TERRITORIAL BEHAVIOR AND POPULATION REGULATION IN BIRDS

A Review and Re-evaluation

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A close relationship between territorial behavior and population regulation in birds was claimed by Howard (1920) in his classic essay on territoriality and has been emphasized by both earlier and more recent authors (see Wynne-Edwards, 1962). At present, opinions on this matter vary considerably; but there seems to be widespread entertainment, and in some circles acceptance, of the idea that territorial behavior significantly limits many avian populations. Frequently appended is the theory that territoriality has evolved because of this effect through a process which has been called "group selection" but which might better be referred to as "interpopulation or interdemic selection" (Brown, 1966). These ideas apparently were first fully developed by Kalela (1954:2, 18, 41) and have recently been elaborated in the ecological literature by Wynne-Edwards (1962, 1963, and elsewhere) and in the popular press by Lorenz (1966:31). The role of territorial behavior in population regulation is now regularly covered in college textbooks of ecology and behavior (e. g. Andrewartha and Birch, 1954:490; Odum, 1959:222; Kendeigh, 1961:222; Macfadyen, 1963:264; Davis, 1966:68; Smith, 1966:372; MacArthur and Connell, 1966:139; Etkin, 1967:32), despite the claims of some ecologists (e. g. Lack, 1954, 1966) that it is of relatively little importance.

Surprisingly, the facts necessary for an evaluation of the role of territorial behavior in population regulation have received relatively little critical attention except in parts of works with a more general orientation. As a result the various ways in which territorial behavior may affect a population do not appear to have been as clearly distinguished and as thoroughly studied as their presumed importance might suggest. This review attempts to identify and evaluate the effects of territorial behavior on population density by examining the evidence from the best studied territorial species. The approach employed, which stresses comparative population dynamics, also enables new insight into the evolution of certain perplexing types of social organization and behavior in birds.

Consideration will be limited mainly to species in which the same territory is used for feeding, mating, and nesting, Nice's (1941, 1943) Type A territories, since these species offer the most persuasive evidence for the population limiting effects of territorial behavior.

EFFECTS ON REPRODUCTION

General.—Territorial individuals tend to occur in a *regular* dispersion pattern, which is more evenly dispersed than a *random* one; *clumping* of territorial individuals is rare. Operationally, territories are best defined in terms of areas "defended" over a period of time—that is, by collections of points in space and time which are characterized not only by the presence of the individual but also by the manifestation of a particular pattern of behavior, such as attack or threat toward intruders or proclamation of ownership (Noble, 1939; Emlen, 1957), the dissenting opinion of Pitelka (1959) notwithstanding. In many species the defended area is essentially equal to the "home range", "utilized area", or "activity space", although this may be true only in certain phases of the reproductive sequence in some species, such as the Black-capped Chickadee (*Parus atricapillus*) (Stefanski, 1967). In these species the analogy to a mosaic is especially clear; the defended areas abut extensively but do not overlap significantly (over a short period of time). The use of the word "territory" implies this mosaic effect at least to a certain extent. When activity spaces of different individuals overlap broadly and the areas defended, if any, are not clearly demarcated, then use of the term "territory" is not justified. One may then speak more simply of overlapping home ranges, with or without some degree of intolerance of other individuals. A regular or uniform pattern of dispersion may occur in the latter situation without recognizable territories. It is consequently not safe to infer the existence of territoriality from dispersion data alone.

Theoretically, if the territories were made small enough, all members of the population, regardless of its size, could fit into the available living space. But it is the special attribute of territoriality that at higher population densities some individuals may defend more than their proportional share of area in the more productive habitats. The ecological effects of this attribute are complex.

The critical density levels.—The principal ways by which territorial behavior might be hypothesized to influence reproductive rate at different population densities and in different habitats are summarized in Table 1. Three critical levels of population density may be recognized according to the presumed effects of territoriality on patterns of dispersion. At *Level 1* in the table territorial behavior assures a mosaic pattern of dispersion; the population is not sufficiently dense that any individual would be prevented from breeding in its preferred habitat by the territorial behavior of other individuals. At *Level* 2 some individuals become dissuaded from breeding in the preferred habitat by the territorial behavior of the birds already established there; but these birds typically breed in other, less productive habitats. At *Level 3* all habitats where breeding could possibly occur are occupied by territorial individuals, and a *surplus* of potential breeders exists as non-breeding *floaters*, the *population reserve* of Meunier (1960) and others.

The classification of populations into levels according to the effects of territorial behavior on them is intended as a model to be tested and as an aid to conceptualization of the processes supposed to be involved rather than as an arbitrary means of pigeonholing populations. The three levels need not be mutually exclusive. Some species may remain at one level for many generations while other species may contain in various parts of their ranges populations at all levels. Similarly single populations may change levels in successive years. Consequently, in general an entire species cannot safely be assigned to one level; statements in this paper which do so usually refer to a specific population which was studied.

