will be necessary to first present some ideas about the factors which lead to birds being present in one place or another, at one level of abundance or another. By considering concepts related to overcrowding and evolutionary optima, we will develop a theory to describe a particular way in which bird populations might distribute themselves over the available living places. This distribution will be called the ideal free distribution. We then will define three hypotheses for the role of territorial behavior. One hypothesis describes how territorial behavior might be part of the mechanism by which the ideal free distribution is achieved. Another describes how territorial behavior might modify the distribution from the ideal free form. A third hypothesis contends that territorial behavior has a role that is unrelated to the ideal free distribution.

Theory of Habitat Distribution

In order to describe these hypotheses clearly, an agreed upon statement of the problem of habitat distribution in general must be developed. Only with such agreement can the possible relationships of territorial behavior to habitat distribution be differentiated. We proceed with the following definitions:

Definitions

Habitat. A habitat of a species is any portion of the surface of the earth¹ where the species is able to colonize and live. The total area available to a species can be divided into different habitats. The area of any one habitat can be large or small, and different habitats of the same species may be of different sizes. A given habitat can consist of several subdivisions which are not contiguous. We will define habitats so that all of the area within each habitat is, at zero density of the species, essentially homogeneous with respect to the physical and biological features which we believe to be most relevant to the behavior and survival of the species. We will also frame our definitions so that different habitats are not identical with respect to those same physical and biological features.

This definition does not imply that all measurable variables within a single habitat must take constant values over

¹In a number of cases, a habitat may be restricted to a layer parallel to the surface of the earth.

all of that habitat. Some variables may be irrelevant. Others, such as temperature and humidity may compensate for one another. In the later case, the "relevant feature" which is "homogeneous" is some function of the compensating variables. Thus evaporative heat loss rate which depends on temperature and humidity may be the relevant feature which is homogeneous, in which case temperature and humidity may still vary over a single habitat. Because of compensating variables, all of the area within a habitat does not need to appear homogeneous to our measuring devices. However, if an area is uniform in all measurable variables, it is in a single habitat.

Habitat distribution of a species. Suppose the total area available to a species is divided into different habitats and that the area of each habitat is known. The habitat distribution of the species is the set of numbers which state the number of individuals resident in each of the habitats. It can also be expressed as the proportions of the total population resident in the different habitats, or as the density in each habitat.

Factors affecting habitat distribution

Habitat selection. We can now consider how the habitat distribution is achieved. Habitat distribution in birds is usually based on habitat selection, at least some individual birds being exposed to a variety of habitats of which just one is chosen for residence. Therefore, the distribution may be considered as a behavioral phenomenon, involving stimuli

and responses. This means that an understanding of the habitat selection responses in given environmental circumstances will lead to an understanding of the habitat distribution. In order to understand behavioral responses, we should consider the environmental factors (excluding direct within-species individual interactions) which caused the natural selection leading to the evolution of the behavior.

Suitability. In the case of habitat choice, these factors include differences in goodness or suitability of habitat because individuals which choose relatively poor habitats are selected against. Although the stimuli directly influencing the choice of habitat may be no more than correlated with habitat goodness, it is the goodness itself which is a basic (or ultimate - see below) determinate of the behavior. To summarize, the relative suitabilities of the different habitats give rise to habitat selection which in turn determines the habitat distribution. The habitat distribution then depends on the relative goodness of the habitats.

In developing an agreed upon statement of habitat distribution, the next matter is to examine the relative suitability of the various habitats. Suppose the habitats are indexed i , $i = 1, 2, \dots, N$, where N is the total number of habitats. The goodness of each occupied habitat is related to the average potential contribution from that habitat to the gene pool of succeeding generations of the species. We are interested in some measure of that goodness, which may be called the suitability, and denoted for the i th habitat as S_i . The

suitability of the habitat cannot here be precisely defined, but may be thought of as the average success rate in the context of evolution (and/or "adaptedness") of adults resident in the habitat. Stated formally, if s_{iq} is the expected success rate of the q th individual ($q = 1, 2, \dots, n_i$, n_i = number of birds resident in the i th habitat), then

$$S_i = \frac{1}{n_i} \sum_{q=1}^{n_i} s_{iq} \quad (1)$$

The habitat suitability will be determined by several factors such as food supply and predators. The influence of some of these factors is density dependent so that the suitability in a habitat is affected by the density of birds there. Let us assume for the moment that the effect of density is always a decrease in suitability with an increase in density. This assumption would imply that Allee's principle does not operate (Allee, et al., 1949), and it may be truly valid only when densities are not close to zero. Allee's principle states that survival and reproductive rates increase with population size up to some maximum. Further increase in population size leads to a decrease in survival and reproduction, as assumed here. Allee's principle certainly holds at very low densities. A solitary male, for example, cannot have as high a reproductive rate as a male-female pair. At moderate densities, the assumption that suitability decreases with increased density is reasonable since predators may become more active at higher densities and competition for food more severe (Lack, 1966).

We can now define a habitat distribution which will provide a reference for the discussion of the role of territorial behavior. This is the ideal free distribution noted previously, and rests on assumptions about habitat suitability and the adaptive state of birds.

Ideal free distribution

Assumptions on suitability. Ignoring Allee's principle, if we assume that suitability always decreases with density, then it would follow that the maximum suitability occurs when the density approaches zero. Let us call this maximum value the basic suitability, denoted for the ith habitat as B_i . The basic suitability of the ith habitat is affected by such factors as potential predators, food density, and cover.

These considerations lead to an equation expressing the suitability of the ith habitat as a function of the basic suitability there, and the density (denoted d_i). We write

$$S_i = B_i - f_i(d_i), \quad i = 1, 2, \dots, N. \quad (2)$$

The term $f_i(d_i)$ expresses the lowering effect on suitability of an increase in habitat density. Since $f_i(d_i)$ always increases with density, S_i always decreases. The Equations (2) will here be assumed to be the same through time. A possible example of Equation (2) for some value of i is plotted in Figure 1.

Before going any further, let us order the habitats in terms of their basic suitabilities, so that $B_1 > B_2 > \dots > B_n$. By definition, no two habitats have equal basic suitabilities. This is consistent with our restriction on habitat definition

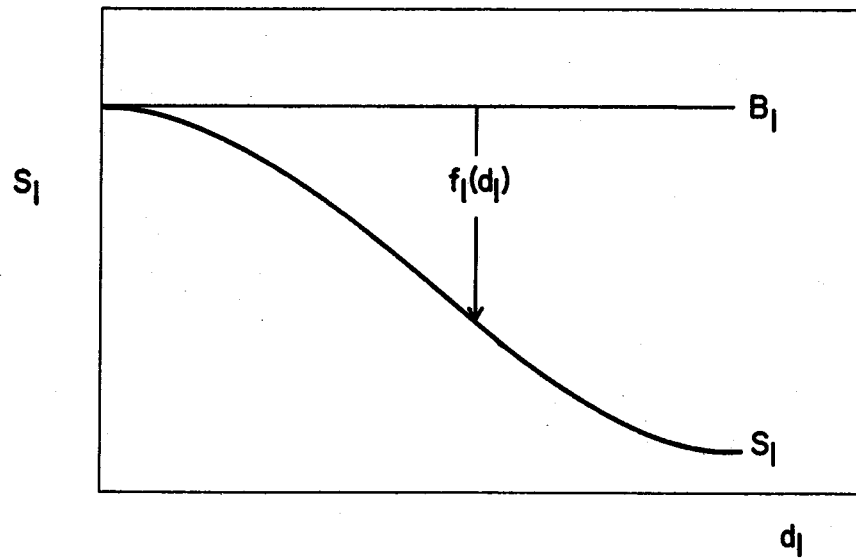


Figure 1. Suitability versus density: 1st habitat (see text)

(stated above), that no two habitats are identical with respect to relevant features.

Assumptions on birds. A description of the suitabilities of the various habitats has been considered in order to understand the habitat selection behavior and the habitat distribution. In applying this description, we make two additional assumptions. These are (1) all individuals settle in the habitat most suitable to them, and (2) all individuals within a habitat have identical expected success rates.

The first assumption demands that the birds have habitat selection behavior which is ideal, in the sense that each bird selects the habitat best suited to its survival and reproduction. Such birds will be referred to as ideal individuals. It is not an unreasonable assumption since individuals which are closest to being ideal will be selected for in the evolution of the species. Therefore, if the environment has sustained the same selective pressures for a large number of generations, the behavior of actual individuals should be approximately ideal.