Table 1 also shows the algebraic relationships involved in comparing net reproduction in habitats of different quality under the three critical conditions of population density. For simplification only two qualities of habitat are considered, an assumption which, although unrealistic, should not alter fundamentally the relationships discussed. The expressions in Table 1 are derived from the fact that the net reproductive rate for the whole population, R_T, can be expressed as the total number of young produced to maturity in both habitats divided by the total number of mature adults there, including breeders and floaters.

$$R_T = \frac{R_p N_{Bp} + R_r\, N_{Br}}{N_{Bp} + N_{Br} + N_{Fp} + N_{Fr}} = \frac{\text{number of young produced to maturity in poor and rich habitats combined}}{\text{number of breeding and non-breeding adults in poor and rich habitats combined}}$$

TABLE 1

HYPOTHETICAL EFFECTS OF TERRITORIAL BEHAVIOR ON BREEDING DENSITY AND REPRODUCTION IN RICH AND POOR HABITATS AT THREE CRITICAL LEVELS OF TOTAL POPULATION DENSITY.

Critical Population Density Level	NUMBERS		NET REPRODUCTION					
	Rich Habitat	Poor Habitat	Rich Habitat		Poor Habitat		Total Population	
			Rate*	Total	Rate*	Total	Rate*	Total
1	N_{Br} $N_{Fr} = 0$	$N_{Bp} = 0$ $N_{Fp} = 0$	R_r	R_rN_{Br}	—	0	R_r	R_rN_{Br}
2	N_{Br} $N_{Fr} = 0$	N_{Bp} $N_{Fp} = 0$	R_r	** R_rN_{Br}	R_p	R_pN_{Bp}	$\frac{R_rN_{Br} + R_pN_{Bp}}{N_{Br} + N_{Bp}}$	$R_rN_{Br} + R_pN_{Bp}$
3	$N_{Br} + N_{Fr}$	$N_{Bp} + N_{Fp}$	$R_r \frac{N_{Br}}{N_{Br} + N_{Fr}}$	** R_rN_{Br}	$R_p \frac{N_{Bp}}{N_{Bp} + N_{Fp}}$	** R_pN_{Bp}	$\frac{R_rN_{Br} + R_pN_{Bp}}{N_{Br} + N_{Fr} + N_{Bp} + N_{Fp}}$	** $R_rN_{Br} + R_pN_{Bp}$

N = number of individuals of breeding age
B = breeders
F = floaters; potential breeders
R = net reproductive rate per breeding individual

r = rich habitat
p = poor habitat
* Rate per individual in population (breeding and non-breeding)
** Total reproduction limited by number of territories

The various expressions in Table 1 represent restatements of this relationship as it is affected by the different patterns of dispersion at the three critical levels. Examples of natural populations at each of these three levels will now be examined.

Level 1: no limits.—At level 1 marginal habitats need not be occupied and there are no floaters. At this level preferred habitats should not be settled as densely as they would be in years when less desirable habitats are occupied. Since the concept of a Level 1 population requires that individuals not be forced out of optimal habitat into marginal habitat by aggressive competition for territories, the habitats actually occupied should not differ greatly in quality. Such appears to be the case in the Kirtland's Warbler (*Dendroica kirtlandii*), for which "there is plenty of habitat available to all without crowding" (Mayfield, 1960:51). Due in part to cowbird (*Molothrus ater*) parasitism the species is unable to populate all available seemingly optimal areas, so it has no need to occupy marginal ones.

A different situation was encountered in the Tree Sparrow (*Spizella arborea*) population studied by Weeden (1965) for three seasons in Alaska, in which "seemingly suitable habitat remained unused" (p. 205) and denser population levels were accommodated simply by reduction of territory size through elimination of the least used parts of the territories, no irreducible minimum being reached.

Some populations may reach Level 1 conditions only rarely. In Kluyver and Tinbergen's (1953) studies on Great (*Parus major*) and Blue (*Parus caeruleus*) Tits at Hulshorst, Holland there appeared to be overflow from the preferred habitat (mixed wood) into the marginal habitat (pine wood) in most years, but in a few years there seemed to be too few tits to fully occupy the area of preferred habitat. These would be years at Level 1.

Cyclic species, such as the ptarmigans (*Lagopus* spp.) probably return to Level 1 conditions periodically.

It seems likely that some species, especially those with relict or very small populations, such as those whose populations have been decimated by man through hunting (rather than habitat alteration) could be classified at Level 1, for example the Eskimo Curlew (*Numenius borealis*) and certain other shorebirds.

Regardless of the reasons why a population may have been kept to such a low density, the essential point is that since there is no ecologically significant competition for territories under such conditions, territorial behavior can have no significant limiting effect on the reproduction in the population. On the contrary, as most authors agree, territoriality under conditions of low density should aid in raising subsequent densities by helping to ensure for each family a near optimal area for nesting.

Level 2: buffer mechanisms.—When optimal habitats become so crowded that some individuals set up territories in habitats that are clearly poorer in the requisites for reproduction but are not crowded, Level 2 densities exist. Under these conditions the most attractive habitats (defined as those which have the highest population densities) tend to fill up first (i.e. Chaffinch (*Fringilla coelebs*), Glas, 1960). If the size of territories in the population were rigidly fixed and constant from year to year, this would result in a stable number of territories and a constant density of pairs in the preferred habitat, where all space would be occupied, and in a variable number of territories and density of pairs in the marginal habitats, so long as the latter had not reached their saturation limits.

Kluyver and Tinbergen (1953) in a classic study of population densities of three species of titmice in two adjacent habitats over a long period of years demonstrated that in the mixed wood habitat, where densities were high and food supply superior

(Kluijver, 1951:83, 1963), the year to year variation in density was relatively small and not proportional in magnitude to the variation in the total population in the study area. On the other hand, in the pine-wood part of the study area the food supply was poorer, densities were lower and more variable. These authors showed that the density in the preferred habitat, the mixed wood, was in effect buffered; while that in the pines was not. They referred to this phenomenon as the *buffer effect* and concluded that it was due primarily to a balance between habitat preference for the mixed wood and the repelling influence of individuals defending their territories there. In a study of the buffer effect in the Chaffinch, Glas (1960) provided similar data. Lack (1958, 1964, 1966) was unable to demonstrate the buffer effect in his British populations of Great and Blue Tits, the principal species studied by Kluyver and Tinbergen.

The buffer effect has not been clearly demonstrated in other species, but the explanation that it is due in part to territoriality has been widely accepted.

In a few species the existence of a buffer effect is suggested by observations that certain "poor" habitats of notably lower breeding density are not occupied at all in years when the density of the species in "better" habitats is lower. This was true for the Skylark (*Alauda arvensis*) population studied by Delius (1965). Similarly, the emigration of Song Sparrows (*Melospiza melodia*) in fall from a dense population to less dense ones (Tompa, 1962) suggests that a buffer effect might be present.

Lack's (1958, 1964) failure to find evidence of a buffer effect might be due to differences in the study areas used. A peculiarity of the region where Kluyver, Tinbergen, and Glas worked was that the habitat with a stable population (mixed wood) was *small* in area compared with the habitat with the more variable population (pine wood), which was typical of large areas adjacent to the studied population. Furthermore, in the Dutch work the two habitats studied were extensively *contiguous* on the study areas. Neither of these peculiarities was true for the populations reported on by Lack.

In order for the causative mechanism of the buffer effect to operate in the manner conceived by Kluyver and Tinbergen individual birds must be presented with a *choice* of habitats within the small region where the individual is likely to seek a territory. Since titmice, chaffinches, and other territorial species show a strong propensity to set up territories in the same places in successive years or in the local region where they were hatched, most individuals probably would not search over a wide area. If they did not encounter a choice between rich and poor habitats in the area of their search, they could not take part in the buffer effect. It would seem then that the amount of *contiguity* between rich and poor habitats might be critical for the buffer effect to operate. This is a point on which adequate field data are lacking.

The prediction that dense breeding populations of a territorial species should show less yearly variation than other less dense populations of the same species was tested by Brewer (1963) using data from yearly breeding bird censuses in five localities as reported in Audubon Field Notes. The predicted inverse relationship between mean density and variability was *not* obtained when species were considered singly. Brewer ascribed the failure of his data to show the predicted inverse relationship to the long distances separating most of the census areas, which ranged from Minnesota to Maryland, and stated that in two areas "only" 60 miles apart variability was, as postulated, negatively correlated with density in seven species and positively correlated in only two, all of which are territorial. In interpreting such data it must be realized that what constitutes optimal habitat in one geographical region may quite logically support a lower density than certain suboptimal habitats in another region simply because the former habitat is located near the periphery of the species range or in a region which is not well suited to the species for climatic reasons. Consequently, Brewer's test, although inconclusive when rigorously interpreted, does serve to point out complexities which must be taken into account in future studies of the buffer effect.

Still another factor must be considered when looking for the buffer effect. According to the model in Table 1 a buffer effect can be predicted for populations at Level 2, but its effect should be much less or absent at Levels 1 and 3. Before stating for any given population that a buffer effect might be expected, it must be shown that the birds are nesting in habitats differing sharply in density or productivity (and presumably attractiveness) (therefore not at Level 1) and that floaters are not prominent (therefore not at Level 3). Apparently because of the census methods employed (nest box occupancy, singing male) it was not possible to calculate the density of floaters in any of the populations which have been studied in respect to the buffer effect (or there were none).

Only further field studies will be able to show whether the buffer effect is widespread and has an important effect on dispersion among bird populations or is only the result of a certain set of conditions not yet empirically identifiable which were found locally in the study areas of Kluyver and Tinbergen (1953) and Glas (1960). In view of the small number of populations (6), species (4), study areas (2), and geographical regions (1) in which the buffer effect has been shown and of the conflicting evidence from studies of other populations including some of the same species (Lack, 1958; Brewer, 1963), I share Lack's (1964, 1966) reservations and believe that judgement on the significance of the buffer effect in bird populations ought to be suspended until more data on natural populations become available. Certainly, until such are available, there is no justification for pointing to the buffer effect as a widespread and important means by which territorial behavior limits breeding density. Its present status is that of an hypothesis accompanied by little and conflicting evidence.