The second assumption demands, first of all, that the birds be free to enter any habitat on an equal basis with residents, socially or otherwise. For example, if a population in a habitat is limited by nest holes and if all these nest holes are occupied by residents which neither share nor are displaced, then a newly settling individual may expect to be totally unsuccessful, although the average of all residents is rather high. In this case, newly settling individuals are not free to enter the habitat on an equal basis with

residents. If, when a new bird arrived, all of the occupants of the habitat came together to draw lots for the nesting holes, and those losing remained in the habitat, then the individuals would be free. This, of course, is unrealistic.

The second assumption demands also that individuals are alike, genetically and otherwise. This aspect of the assumption may heavily restrict the application of this theory, at best to local populations.

A particular difficulty which arises from this assumption concerns habitat accessibility. According to this assumption, if accessibility is relevant, every habitat must be equally accessible to all members of the species. This is absurd when we regard widely distributed bird species and only local habitats. However, if we restrict attention to habitats as widely distributed as the bird species, or to local populations as narrowly distributed as the habitats, then this difficulty is bypassed.

Note that the second assumption, and Equation (1), imply

$$S_i = s_i .$$

Each bird expects success equal to the habitat average.

The ideal free distribution. With these assumptions we now use the suitability Equations (2) to determine the habitat selection of the individuals in the population. The ideal assumption states that each individual will go where his chance of success is highest. The assumption of homogeneity states that each individual's chance of success is highest in the habitat of highest suitability. The two assumptions

together then assert that each individual will go to the habitat of highest suitability. Thus, a description of the relative habitat suitabilities to some degree determines the choices of ideal free individuals. These choices in turn determine a distribution, which may be called the ideal free distribution. This distribution, which is formally described below, will form a convenient basis for discussing the hypothesized relationships of territoriality to distribution.

If all individuals choose the habitat of highest suitability, then from the point of unoccupied individuals, the suitability in all occupied habitats must be approximately equal and larger than or equal to the suitability in all unoccupied habitats. This is true because if some habitats had a clearly lower suitability, then some of the birds in that habitat could improve their chance of success by moving to the habitats of higher suitability. If they did not make that move, they would not have ideally adapted habitat selection behavior, contradicting the ideality assumption. The distribution is stable only when suitabilities are equal in all habitats. With Equations (2), a fixed set of habitat areas, and given population size, the condition of equal suitabilities in all occupied habitats completely determines the ideal free distribution. To prove this, let a_i be the area of the i th habitat, and M the population size. If exactly l habitats are occupied, then the equal suitabilities condition says that

$$S_1 = S_2 = \dots = S_l . \quad (3)$$

Note that the first ℓ habitats are the ℓ occupied habitats. These are the ℓ habitats with the highest basic suitabilities, B_1 . In fact, if the $(\ell + p)^{\text{th}}$ habitat were occupied, some $(\ell - q)^{\text{th}}$ habitat must be unoccupied (p, q positive integers such that $0 < p \leq N - \ell$ and $0 < q < \ell$), since only ℓ habitats are occupied. But, because $d_{\ell - q}$ equals zero, the suitability in habitat $\ell - q$ is $B_{\ell - q}$ and

$$S_{\ell - q} = B_{\ell - q} > B_{\ell + p} \geq S_{\ell + p},$$

or

$$S_{\ell - q} > S_{\ell + p}. \quad (4)$$

Because under our assumptions individuals settle where the habitat suitability is highest, the birds in habitat $\ell + p$ would move to $\ell - q$ where by (4) the suitability is higher. Thus, if there are ℓ occupied habitats, they are the first ℓ .

It is also true that M , the total population size of a given species over all its occupied habitat, is given by

$$M = a_1 d_1 + a_2 d_2 + \dots + a_\ell d_\ell, \quad (5)$$

since

$a_i d_i$ is the number of birds in the i th habitat, and the total population is the sum of all the birds in all occupied habitats.

From Equations (2),

$$S_i = B_i - f_i(d_i), \quad i = 1, \dots, \ell$$

so that $S_i = S_{i+1}$ in (3) implies

$$B_i - f_i(d_i) = B_{i+1} - f_{i+1}(d_{i+1}), \quad i = 1, \dots, \ell - 1. \quad (6)$$

There are $\ell - 1$ of these equations in ℓ unknowns; d_1, d_2, \dots, d_ℓ . With Equation (5), there are ℓ equations. These ℓ

equations can be solved uniquely² for the $d_i (i = 1, \dots, \ell)$ in terms of the constants M and the a_i . The distribution can be expressed as the proportion of birds in each habitat.

Denote the proportion in the i th habitat as P_i . Then clearly

$$P_i = \frac{d_i a_i}{M},$$

and the distribution is seen to be a function of the density in each habitat. Since the densities are determined by the condition of equal suitabilities, so is the distribution.

As example of the solution of the equations is given in Figure 2 for $\ell = 1, 2,$ and 3 . The suitability curves are drawn for three habitats, 1, 2, and 3. When no birds are present, the suitability is highest in 1 and equals B_1 . Therefore, if a small number of birds now settle in the habitats, they will all go to 1, because they settle where the suitability is highest. Then the density in 1 will increase from zero, and the suitability will decrease, following the curve labeled S_1 . As the population size increases, more and more individuals will settle in 1, until the density there is so high that the suitability is equal to the basic suitability in 2 (B_2). Now, any additional birds have a choice of habitats; 1 and 2 are equally suitable. However, these additional birds must increase the density in both habitats, and in such proportions that the suitabilities in both remain equal. Further increases in population size will raise the density in both habitats. If the population increases enough, the

²Because the $f_i(d_i)$ are always increasing.

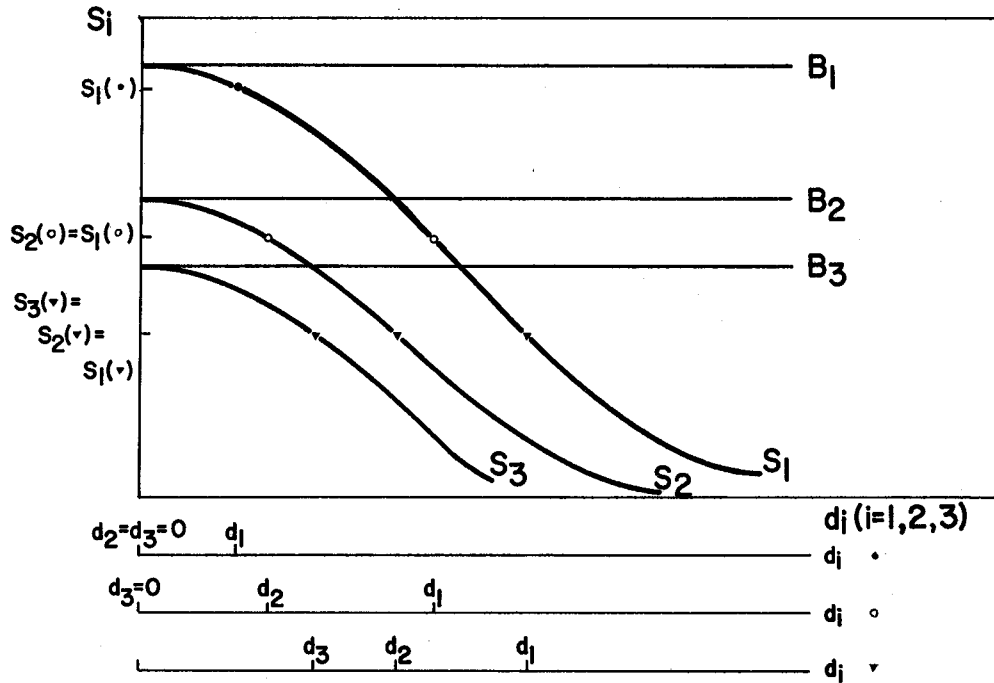


Figure 2. Suitability versus density: Habitats 1, 2, and 3. The ideal free densities are shown on the extra density coordinates at three values for the total population size, $M' < M'' < M'''$. The situation at each population size is denoted by (●) for M' , (○) for M'' , (▼) for M''' . At M' , the lowest population size, all the population is in 1; the densities in 2 and 3 are zero. At M''' , the largest population size, all three habitats are occupied.

densities in 1 and 2 will be so high that the suitabilities in both habitats are reduced to B_3 , the basic suitability in habitat 3. Any additional birds must increase the density in all three habitats in such proportions that the suitabilities in all three remain equal.