Since it is known for a number of species (e.g. Great Tit, Kluijver, 1951:83, 1963; Lack, 1955, 1958, 1964; Pomarine Jaeger (*Stercorarius pomarinus*) and Snowy Owl (*Nyctea scandiaca*) Pitelka, Tomich, and Treichel, 1955; Buzzard (*Buteo buteo*) Mebs, 1964; Ovenbird (*Seiurus aurocapillus*) Stenger, 1958) and undoubtedly in others that density of territories is directly correlated with the richness of the food supply, it is reasonable to assume that avian productivity in the preferred areas (judged by density) would exceed that in the marginal areas if all other factors (including density) were equal. Data of Kluijver for the Great Tit indicate that the number of young fledged per breeding pair per season would be higher in the habitat of highest density than in the habitat with normally lower densities if the densities were equal in the two habitats (which they usually were not).

Territorial behavior at Level 2, according to the model in Table 1, should result in lower production per pair in the marginal habitats than in the rich ones. This would result in a *lower rate* of production for the population as a whole including rich and poor habitats but would *increase the total production of the population*, not decrease it as N. Tinbergen (1957:20–21) has claimed: in addition to the regular production from the rich habitats there would be an increment from marginal habitats that were not previously being utilized. (These relationships may be seen in Table 1 by comparing the rate and amount of reproduction for the whole population at Levels 1 and 2.) Consequently, competition for territories would be increased until all possible habitats were fully exploited, at which time the buffer mechanism in its simplest form would cease to operate. It is obvious that territorial behavior at Level 2 is not a mechanism of population control when the whole population is considered. It would be significant *only in preferred habitats* and primarily for the range of population sizes and densities in which preferred habitats were filled but possible marginal habitats were not. Its effect for the population as a whole should be viewed not simply as curtailing production and preventing overpopulation (Wynne-Edwards, 1962:149) but as insuring the maximum production from the available habitat. This in turn would tend toward greater competition for territories in favorable as well as unfavorable habitats.

In view of these logical considerations it is clear that some authors have oversimplified the situation. For instance, N. Tinbergen, (1957:20) who then apparently believed that the general "function" of territoriality was dispersion, has written, "The existence of a dispersion mechanism [territorial behavior] means that density is reduced in the most desirable habitats. If the less desirable habitats are occupied as a consequence of this, but offer less good chances of success (or, of course, if many birds are prevented from settling down and breeding at all) this would mean that the dispersion mechanism would reduce absolute numbers by reducing overall breeding success." Although a reduction is spoken of, such a reduction could never actually occur since it would be a reduction from a situation that does not exist. Tinbergen was, in my interpretation, comparing the situation as it is with the situation which might exist if the species were suddenly to become non-territorial and all floaters were allowed to breed in the most desirable habitats. As I have shown above, in going from Level 1 to Level 2 an increase in absolute numbers would occur in a real population, *not a reduction*, nor would there be a reduction in density. A further complication, which cannot be considered here, arises from depressions in productivity due to high densities. Because of this complication reproductive rate in a "poor" habitat sparsely populated might exceed that in a "rich" habitat densely populated (Perrins, 1963, 1965).

Some other population studies, although not concerned specifically with the buffer effect, yield some insight into how the movements of individuals are affected. The dynamics of European Blackbird (*Turdus merula*) populations have been studied in a number of areas (e.g. England, Snow, 1958; Poland, Graczyk, 1959; Germany, Erz, 1964; Czechoslovakia, Havlin, 1962, 1963; Switzerland, Ribaut, 1964). It has been found that in populations of high density many young individuals are unsuccessful in establishing territories apparently because of territorial behavior. Under these conditions some first-year birds remain as floaters in the dense populations and some probably seek territories elsewhere, where the density is lower. Since some populations seem to produce either more or less than is needed for simple replacement of losses, it can be inferred that there is probably movement from the more productive into the less productive populations. At Oxford (Snow, 1958) the high density populations produced more birds than could breed there, and probably supplied the low-density populations with some breeders. In contrast, on the continent some high-density populations which were studied produced less than enough to maintain their high density, hence must have depended on immigration from other populations, presumably of lower density. Thus the flow of individuals, although always going from the over-productive to the underproductive populations, need not always go from high-density to low-density populations, despite the known limiting actions of territoriality at high densities in the populations studied. This anomaly is due to reasons other than the limiting of breeding density by territoriality (see below), and is, therefore, not inconsistent with the model described in Table 1.

Level 3: floaters.—In theory, when the number of potential breeders is sufficiently great, a point is reached at which an upper limit is imposed on breeding density by means of territorial behavior; this condition is designated as Level 3 in Table 1. Individuals above this limit, by definition, would be prevented from breeding anywhere, except in completely unsuitable habitat, by the territorial behavior of the breeders. This level is distinguishable from Level 2 (in theory) by the absence of suitable unutilized habitat and by the presence of floaters in at least the rich habitat. The model described in Table 1 requires that total reproduction at Level 3 be limited in poor as well as in rich habitats.