Allee-type ideal free distribution

Let us now briefly consider the effect on the distribution of Allee's principle which we have heretofore assumed does not apply. In this case, the S_1 curves first increase with density up to a maximum then decrease. These curves do not always have unique inverses; there are sometimes two densities corresponding to a single suitability. Therefore, the Equations (3) and (5) do not necessarily have a unique solution. Consideration of Allee's principle suitability curves is best done graphically as in Figure 3. At low population sizes, the birds will presumably go to habitat 1, and as the population increases, will enjoy an increasing suitability up to some maximum. Further increases in population size with all birds settling in 1, will cause a decrease in suitability in habitat 1 until at some higher population size (A), the density (d_1) in 1 is such that the suitability there equals the suitability in 2 at density 0. Now a remarkable event may occur. With a further slight increase in population size (A+), some birds will settle in 2 and perhaps some in 1. But the suitability in 2 increases with an increase in density, while the suitability in 1 decreases; therefore, $S_1 < S_2$, and suddenly it

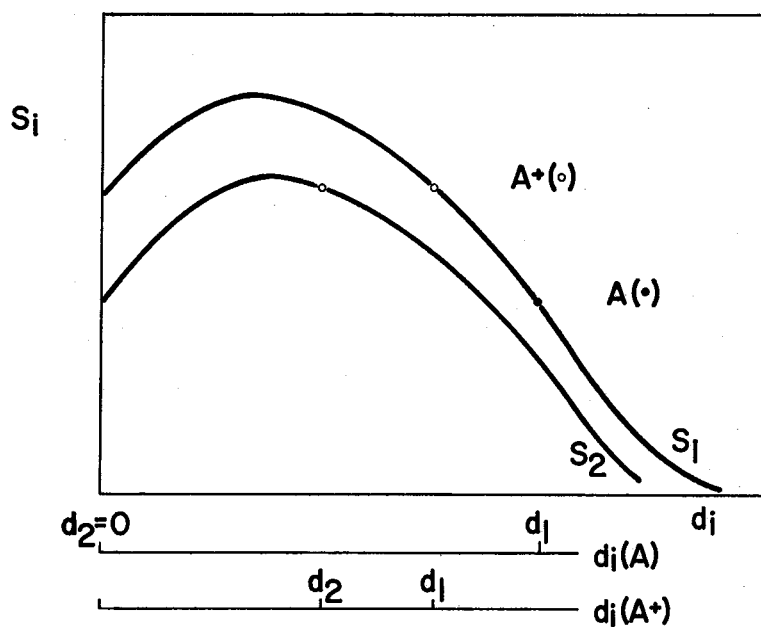


Figure 3. Suitability versus density under Allee's principle. At population size A the density in habitat 1 is $d_1(A)$. At population size $A+$ the density in 1 is $d_1(A+)$ while the density in 2 has increased to $d_2(A+)$. See text for explanation.

becomes advantageous for birds in 1 to go to 2. Being ideal, they will so move, and may continue to move until the suitability in 2 is maximal. They would then fill the two habitats in such a way that $S_1 = S_2$, and may well become common in both (open circles in Figure 3). Thus, a very small increase in population size may result in a very large change in the distribution. By manipulating the S_1 curves, many such changes can be produced, and one can generally conclude that under the conditions of this theory, species following Allee's principle may demonstrate erratic changes in distribution with small changes in population. One can imagine curves which lead to complete shifts in population while other curves may lead to no erratic behavior at all.

Unless otherwise noted, the Allee-type ideal free distribution will not be considered in the following Section.

Territorial Hypotheses and Effects on Distribution

We can now discuss the possible relationships of territoriality to distribution. We will consider three distinct hypotheses and put them in the framework of the preceding discussion. In order to do this, a general definition of territorial behavior will be made which does not imply any particular role for the behavior.

Territorial behavior is defined as any site dependent display behavior that results in conspicuousness, and in the avoidance of other similar behaving individuals. Territorial behavior is specifically not restricted to defensive and/or aggressive behavior nor are they excluded. The following hypotheses to be discussed were in each case inspired by the authors cited in connection with them.

The density assessment hypothesis

This first hypothesis ascribes a role to territoriality which permits achieving the ideal free distribution (non-Allee). It was first described by Kluyver and Tinbergen (1953). Before discussing the hypothesis and its consequences in distribution, some preliminary discussion on the achieving of an ideal free distribution will be presented.

Given the total population size M , the habitat areas a_i and the equations in S_1 (2), the density in each habitat is determined. The density in turn determines the proportion of the population in each habitat, or an ideal free distribution. The actual values will be expressed in terms of M and the a_i which for a given year are constants for

the purpose of the present discussion. However, M , and perhaps the a_i vary with time in a somewhat irregular fashion. Therefore, the proportion of the population in a given habitat may also vary between different years. This is demonstrated in Figure 2. The suitability curves for three habitats are drawn, and the habitat densities at three population sizes shown. The relative densities in each of the three habitats are shown on the extra abscissas, and are markedly different at the three population sizes.

If the total population size does not vary, then a species could consistently achieve an ideal free distribution by being composed of individuals, a fixed proportion of which prefer each habitat at all times, or by being composed of individuals which prefer each habitat a fixed proportion of the time. However, if the variation in population size does occur and leads to considerable variation in the ideal free distribution, then such a fixed habitat selection scheme will usually not work. In this case, the habitat selection of the individuals, if it is to be ideal, must adjust to the changing conditions.

In order for individuals to be able to modify their habitat selection in accordance with changes in the ideal free distribution, there must be some cue or cues which reflect these changes. The changes come about due to variation in population size and possibly habitat areas. These variables affect the densities in the various habitats and therefore the relative suitabilities. Any cue, such as foot-print abundance, which would reflect habitat densities, or any cues

which would reflect population size and perhaps habitat areas could be used by ideal individuals in achieving the ideal free distribution. The individuals would have their preference for a given habitat depend on the state of the cue.

Kluyver and Tinbergen (1953) suggested that the territorial behavior of resident individuals is used as a density cue by unsettled individuals so that they can avoid highly populated habitats where the chance of breeding success is presumably lower than elsewhere. These authors observed that the habitat distribution of some Paridae (tits) was dependent on population size. At low population levels, most of the individuals were found in a single habitat type, while at higher levels many individuals occupied another habitat type, but at a lower density (compare this with population sizes M' and M'' in Figure 2 of this paper). They emphasized that breeding success (and therefore, suitability) was not noticeably different in the two habitats. Thus, the distribution of the tits was apparently nearly ideal free, despite changing population size. No appropriate cue for density other than territoriality was observed, nor was there evidence for a cue for population size.

There is no evolutionary difficulty in supposing that territorial behavior serves as a density index. It is obviously to the residents' advantage to provide such a cue, since they suffer if their habitat is crowded to the extent that its suitability is lower than that in other habitats. It is also the advantage of the settling individuals to respond to such a cue,

for by so doing they avoid habitats where high density makes their chance of success lower than elsewhere. Since the population size of tits varies considerably, the development and use of some density cue, such as territorial behavior, might be expected.

The density limiting hypothesis

Introduction. The second territorial hypothesis is based on a model from Huxley (1934), who described a territory as a rubber disk. The disk can be compressed, but with an increased amount of force necessary as it gets smaller. This hypothesis is relevant to the free aspect of the homogeneity assumption about birds in the ideal free model. That assumption states that any individual is free and may therefore enter any habitat on an equal basis with the birds already resident there. With the rest of the homogeneity assumption, this means that the average success of the occupants of a habitat is also the suitability that an unsettled bird will have (on the average) on settling in that habitat. The free assumption, as already mentioned, fails if the species is limited by nest holes which, once occupied by a resident, are not relinquished or shared. The second territorial hypothesis describes another possible way in which this assumption might fail. Suppose the residents of the habitat, by their territorial behavior, made it dangerous for unsettled individuals to enter the habitat. Then the average success of newly settling individuals will be lower than the habitat average, and the assumption fails. If so, ideal individuals maximizing their own success would not necessarily settle

where the habitat suitability is highest, and the habitat suitabilities no longer must be equal. Since Equation (6) no longer holds, the distribution is not determined as before. There exists a new, different distribution.

The supposition that the territorial behavior of residents restricts non-residents from settling is reasonable. In evolution such behavior effectively prevents the density in the habitat from increasing, maintaining the suitability (see Figure 4). This would give the aggressive residents a selective advantage and the behavior, as suggested by Brown (1964), would spread throughout the population. However, if all the individuals, settled and unsettled alike, became equally aggressive, it might not then be possible for the settled birds to make a habitat less suitable to unestablished birds. This is perhaps unlikely; for example, dominance seems to depend on experience (Nice, 1936; Sabine, 1955) which for a given area should vary considerably from bird to bird. In the following discussions we will assume that all individuals are not equally aggressive, so that social dominance hierarchies are established and the free assumption does not hold.

Consequence of hypothesis on the distribution. We consider in more detail the altered ideal distribution which would arise from this hypothesis. By definition the ideal bird always goes to the habitat where his potential success is highest. In the ideal free distribution, the potential success of a new individual settling in a given habitat is equal to the average of all individuals resident there, including the new one. This

is the habitat suitability described by Equation(2). If the unsettled birds are restricted by the territorial behavior of residents, then their potential success is less than the average of the habitat. This suggests that we define some quantity t , $0 \leq t \leq 1$, which can be subtracted from one and multiplied into the S_1 , to yield the apparent habitat suitability from the point of view of the unsettled bird. This apparent habitat suitability may be denoted by T_1 , defined symbolically in Equation (7):

$$T_1 = S_1(1 - t) \quad (7)$$

Let us now consider some of the properties of t . This quantity will depend on density, and can be reasonably assumed to always increase as the density in a habitat increases. This assumption is justified because t is related to the resistance of the established birds. The resistance from each male evidently increases as the territory size diminishes (Huxley, 1934); that is, as the density increases. Thus, the per bird resistance always increases with density. Also, the number of birds increases with density. Therefore, the overall resistance, and t , must increase with density. We will assume that t does not vary with habitat, since it is unlikely that the territorial resistance is dependent on habitat, except as density varies. Thus, Equation (7) may be rewritten

$$T_1 = S_1(1 - t(d_1)) \quad (8)$$

The function T_1 , like S_1 , always decreases with density, since S_1 always decreases and $t(d_1)$ always increases with density. Also, T_1 is always less than or equal to S_1 . The actual suitability of the habitat remains S_1 ; T_1 is just the apparent suitability from the point of view of the unsettled bird.

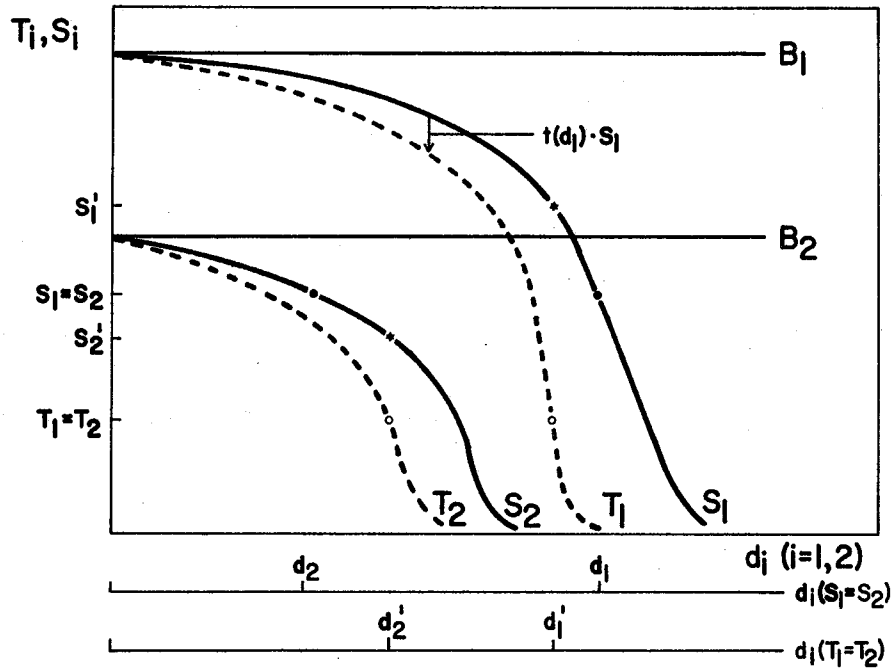


Figure 4. A comparison between ideal free and ideal dominance distributions: Habitats 1 and 2. Population size and habitat areas are constant. S_i is the suitability for established birds. T_i , the apparent suitability to unestablished birds. The filled circles represent equilibrium conditions $S_1 = S_2$ for the ideal free distribution, and densities for that distribution are given below as (d_1, d_2) on the abscissa labelled $(S_1 = S_2)$. The open circles represent equilibrium conditions $T_1 = T_2$ for the territorial distribution, and densities for that distribution are given as (d_1', d_2') on the abscissa $(T_1 = T_2)$. At $T_1 = T_2$ the actual suitabilities are given as (S_1', S_2') , marked on the S_1 curves with a star. Note that in going from the ideal free to the ideal dominance distribution, at constant population size and habitat areas, the density in 1 decreases ($d_1' < d_1$) while the density in 2 increases ($d_2' > d_2$). Some individuals have in principle been forced from habitat 1 into habitat 2. See text for further discussion.

The T_1 in (8) are defined such that an ideally adapted individual will always go to the habitat where T is highest, assuming as before that all (unsettled) individuals are alike in their adaptation to the habitats. This leads, as with the S_1 , to an equilibrium condition where the T_1 are equal in all occupied habitats. The resultant equations, with (5), completely define a set of habitat densities and a new distribution. This distribution may be called the ideal dominance distribution. Like the ideal free distribution, the ideal dominance distribution is a useful basis for discussion, but because of the underlying assumptions, can only approximate any real life situation.

Interpretation. Some remarks about the T_1 in (8) may make them easier to understand. If within an area some habitats are better than others then the territorial restrictions may just restrict newly settling individuals to the less good habitats. Then T_1 represents the average success expected in the area for individuals in the less good areas. However, in a uniform habitat where no less favorable regions exist, then the territories of all occupants will be, on the average, about equally suitable. In this case, $t(d_1)$ represents only an entering risk to unsettled individuals. If they can successfully settle in the habitats, they may expect to be as successful as the habitat average. But the act of settling may involve a serious risk of physical harm. There may be a high probability of failure with accompanying mortality. Thus, the T_1 may not be a measure of the success of some members of the habitat, but

a measure of the average success of a hypothetical group of individuals which tried to enter a habitat until either successful or dead.

These two territorial hypotheses exemplify the distinction between ultimate and proximate determinants of behavior. These are defined as follows. Ultimate determinants of behavior are the environmental factors which produce the natural selection that leads to the genetic basis for the behavior. Proximate determinants are the stimuli that prompt the behavior. The behavior that we are considering is the habitat selection of individuals. The first hypothesis is that territorial behavior is only a proximate factor providing information about density. The second hypothesis is that territorial behavior is an ultimate factor which by directly influencing the survival of past individuals which selected certain habitats to breed in has actually caused the population-genetic basis for the habitat selection to change in some way. And since the distribution is determined by the habitat selection, the territorial behavior is an ultimate cause of the phenomenon as well. However, in the second hypothesis territorial behavior is probably also a proximate factor. It could easily provide information about itself and provide a stimulus to which unsettled individuals could respond. This is quite likely because territorial behavior generally involves display and vocal announcement as a substantial part of the "defense" of boundaries.

The spacing hypothesis

Lack (1964) and Johnston (1961) have supported a third territorial hypothesis, that the territorial behavior has been

evolved only to space individuals within a habitat. This means that the density in a habitat is determined independently of the behavior, but that given a certain density, the individuals separate as much as possible and have non-overlapping home ranges. For example, suppose a population of a territorial species can achieve distribution without the territorial behavior either cueing density variation or restricting habitat occupancy. Then the role of the territorial behavior may be purely behavioral, isolating mating adults to strengthen pair bonds (Lack, 1954). Or the behavior could prevent the spread of disease by a quarantine effect. Whatever its role, if the territorial behavior only spaces individuals, it has nothing to do with whether or not an individual will settle in one habitat or another. It only affects the movements of the individuals within the habitat. The effect of spacing is to keep the instantaneous distribution of individuals within the habitat fairly uniform. It does not alter the number of occupants of the habitats, nor does it affect the average number of individuals using any portion of the area within the habitat (the average being taken over some time period). Thus, the average density over any piece of land (i.e., any habitat) is not influenced by territorial behavior under this hypothesis. If territorial behavior only spaces individuals, it has no effect on the habitat distribution, either ultimately or proximately.