It should be noted that in the model although the rate of reproduction for the population as a whole becomes lower as the proportion of floaters becomes greater, *total* production is, nevertheless, *greater* than at Level 2, no matter how low the *rate* may become. Reproduction, according to the model, is constant because the number, density, and rate of reproduction of actual breeders is constant (in an unchanging environment); the number of floaters and the reproductive rate for the population as a whole is irrelevant to total reproduction (in the model). In nature, reproductive rate of the breeders may be lowered at Level 3 for reasons other than the exclusion of surplus individuals from breeding. The model states only the predictions of reproduction according to the theory of population limitation by territorial behavior; it is not intended to predict the action of other density-dependent factors, some of which are discussed later.

Since it is Level 3 at which the classical limiting effects of territoriality should be best shown, it is desirable to examine the evidence for the existence and operation of Level 3 conditions. The foundation of the argument that territorial behavior limits breeding density consists of a *combination of behavioral and ecological observations.* The behavioral evidence involves observations of individuals being prevented from establishing new territories in areas already claimed by other individuals through aggressive behavior of the owners. The ecological evidence consists of data on the stability of breeding populations and on the existence of a fraction of the population which is capable of breeding but does not do so except when some or all of the breeding population is removed.

The behavioral evidence alone is insufficient to indicate whether or not territorial behavior is exerting any limiting effect on total reproduction. An individual prevented from establishing a territory in one place may be successful elsewhere or even at the same place at a later time. Many observations of both successes and failures of birds attempting to set up territories on already occupied areas have been published (e. g. Lack and Lack, 1933; Lack, 1954; Hinde, 1956).

The ecological evidence concerning stability of breeding density is also insufficient by itself to conclude anything about the effects of territorial behavior on a population. Lack (1966) has argued that territorial behavior, if it is significant, ought to impart greater stability to breeding density than might otherwise be the case. But under Level 1 conditions territorial behavior would not necessitate stability because the limit to breeding density would not have been reached. At Level 2 stability might be expected in the better habitats but not in the poorer ones; however, even in this case stability is a relative matter. At Level 3 one might predict a stable breeding density, but again there are exceptions and a rigid upper limit is not required for territoriality to be effective. Stability need not necessarily occur if there is variation in the environmental factors which set the behavioral limit. For example, in the Red Grouse (*Lagopus lagopus scoticus*) Jenkins (1963) felt that territorial behavior was preventing some individuals from breeding in all years, yet breeding density varied from 14 to 34 birds/40 ha in different years. This variability was attributed to environmental factors acting on the birds' behavior.

If stability does occur, it might be caused by other factors, such as stability in winter food supply, number of nest sites, winter survival, and need not be wholly attributed to territorial behavior. In general, one cannot safely conclude anything about the presence, absence, or importance of territorial behavior in population regulation from data on population stability alone; nor is conspicuous stability of breeding densities a necessary consequence of partial limitation of breeding densities by territorial behavior.

In polygamous species with Type A territories the numbers of females may constitute a unique "control" against which to compare those of the males. Brenner (1966) in a study of Red-winged Blackbirds (*Agelaius phoeniceus*) in a Pennsylvania cattail marsh found that although the density of females in the marsh varied considerably over five years (from 7 to 42) the number of males remained remarkably stable (17 to 21). This suggests that the marsh was always saturated (Level 2 or 3) in respect to males but not with respect to females. Large yearly changes in the numbers of females (and, presumably, the total population of males), which were directly correlated with rainfall, nesting cover, and insect biomass, were masked in the numbers of territorial males. If the number of females can be accepted as a reasonable index of the abundance of potential male territory holders (adult and yearling), then this population study would appear to constitute an unusually clear case of the buffering of breeding density among males through their territorial behavior.

The ecological evidence concerning the existence of a *surplus* of potential breeders during the breeding season is critical, since the theory that territorial behavior prevents some individuals from breeding by denying them territories requires that a surplus be present. If it can be shown for a territorial species that a surplus is present and that surplus individuals will establish territories and breed when the previous owners are removed, it would seem safe to conclude that the presence of the previous owners was somehow preventing the surplus from breeding, most likely by territorial defense. Consequently, *from the standpoint of the limitation of breeding density information on the existence and magnitude of breeding surpluses is crucial.*

The existence of a floating population of mature but non-territorial adults is not easily demonstrable, since the commonest census techniques, counting singing males or occupied nest boxes, tend to miss floaters or not to distinguish them from breeders. A method for identifying individuals, or at least preventing confusion between them, is required.

The most abundant type of information suggesting the existence of a surplus consists of observations of rapid replacement of lost mates. Many examples of this phenomenon were described by Darwin (1871:738–741) and many more since (references in Meunier, 1960; Wynne-Edwards, 1962). Although such cases are suggestive, they concern individuals rather than populations, and they give little information on the relative size of the surplus, its ecological distribution, or its existence from year to year. Furthermore, negative results such as failure of a female chickadee to replace her lost mate (Smith, 1967) usually are not reported, making it difficult to evaluate the positive ones. Consequently, none of these observations by themselves can be taken as conclusive evidence that a surplus of significant proportions is widespread and of regular yearly occurrence in the population concerned.

In a few studies breeding birds have been removed from their territories in larger numbers. Such studies have been widely accepted as providing dramatic proof of the limiting effects of territorial behavior on total reproduction, but there are reasons to doubt whether this conclusion is justified.

The experiments of Stewart and Aldrich (1951) and Hensley and Cope (1951), during an outbreak of the spruce budworm (*Choristoneura fumiferana*) in northern Maine, in which a large percentage of all individuals of all avian species was removed by shooting from a 40-acre tract of spruce-fir forest showed that a spectacular replacement of territorial males over a short period of time occurred. In 1949, only 148 territorial males were censused before collecting began; but collecting from June 15 to July 8, yielded 420 adults (original owners plus their replacements). In the following year the experiment was repeated; 154 pairs were censused, and 528 adults were subsequently collected. Although a rapid replacement of males was demonstrated in both 1949 and 1950, *none of the females of the 10 most abundant species removed was replaced* (Table 1 of Hensley and Cope). Consequently, there is no evidence 1) that a surplus of females existed, 2) that any females were denied opportunity to breed by territorial behavior, or 3) that reproduction in the population was being limited to the slightest degree by territorial behavior. The replacements in these species consisted entirely of males (and a very few individuals labelled "undetermined"). Moreover, even in the original populations which were first collected, males outnumbered females in the abundant warbler species by from 1.7 : 1 to 9 : 1, the excess of males being generally less conspicuous in the second summer. The reasons for this apparently uneven sex ratio in the adult population are not clear.

In the Pied Flycatcher (*Ficedula hypoleuca*), in which 30 per cent of males were unpaired in Curio's (1959) population, the greater mortality of females than males, claimed by Curio (but see Lack, 1966:112), was suggested by Meunier (1960) as the cause of the surplus and the limiting factor for the number of breeding pairs. For a number of European species other than strictly hole-nesters Meunier has pointed out that the non-breeding individuals in populations studied by various authors were almost all males.

A surplus of non-territorial males has been demonstrated by shooting of territorial males in August in Red Grouse (Jenkins, Watson, and Miller, 1964) and in mid-March in Rock Ptarmigan (*Lagopus mutus*; Watson, 1965*a*). In the removal experiments of Orians (1961) on Red-winged Blackbirds only males were shot, and these were repeatedly and rapidly replaced. Removal experiments with females were apparently not performed, but since this species is polygynous, the existence of a surplus population of females would not necessarily be expected (although female territoriality does occur in the species, Nero, 1956).

Holmes (1966) conducted removal experiments on Dunlins (*Erolia alpina*) in Alaska, where the species holds Type A territories through the incubation period. A total of 31 adults of both sexes in two years was collected during the period of arrival on the breeding grounds from a plot which normally supported 4 or 5 pairs. However, birds deserting their territories in late June or early July because of the nest predation by jaegers (*Stercorarius* spp.) were not replaced, despite the continuance of territorial activity through mid July.

Systematic experiments on the promiscuous Blue Grouse (*Dendragapus obscurus fuliginosus*) in British Columbia revealed no significant evidence of a surplus of adult males (Bendell and Elliott, 1967). Of the yearling males only about 11 per cent normally entered the territorial population, but on plots where all territorial birds were removed 64 per cent did so. This suggests that the establishment of breeding territories was being inhibited in about half of the yearlings by the normal breeding population.

There was no evidence of a surplus of hens. Similarly the removal of 10 territorial male Ruffed Grouse (*Bonasa umbellus*), also promiscuous, from a 360 acre area in spring resulted in replacement by only 2 birds, both yearlings (Dorney, 1960, cited by Bendell and Elliott).

In a few studies floaters have been detected by means of the individual recognition enabled by banding. Kendeigh (1941) and Kendeigh and Baldwin (1937) have analyzed data on non-breeders from a 19-year study of a dense breeding population of House Wrens (*Troglodytes aedon*). Kendeigh (1941:42) wrote: "The size of the house wren's territory is compressible with increasing number of birds present, at least down to a minimum. When the territories are reduced on an average to that minimum, resistance to invasion by more individuals becomes exceptionally increased . . . and the population tends to be thereby limited." This conforms well with Huxley's (1934) analogy to "elastic discs". Restricting the analysis to the 10-year period of most efficient trapping Kendeigh (1941) estimated that during the first period of breeding 15 per cent of the males and 13 per cent of the females "did not make serious attempts at nesting"; for the second period of breeding the figures were 20 and 25 per cent respectively. If males which held territories but failed to attract mates are included, the figures rise to 28 per cent for the first period and 35 per cent for the second. A closer analysis of the non-breeders showed that they varied considerably in their "reproductive vigor," from those who did not hold territories in either breeding period to those who did in both but lacked only a mate. The percentage of first-year males was higher among the unmated birds (80 per cent) than among the mated ones (57 per cent). The reasons for non-breeding in these individuals are not known and it cannot be simply assumed that the territorial behavior of their neighbors was responsible (see below).