Application of the theoretical development

Approach. The next matter is to consider the problem of identifying the actual role of the behavior relative to

habitat distribution in a given species. We have defined two theoretical distributions under certain assumptions and three different territory hypotheses. We may, as a first approximation, assume that if territorial behavior has one of the hypothesized roles in a given species the actual habitat distribution will be similar to the theoretical distribution described for that hypothesis. Thus, if we can show that the actual species distribution is approximately ideal dominance, this may be taken as evidence in the support of the hypothesis that the role of the behavior is to limit density. Or if we can show that the distribution is consistently ideal free in spite of variation in population size, and can find no other evident cues for density and/or population size variation being used by the species, then this may be taken as evidence in the support of the hypothesis that the behavior is used for density assessment. If we can show that the distribution is not consistently ideal free in the face of variation in population size, nor ideal dominance, then this may be taken as evidence for a lack of any density assessment or density limiting mechanism, and spacing remains as the most tenable of the hypotheses offered. (Other hypotheses may exist, but we will not pursue them here.) The approach to the problem rests on identifying the distribution as (approximately) ideal free, ideal dominance, or neither.

Density and habitat suitability. If a population has an ideal free distribution, then by definition the suitability of all habitats is equal. We used this to show that the ideal

free assumptions determine a distribution. However, the densities in the different habitats are not necessarily equal (see Figure 2). Thus, if a species has a nearly ideal free distribution, habitats with different densities will show similar success rates.

If a population has an ideal dominance distribution, then the suitability of all habitats is not necessarily equal. Only the apparent suitabilities (the T_1) will be everywhere equal, assuming ideally adapted individuals. In this case, it will now be shown that, for two occupied habitats, p and q, if $d_p > d_q$ then $S_p > S_q$: the suitability is higher in habitats of higher density. From the equilibrium condition, for occupied habitats q and p,

$$T_q = T_p . \quad (9)$$

Since, by (8)

$$T_q = S_q (1 - t(d_q)) ,$$

$$T_p = S_p (1 - t(d_p)) ,$$

then substituting in (9) we obtain

$$S_p (1 - t(d_p)) = S_q (1 - t(d_q))$$

and

$$S_p/S_q = (1 - t(d_q))/(1 - t(d_p)) . \quad (10)$$

If $d_p > d_q$, then $t(d_p) > t(d_q)$, since the t function always increases with density. Then

$$(1 - t(d_q)) > (1 - t(d_p)) ,$$

$$(1 - t(d_q))/(1 - t(d_p)) > 1 ,$$

and therefore, by (10),

$$S_p/S_q > 1 .$$

From this it follows that $S_p > S_q$ as asserted. Thus, if a species has an ideal territorial distribution, then the success rate in habitats with higher densities of residents will be higher. This assumes that the t function does not depend on habitat, and always increases with density.

It is possible using another approach to show that this relationship between density and suitability exists. Assume that territory size is inversely related to the number of birds against which it is defended (Huxley, 1934). The better a territory is, the more there are that are less good, and there are more birds potentially trying to overtake it. Since the territory must be defended against more birds, it must be smaller. Hence, more suitable territories are smaller, and density, which is inversely related to territory size, is seen to be higher in high suitability habitats.

Figure 4 shows examples of the S_1 and T_1 curves for $N = 2$, and a sample population distributed freely (filled circles) and territorially (open circles). Note that the suitability in the ideal free distribution is equal in both habitats ($S_1(\bullet) = S_2(\bullet)$). In the territorial distribution, the suitability and the density are higher in habitat 1 than in habitat 2 ($S_1(*) > S_2(*)$, $d_1 > d_2$).³

These conclusions suggest that the role of territorial behavior in the habitat distribution of a territorial species

³We should note the discussion of Gibb (1961) in which attention is drawn to the relationship between the role of territorial behavior and differences in habitat suitability. Gibb's remarks are not formally developed, and do not distinguish the density assessment and density limiting hypotheses. But they do foreshadow several of the ideas presented above.

can be ascertained as follows: If the high density habitats show consistently higher success rates, and if no density limiting mechanism other than territorial behavior is evident, then the role of the territorial behavior is evidently to limit density. If suitabilities in all habitats are equal, even though densities are not, if the distribution changes with changing population size, and if no alternative density or population size cue is apparent, then the role of the territorial behavior is evidently to serve as a density assessment mechanism. If neither of the above two criteria are met, then the role of territorial behavior seems to be only to space individuals. Underlying this approach is the assumption that the birds are approximately ideally adapted. This assumption may well fail, and this possibility should always be considered. There is also the possibility, ever present, of hypotheses different from those considered here.

Uncertainties in application. There are a number of uncertainties involved in these conclusions which should be given careful consideration. Some of this uncertainty is inherent in the theory, which describes the relationships of expected values or population means. Any given realization of the theory (e.g., the observed habitat suitabilities in a given year) is expected to deviate from the average values, even if the assumptions of the theory are met. This deviation will alter the succeeding year's distribution somewhat (by accidental selection), and so some fluctuation in the distribution may also be expected.

Another source of uncertainty lies in inherent failure of the assumptions, particularly the ideality assumption. For example, the sensory reception of the bird cannot be perfect, and so the bird can be expected to misread whatever environmental cues it uses to assess the suitability of a habitat. Also, the correlation between these cues and suitability is probably never perfect. Finally, the birds may reasonably be expected to be always evolving towards the ideal state without ever achieving it. These failures of the ideal assumption will lead to errors in the individual judgments of habitat suitability.

Hopefully the uncertainties in our predictions will be generally independent in different years, or even in different regions in the same year. Probably, most of the error-causing factors are rather local in effect. A major exception is weather, but even this factor changes from year to year. Thus, in most cases, sampling over several years, or perhaps over widely separated regions in the same year should provide a way of estimating or controlling these errors. If the errors are not independent even over years, then the species may be considered to be evolving and changes over time should be detected. Thus, results which are consistently obtained over a number of years may be reasonably considered free from these errors.

Measurement of suitability. The problem of measuring suitability remains. The suitability of a habitat is a reflection of the average genetic contribution of resident

adults to the next generation, and must be closely related to the average lifetime production of reproducing offspring in the habitat. Therefore, it must depend on several components, including reproductive rate, and survival of adults and immatures. Since territoriality is normally associated with breeding behavior and habitat distribution during the breeding season, we will usually associate suitability with such things as nesting success, feeding rates, and clutch size.

PART II
EXAMPLES OF APPLICATIONS OF THEORY

Introduction

Although the main intent of this thesis is to provide clearer definitions of the territorial hypotheses that have been debated, it is possible that non-theorists might have difficulty in relating these definitions to the sort of observations commonly made. Therefore, I will provide two examples of the way in which the theory is intended to be used. The format of each example is the same. We wish to compare density and suitability in a territorial species. In order to do so, we must assume that suitability (which is not well defined) is related to some measurable feature of the bird-habitat interaction. In each case, we make this assumption carefully, as the interpretation of the following data depends on it. Having made the assumption, we proceed to measure our supposedly suitability-related feature for comparison with the habitat variation in density. If the suitability index does not vary appreciably, we conclude that the distribution may be nearly ideal free. If, at the same time, there is annual and habitat variation in densities, some density cue, perhaps territorial behavior, is implicated. If there is appreciable variation in the suitability index, which is positively correlated with density, then, since this correlation is a characteristic of the ideal territorial distribution defined in Equation (9), we conclude that the actual distribution may be nearly ideal territorial. In the absence of evidence of some other

density limiting factor, we conclude that the function of territorial behavior may be to limit density. If there is appreciable variation in the suitability index, which is not positively correlated with density, then there is no evidence to support the conclusion that the distribution may be either the density cueing or density limiting hypotheses, and the spacing hypothesis becomes the most likely of the three.

It is worth repeating that this method of evaluating the role of territorial behavior rests on a number of assumptions. The birds must be ideally adapted in their habitat selection behavior. The suitability index must be truly related to the potential genetic contribution of the individuals. Suitability within a habitat must decrease as density increases, at least over normal ranges of density variation. The presence of these assumptions emphasizes the complexity of the problem, which will not be solved easily for a given species. The studies presented in this section are a first step, from which one may find direction, but not final conclusions.

Sex Ratio Variation in the Dickcissel
(Spiza americana)

Introduction

Consider a species where all females have a choice of males (either because there are more males than females or because males are polygynous). Suppose further that only the males are territorial, that the females are free, and that all individuals are ideally adapted. Then it follows that the suitability for males is validly indexed by the sex ratio (females/male). This is so because the genetic contribution of males is achieved through the females. If all females have identical suitabilities, then males with equal numbers of mates will have equal suitabilities. Males with more mates will have higher suitabilities; males with fewer mates will have reduced suitability. Therefore, male suitability can be measured by the sex ratio, and we can study the role of male territoriality by comparing sex ratios in habitats occupied by the males at different densities.

One may look at the sex ratio-density correlation in situations where only males are territorial and females have choice of males. These conditions are satisfied by the Dickcissel which breeds throughout the Midwest. The males are strongly territorial and the females breed in the territories of the males but show no aggression. We⁴ noted that females

⁴The observations were made with Steve Calver, student at Duke University.

were more frequently encountered in some habitats than others and that many males were apparently mateless. This implied that all females had a choice of mates. Zimmerman (1966) has recently shown that the male Dickcissel is polygynous. On making these observations we decided to measure the variation in the sex ratio from habitat to habitat and from geographic region to geographic region to see if the variation was in conformity with the expectations of the ideal dominance, or the ideal free distribution.

Measurement of a Sex Ratio Index

A sex ratio index was estimated as the percent of mated (or potentially mated--see below) males. A criterion for scoring a male as mated or unmated was decided first. We noticed that singing males when approached showed two distinctive behavioral responses. Some males stopped singing and gave persistent alarm notes which were high pitched at first but which often changed to "chek". These males when watched carefully were found to have mates. Other males when approached persistently continued singing, flying from perch to perch when chased. A few males simply flew out of sight, or flew into the ground cover. These males which persistently sang, or otherwise failed to give alarm notes were almost always determined to be unmated. We checked the possibility of incubating or hiding females in 12 test cases by dragging a rope between us in the "unmated" male's territory. This never produced any females. Occasionally a female was seen in the territory of the non-alarm giving males, but these females

did not appear to be nesting, nor in any way bound to the territory in which they were first seen. Any males which gave persistent alarm notes were scored as mated; any male which failed to give such alarm notes was scored as unmated. Any unmated male with a female in its territory was scored as potentially mated and counted in with the truly mated birds. The territories of all unmated males were searched carefully in order to find females. All observations were made between 10 June and 20 June, 1965.

We recognize that our index does not correspond exactly to the true sex ratio since males may have had mates which they did not defend, some unmated females may have been missed, some non-territorial males may have been missed, some males may have given persistent alarm although they did not have a mate, and some mated males may have had two mates. However, since we are only concerned with differences, we need only assume that the discrepancies involved were alike in all areas. We found no reason to reject this assumption. The birds' behavior was similar wherever we went, and there was no evident variation in the stage of the nesting cycle from one study area to another.

The local study

Introduction. In making preliminary observations, we found that two particular local habitat types (clover fields and pastures) were both frequently encountered and frequently occupied by Dickcissels. Therefore, we concentrated our efforts in those two habitats. The Dickcissels were clearly

more dense in clover fields than in pastures (see Graber and Graber, 1963). Therefore, the prediction of the ideal territorial distribution model is that the sex ratio be higher in the clover fields than in the pastures. This is the prediction that will be tested in this section, using the sex ratio index.

Results. The sex ratios in clover fields and pastures were estimated in six different regions across the range of the Dickcissel. A total of 252 males were observed, 171 in clover fields, 81 in pastures. The regions are marked by Roman numerals on the map in Figure 5. Above each point on the map are plotted the estimates for the two habitats sampled. The points are connected by a line--dashed for clover fields, dotted for pastures. In all six regions, the proportion of mated males (the sex ratio index) was estimated to be higher in clover fields than in pastures. This is consistent with the prediction of the ideal dominance distribution model. We find support, therefore, for the hypothesis that the territorial behavior of the males apparently limits the density in the clover fields, forcing some males to settle in less suitable pastures.

The Geographic Study

Introduction. We made a transect across the range of the Dickcissel, as shown on the map in Figure 1, (points A to G). The apparent center (mode) of the Dickcissel's distribution across the transect was in the Mississippi River Valley, with the bird becoming less abundant to the east and to the west.

The density in a clover field in the Mississippi River Valley was estimated to be more than 5 males/acre from a sample of about 6 acres. Densities elsewhere were estimated roughly to be below 2 males/acre, (see, for example, Graber and Graber, 1963), and at the edges of the range were on the order of .01 birds per acre, all estimates in clover fields. We supposed then, that if the Dickcissel had an ideal territorial distribution, which affected geographic as well as field to field distribution, then we should observe a decrease in the sex ratio index as we moved from the Mississippi River Valley either to the east or to the west.

Methods. In order to test this prediction, we selected for careful sampling a series of geographic regions which were along a west-east transect of the species' range. Seven regions from 60 to 300 miles apart were sampled; these regions are marked by capital letters on the map in Figure 1. In order to fairly sample a region, we selected 2-6 whole colonies within the region being studied, scoring all the males in each colony for mates or potential mates. The males thus scored were considered to be random samples from the region, containing no habitat bias. In all cases, a colony occupied most of the habitats in that region. The colonies sampled were generally the first that we found. Those protected by No Trespassing signs and, in the Springfield, Illinois sample, those which were extremely large were not sampled. In the Mississippi River Valley sample, matelessness and the number of males in the most densely occupied habitat

in two colonies were estimated from a sample. These estimates were used to estimate for that particular habitat the number of mated and the number of unmated males. These estimates were tabulated with the rest of the data collected from the region. A total of 390 males were scored.

Results. The results are shown in Figure 5 (solid line). Above each point on the map marked with a capital letter is plotted the regional sex ratio index there. These are connected with a solid line, the line being drawn below that drawn for the clover fields (see above), since the regional value must always fall below that in the optimal habitat, clover fields. The trend is clear and significant. The regional estimated sex ratio index drops from nearly 1 in the (modal) center of the range where the Dickcissel is very common to nearly zero at the edges of the range where the species is found in very low numbers. We conclude that the habitat distribution defined geographically also appears to be territorially limited and that some males are evidently forced to settle in less suitable regions.

Discussion

While these results do not prove that the territorial behavior of male Dickcissels limits the density in better habitats, they are not inconsistent with the hypothesis. Further, they are not consistent with the hypothesis that the distribution is perfectly adapted and free from restrictions. Besides territoriality, we know of no other difference between males and females which would explain the observed sex difference in distribution.

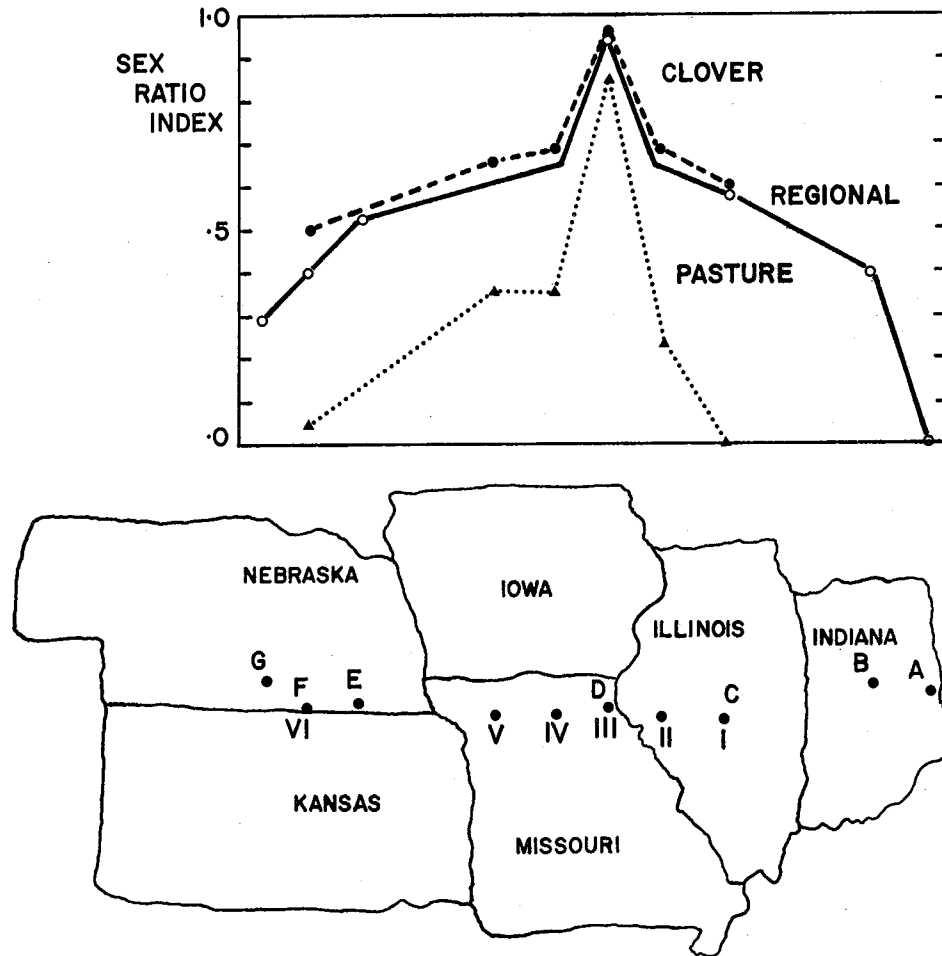


Figure 5. Local and regional variation in a sex ratio index of the Dickcissel. On the map are shown the study areas. Above, the estimates of overall regional indexes are plotted as open circles and connected with a solid line. The estimates of regional clover field indexes are plotted as solid circles and connected with a dashed line. The estimates of regional pasture sex ratio indexes are plotted as solid triangles and connected with a dotted line. The graph of the overall regional sex ratio index is drawn below the graph of the clover field sex ratio.