In a five year study of a color-marked population of Skylarks Delius (1965) estimated the proportion of non-territorial floaters at 10 per cent in most years, with males predominating. Some of these individuals replaced breeding males which had disappeared, thus showing that they were not inherently unable to breed. Most seemed to be one-year-old birds. In one year when the density of breeders was 20 per cent lower than usual no non-breeders were seen.

In a population of the European Blackbird Ribaut (1964) found in two successive breeding seasons a non-breeding fraction constituting about 14 per cent of the total population (64 birds). Breeders which died were quickly replaced from the reserve population, which included females as well as males. Reserve males attempted to hold territories but were prevented from doing so by the established owners. It should be mentioned that this was an urban population and showed some of the characteristics of urban and suburban Blackbird populations in Europe (Erz, 1964; Graczyk, 1959; Havlin, 1962, 1963; Lack, 1966), rich winter food resources, high population density, and high survival rates. Despite the high survival rate and abundant food supplies of the urban populations studied by Erz and Ribaut, the population density could not apparently be maintained by reproduction of the populations studied but depended on immigration from other populations. In the case of Ribaut's population this failure of reproduction to keep pace even with a low mortality rate was due primarily to a high frequency of nest desertions, not to limitation of the numbers of breeders.

A surplus of non-territorial cock Ring-necked Pheasants (*Phasianus colchicus*) amounting to 11 per cent of the total male population was detected by Burger (1966) in the year of highest population density in a three-year study in Wisconsin. Few if any surplus birds were found in the other two years.

An unusually large surplus of individuals which were excluded from holding suitable territories existed in the population of Australian Magpies (*Gymnorhina tibicen*) studied by Carrick (1963). The numbers of non-breeders in the breeding season were not given in his preliminary report, but judging from the large surplus in Australian mid-winter, 60 per cent of the population, and the high survival rate, the breeding surplus must have been very large. Vacancies in the breeding population were quickly replaced from the non-breeders, indicating that some of the deprived individuals were physiologically capable of breeding and probably prevented from doing so by the unavailability of territories.

Although many authors have concluded that territorial behavior was limiting the breeding density of a population studied by them, the evidence on which their conclusions were based has sometimes been unsubstantial, such as the observation of an individual bird failing to establish a territory at a particular place at a particular time. I have tried to emphasize in this section what should be, but has not always been, self-evident, namely, that something more than the observation of a few individuals fighting and threatening is necessary to conclude anything about the effects of territorial behavior on population dynamics, specifically about the limiting effects of territorial behavior. A number of critical points must be confirmed on the population level before it can be concluded that breeding density is being limited by territorial behavior in the Level 3 manner and that recruitment is thereby curtailed.

First of all it must be established that some individuals are being deprived of a chance to breed. It must be shown that a surplus exists and that it constitutes a significant fraction of the population. A surplus can exist for reasons other than territoriality, for example, when the number of suitable holes for hole-nesters is limited (references cited by Meunier, 1960; Pfeifer, 1963) or when delayed reproduction is the rule, as in certain colonial seabirds. The second requirement, therefore, is the demonstration that it is the territorial behavior of the established birds that is preventing the floaters from breeding. This can be done by mass depopulation of a particular area, as was done in a number of studies described above, or better, by selective removal of territory owners, leaving the floaters intact. In only two cases known to me has the latter been done after the spring arrival period was over on a population basis with a positive result (Orians, 1961; Bendell and Elliott, 1967). However, some authors working with populations known to have a surplus have noted that accidental losses from the established breeding population were quickly replaced from the non-breeding fraction (e.g. Delius, 1965; Ribaut, 1964; Snow, 1958; Carrick, 1963; Rowan, 1966).

Furthermore, if the conclusions are to be extended to include limitation of total reproduction, a third requirement must be added. It must be shown that territoriality prevents some females from breeding. Most workers have concentrated on the males, probably because they are the more territorial sex and more conspicuous. Nevertheless, as we have seen, generalizations valid for males are not valid for females until proven so. The data of Delius (1965) on Skylarks, Ribaut (1964) on European Blackbirds, and Carrick (1963) on Australian Magpies show that some females are prevented from breeding in these species by territorial behavior, but in a number of other important studies data on females is lacking or suggest that females are not limited, as in polygynous species and the depopulation studies of Stewart and Aldrich (1951) and Hensley and Cope (1951).

Lastly, even when surpluses including females have been demonstrated as being caused by territoriality, interpretations about the importance of territoriality for the species as a whole and for other species require caution. It is natural that in attempting to demonstrate the existence of limiting effects of territorial behavior an investigator would choose the densest population available. But if this population is not representative of populations of the species in the same region existing under natural conditions, it would be incorrect to generalize. Unfortunately, many study areas owe their unusually high densities to artificial conditions created by man, such as public parks, botanical gardens, managed hunting grounds, and agricultural situations.

For example, as Lack (1966:125) has pointed out, the peak density of Blackbirds in the Oxford Botanic Gardens was about ten times that in Wytham Wood and much greater than in any other known population existing under approximately natural conditions.