Let us consider the interaction between the geographic results and the habitat results. In Figure 6 we plot the differences (as a percentage of the larger value) between the sex ratio indexes in clover fields and pastures, versus the overall regional sex ratio indexes read from the graph in Figure 5. As can easily be seen, the difference between habitats decreases as the overall regional sex ratio index increases. This is as it should be under the hypothesis that it is territorial behavior which is causing the variation. As the overall sex ratio increases, there are relatively fewer males for the females to mate with. Thus, more and more females will be forced to follow those males which were forced to settle in less suitable habitats (pastures). This movement of females into the less suitable habitats tends to make the ratio there more equal to that in the optimal habitat. In a monogamous species where the sex ratio is one, the sex ratios in all habitats would be equal even though the males' distribution be limited by territorial behavior.

In conclusion, the results support the hypothesis that the territorial behavior of male Dickcissels limits density. The distribution of male Dickcissels appears to be ideal dominance, not ideal free.

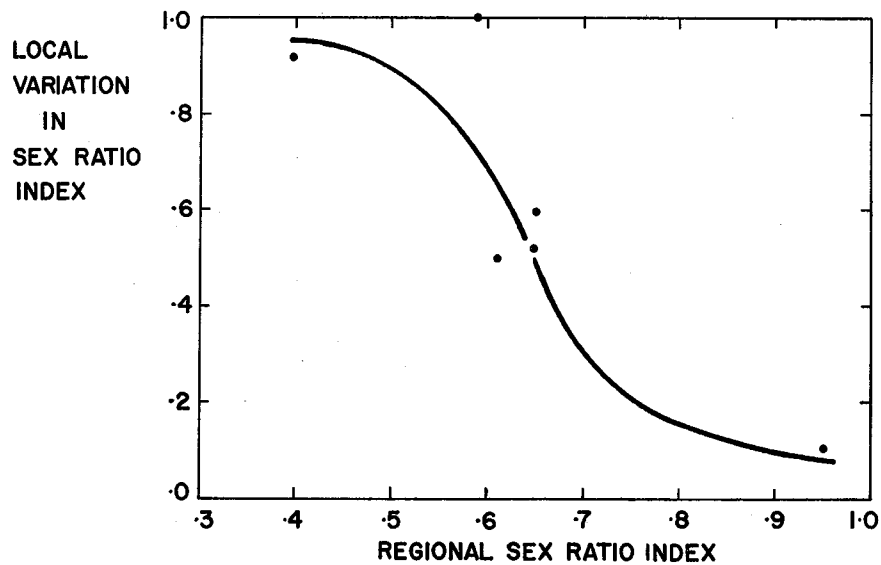


Figure 6. Interaction between local variation in sex ratio and overall regional sex ratio index. The local relative difference in sex ratio indexes is the index in clover fields minus the index in pastures divided by the index in clover fields within each of the six regions sampled. The regional sex ratio index for each point is read from the solid line in Figure 5. See text for explanation.

Breeding Success in a Local Population of
Field Sparrows
(Spizella pusilla)

Introduction

For many species, the assumptions of the previous example do not hold. If these species are to be studied, another set of assumptions are needed. It was previously noted that the suitability of a habitat must be related to the breeding success of individuals resident there. Breeding success has many components in bird populations. It depends on clutch size, nest mortality, food supply, and other factors as well. If we assume that breeding success in general, and its components in particular, are valid indexes of habitat suitability, then we can use the variation in these components to study the territorial behavior of the species. As before, if the birds in high density habitats seem to be raising more offspring than birds in low density habitats, then the observations suggest that a positive correlation between suitability and density exists, as predicted by the density limiting territorial hypothesis. If all the birds seem to be raising about the same number of offspring, irrespective of habitat, then the observations suggest that no significant variation in suitability exists, as predicted by the density cueing territorial hypothesis. If breeding success varies, but is not positively correlated with density, the observations are not consistent with either territorial hypothesis. These predictions depend on ideal adaptedness of the birds under consideration.

This example applies this approach to a local population of Field Sparrows. It should be remarked at the outset that local population studies are vulnerable to the uncertainties described at the close of the first section. Local, random factors could easily produce deviations from the breeding results expected by the population. The following example study is also restricted to a single year, so that random annual differences cannot be distinguished. Therefore, before any firm conclusions about Field Sparrows can be reached, other local populations should be studied, perhaps in a similar way.

The population studied was a local population of Field Sparrows breeding over a variety of habitats bordering Lake Raleigh, Raleigh, North Carolina. The habitats were farm lands, mostly pine plantations of differing ages and overgrown pastures, which border the northwest edge of Lake Raleigh. Field Sparrows are year-round residents there and breed throughout the area. Their nests are open, and may be placed very near the ground or as high as seven feet. The breeding season begins in late February or early March, when most of the territorial chases and displays are observed. Nesting begins in late April and continues at a decreasing rate until early September. The males and females have similar plumages, both being very plainly marked. Only the males seem to display territorial behavior. The territorial behavior apparently does not include song, and is not easily observed.

Specific Study Areas

The area designated as habitat 1 consisted of 14.7 acres of pine planting in which the trees (Pinus taeda) were co-dominant with broomsedge (Andropogon virginicus). Most of the trees were over 6 feet in height. Habitat 2 consisted partly of about 15 acres of another pine planting in which the trees were quite small (less than 3 feet tall) and scattered. The dominant vegetation was Festuca elatior and Lespedeza lineata. Also in habitat 2 were 10 acres of a nearby pasture in which the same vegetation dominated, but pine trees were absent.

Procedure

Between the dates of April 18 and August 30, 1964, nearly 100 field trips were made on 75 different days. Most of these were in the months of May, June and July. They averaged two hours apiece. The total study area was examined thoroughly at least once a week except during August. Other trips were spent in finding and checking nests, or in banding nestlings or newly fledged young. Observations on feeding behavior were made at opportune times.

Density. Density was measured in terms of territorial males per acre by spot mapping. Each male was assigned to one habitat or the other according to where he sang, or, if he did not sing, in which field his mate chose to nest. The observed proportion of birds in each habitat was compared with the proportion of the total area studied in that habitat, and the difference tested for statistical significance. The null hypothesis is that the birds settle over the two habitats in

the same proportions as the relative areas of the habitats, i.e., that the average densities in the two habitats are equal. Under this null hypothesis, there is just one habitat under study. The errors in the proportions were assumed to be binomial. This assumption is based upon the fact that the population size in a given year is fixed. It implies that the birds do not space themselves or flock within this (or any) "single" habitat. This is probably not true; the birds probably do space themselves within any habitat, and so the binomial errors may well overestimate the true density variation within a habitat. Thus, if the proportion of birds in an area differs significantly from the proportion of area in that habitat, then it may be safely presumed that a meaningful difference in density exists. The actual test was a z-test, which depends on the asymptotic normality of the proportion estimate.

Habitat suitability. Habitat suitability was assumed to be proportional to several components of breeding success. Large numbers of observations were obtained on six of these components: matelessness of males, nest mortality, egg failures (infertility?), desertions by female (female mortality?), clutch size, and feeding habits.

Matelessness. Matelessness of males was the average number of days that the males in each habitat were without a mate. The mateless males were identified by their behavior; they sang continually and were rarely seen with another bird. Individuals were distinguished by their songs, which in all

cases were quite distinctive (Borrer, 1961). The date on which mateless males obtained mates was also quite easily noted. The song changed in quantity and length, and after several days disappeared altogether. The number of mateless days were counted for each male, and averages and variances found for each habitat. The separate values obtained are not independent random variables, however, since the obtaining of a mate by one male may well lengthen the period that another goes mateless. Therefore, application of normal statistical testing procedures (e.g., a t-test) is inexact.

Nest mortality. Nest mortality was estimated on a daily rate basis, following the method of Mayfield (1961). The habitat comparisons were made between the daily rate estimates. Given the assumptions that the true rate does not vary with the age of the nest and that all nests are identical, the proportion of observed nest-days which result in failure is binomially distributed. The proportions of failures in each habitat were thus compared in a t-test, again assuming that each was normally distributed. The calculated overall nest mortality rates were also computed for direct comparison.

Egg failures. Egg failures represent eggs which survived to hatching time but which failed to hatch, or to produce a viable young. Only nests followed through hatching were used. The percent of such eggs in each population was estimated, and also the average number per nest. The latter averages may reasonably assumed to be derived from independent samples, and a t-test of significance was conducted.

Female desertion rate. Female desertion rate was calculated on a per nest-day basis from nests which were known to be deserted. In all cases but one, the male was deserted also, and in that one case, he had disappeared several days before. In three cases, the deserted nest was disheveled but the contents left intact. Two additional desertions were of nests containing nestlings. These cases evidently represent female mortality; in the first three, the predator apparently took the female directly off the nest. Because of the probable relation between desertion rate and adult mortality, the former is considered separately from overall nest mortality. The procedure for testing was identical to that given above for nest mortality.

Clutch size. Clutch size is the average number of eggs laid per nesting attempt. It was estimated for each habitat using only unequivocally full clutches. Nests discovered within a day of hatching or showing signs of recent predation were not considered. Averages were compared in a t-test.

Feeding habitat. Feeding habitat was studied by watching the coming and going of adults feeding nestlings. These observations were made from all vantage points, the nest, the feeding area, and some neutral point off to the side.

Results

The density in habitat 1 was 1.51 males/acre (23 males in 14.7 acres) and in 2 was .56 males/acre (14 males in 25 acres). Thus, 62% of 37 males resided in 35% of the studied area. This difference is sufficiently large to reject the hypothesis that

densities are equal ($z = (.62 - .35) / ((.35)(.65) / (37 - 1))^{1/2} = 3.40$, d.f. = 36, $p < .01$).

The average length of time that the males in 1 were mateless was 9.56 days (SE = 4.33 days). The males in 2 were mateless an average of 10.71 days (SE = 5.44 days). The difference of about 1 day is in favor of 1 but is evidently not significant.

Nest mortality computations are given in Table 1. The estimated percentage of nests in 1 which survived to fledge young is 20%. In 2, an estimated 49% were successful. The difference is relatively large, and in favor of 2. The z value at 503 degrees of freedom is 2.02 ($p < .05$).

Twenty-one percent (12) of 57 eggs in 17 nests which survived through hatching time in 1 failed to hatch, an average of .7 eggs per nest. None of the 33 eggs observed in 10 nests in habitat 2 failed. The difference is large, in favor of 2, and statistically significant ($t = 2.1$, d.f. = 25, $p < .05$).

Of 333 nest-days observed in 1, 5 resulted in a female desertion, a rate of .015 desertions/nest-days. Of 172 nest-days observed in 2, 1 desertion was observed, a rate of .006. The difference is again in favor of 2, but is not statistically significant.

The average clutch size in 1 was 3.43 eggs/nest (SE = .11, $n = 21$). In 2, it was 3.56 eggs/nest (SE = .16, $n = 9$). Again, the difference is in favor of 2, but is not significant.

The birds in habitat 1 were observed gathering food for their nestlings from three areas: a 5 acre alfalfa field

Table I. Nest mortality by habitat (1, 2)

A. Per day

	Total		Eggs		Young	
	<u>1</u>	<u>2</u>	<u>1</u>	<u>2</u>	<u>1</u>	<u>2</u>
No. Nest days	333	172	210.5	65.5	122.5	106.5
No. Failures	24	5	13	2	11	3
rate/day	.073	.029	.061	.030	.089	.028
95% confidence limits	.047-.108	.011-.079	-	-	-	-

B. Per Attempt

	<u>1</u>	<u>2</u>
No. days: laying to hatching	14	14
mortality rate/day (eggs)	.061	.030
Survival rate/day (eggs)	.939	.970
Survival rate egg laying and incubation $(.939)^{14} = .42$	$(.970)^{14} = .65$	
No. days: hatching to fledgling	8	8
Mortality rate/day (young)	.089	.028
Survival rate/day (young)	.911	.972
Survival rate hatching to fledgling $(.911)^8 = .47$	$(.972)^8 = .79$	
Survival rate over nesting $.42 \times .47 = .20$	$.65 \times .79 = .49$	

bordering the habitat, a bushy creek tangle also bordering the habitat, and, occasionally, from small patches of Compositae (Erigeron, Astor) within the habitat itself. These latter patches were dominant over about 15% of the total area of habitat 1. The birds in habitat 2 were observed gathering food for their nestlings from a 10 acre alfalfa field bordering habitat 2 and from the Lespedeza-Festuca which covered about 70% of the total area of the habitat. Although the same brushy tangle adjacent to habitat 1 was also adjacent to habitat 2, I did not observe any habitat 2 birds feeding there.

To summarize these results, habitat 1 had a significantly higher density than 2, but most of the suitability components measured indicated that 2 was more suitable. The observed nests in 2 had larger clutches, more fertile eggs, higher survival rate, and fewer female desertions. The feeding areas used by the birds in 2 seemed to be more abundant, more available, and qualitatively similar to those used by birds in 1. However, the males in 1 went mateless somewhat less than the males in 2.

Discussion

The preceding results suggest that territories in habitat 1 were not more suitable for breeding than those in habitat 2. Since habitat 1 had a higher density, this means that there is evidently no positive correlation between density and suitability. Therefore, the distribution is evidently not ideal dominance. The results also suggest that habitat 2 is more

suitable than habitat 1, i.e., that suitability is not equal in the two habitats. If generally true, this would indicate that the population is not ideally adapted to the habitats studied. This might be expected considering the semi-artificial nature of the habitats (pine plantings). The population may not have had time to adapt. However, the components of suitability measured may not reflect actual suitability since annual adult mortality and the survival of fledglings and immatures were not considered. The Field Sparrow typically winters largely in habitats similar to 1 (Quay, 1947), and living or having been raised in the winter habitat type may well enhance over-winter survival. Then the birds which nested in 1 would have a higher survival rate which might compensate for their lower nesting success.

Of course, this study is limited in time and geography, and we have no estimate of the uncertainty associated with these restrictions. However, if we were to accept the suggestion that the distribution is not ideal free or ideal dominance, then we could conclude that territorial behavior in this local population of Field Sparrows neither effects nor affects the distribution. It only spaces individuals. This would support the position of Lack (1964) and Johnston (1961). Further habitat comparisons, with studies of other suitability components, are needed to verify this suggestion.

Summary of Examples

These examples are provided so that non-theorists may see actual applications of the theory previously described. The Dickcissel sex ratio study employed an indirect index of suitability which was found to vary in a way consistent with the hypothesis that territorial behavior in the males of this species limits their density. The Field Sparrow breeding success study considered directly some of the components of habitat suitability, and found these to vary in a way which was inconsistent with hypotheses that territorial behavior either cues, or limits density. Both of these studies provide valid examples of how the problem can be approached and offer first steps in the eventual identification of the role of territorial behavior in the habitat distribution of two common species.

SUMMARY

The first section of this thesis provided a theory of habitat distribution which could be used as a frame in which hypotheses of territorial behavior were precisely defined. Three hypotheses were considered: (1) that territorial behavior was part of a density assessment mechanism, (2) that territorial behavior limited density, and (3) that territorial behavior does not affect density, but only spaces individuals. These three hypotheses, within the framework of the theory, were shown to predict three different relationships between suitability and the density variation between occupied habitats. The density assessment hypothesis predicts no variation in suitability between habitats. The density limiting hypothesis predicts a positive correlation between suitability and density, taken between habitats. The spacing hypothesis predicts neither of the above, given no other factor cueing or limiting density.

A second section provides two examples of the application of the theory. A study of Dickcissel (Spiza americana) sex ratio variation employed an indirect index of suitability which was found to vary in a way consistent with the hypothesis that territorial behavior in the males of this species limits their density. A study of Field Sparrow (Spizella pusilla) breeding success considered directly some of the components of habitat suitability, and found these to vary in a way which was inconsistent with either the density cueing or the density limiting hypotheses. Both of these studies

provide valid examples of how the problem can be approached, and offer first steps in the eventual identification of the role of territorial behavior in the habitat distribution of the species studied.

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