For Australian Magpies (*Gymnorhina* spp.) Robinson (1956:274) has described the human influence as follows: "It appears that it is the dairying districts throughout Australia which are carrying the biggest populations at present. These are all in the higher rainfall belts which produce the maximum of cultivated green feed possible during the year. These are really artificial conditions humanly created, as the habitat has been considerably changed by man. In its natural state it was mostly heavy forest country with no pasture and Magpies were rarely seen. In the drier areas Magpies are not so plentiful, and are seldom seen in the dry interior where average rainfall drops below ten inches and droughts are common." He observed that the population increase on his study area over a ten year period was correlated with clearing and pasturing, as well as the provision of extra water (p. 266). It is not surprising that the simultaneous enrichment of the food supply and destruction of trees used for nesting would produce a surplus of birds which were unable to find nesting territories.

Other species in which surpluses including females have been associated with human manipulation of the environment are the House Wren, Red Grouse, and Partridge. The extent of the human influence in some of these cases is difficult to evaluate. Apparently the only population of a monogamous species with such a surplus in which human influence can be completely excluded is in the Rock Ptarmigan, and even in this species bigamy occasionally occurs (although many hens may remain unpaired; Watson, 1965*b*).

In my opinion, this amount of reliable information is hardly sufficient for sweeping generalizations concerning the limiting effects of territorial behavior on reproduction, which so frequently are seen in textbooks and journal articles.

Lack's views.—In his reviews of avian population studies Lack (1966, 1954, and earlier) has repeatedly de-emphasized the role of territorial behavior as a limiting factor for breeding densities. His principal recent criterion for judging the importance of territorial behavior was not the magnitude and persistence of a breeding surplus which is emphasized in this paper, but was the stability of breeding densities around an upper limit (e.g. 1966:78). For a number of cases cited by recent authors as examples of population regulation through territorial behavior (e.g., in the studies of European Blackbirds, Song Thrushes (*Turdus philomelos*), Song Sparrows, Great Tits, Red Grouse, and Rock Ptarmigan). Lack pointed to sharp differences in densities in different years and in different habitats as objections to this interpretation. He repeatedly took opposition to Huxley's (1934) "elastic disc" hypothesis on these grounds. On the other hand, again using density as a criterion, he accepted territorial behavior as a limiting factor for Tawny Owls (*Strix aluco*), despite a steady increase of nearly 90 per cent in number of breeding pairs in the study area.

In my opinion, stability of breeding density is not an adequate criterion for assessing the limiting effects of territorial behavior, for reasons already stated. It may provide hints, but it is not decisive.

Contrary to Lack, I find no reason why territoriality could not participate in limiting Red Grouse or other species at quite different densities in different years, the variation being attributable to variations in the history, age, or condition of the birds. Nor is it difficult to conceive of territorial behavior helping to limit Song Sparrow populations at different densities in British Columbia and Ohio. In both types of variation, yearly and regional, the limit is a function of the *interactions* between the quality of the environment, the condition and number of competing individuals, and the behavior of the species.

These interactions are strikingly shown in Tompa's (1962, 1964) study of the Song Sparrow on Mandarte Island, British Columbia. This population had been stable at a level about 10 times Nice's (1943) population in Ohio; and Tompa (1962) concluded because of the fully occupied habitat, the stability at high density, and the emigration which was temporally correlated with territorial behavior, that the population was limited by the behavior of the birds. Lack (1966) objected on the grounds that the 1963 population showed an increase of 50 per cent over the allegedly stable population of 1960–62. However, there were surplus, non-territorial males and territorially induced emigrations of males and females in all years of the study. This indicates Level 3 conditions for the males and Level 2 for the females. The increase in 1963, was apparently brought about by a quirk in the weather (Tompa, 1964:52) which by killing many adult territory holders made possible the establishment of an unusually high number of bachelor territories by first year birds in 1962. In 1963, most of these individuals retained their territories and obtained mates, thus accounting for the sudden rise in the breeding population. The important point to note is that the weather played

TABLE 2

ASSIGNMENT OF SELECTED POPULATIONS TO THE CRITICAL LEVELS OF BREEDING DENSITY DESCRIBED IN THE TEXT AND IN TABLE 1. LEVELS 2 AND 3 INDICATE LIMITATIONS OF BREEDING DENSITY MEDIATED BY TERRITORIAL BEHAVIOR DURING THE BREEDING SEASON; LEVEL 1 INDICATES ABSENCE OF TERRITORIAL LIMITATION AT THAT TIME. SURPLUS INDIVIDUALS ARE INDICATED AS PERCENTAGES OF THE TOTAL FOR THE SAME SEX, WHERE POSSIBLE.

Species	Reference	Place	Habitat	Surplus Non-territorial Males	Surplus Non-territorial Females	Level	Comment
Blue Grouse	Bendell and Elliott 1967	B.C.	Conifer	0	0	1	Yearling males at Level 3
Kirtland's Warbler	Mayfield 1960	Michigan	Jack pine	0	0	1	
Tree Sparrow	Weeden 1965	Alaska	Tundra	0	0	1	
Long-billed Marsh Wren	Verner 1964	Washington	Marsh	0	0	1	Bachelor territories 19–36%
Great Tit	Kluyver and Tinbergen 1953	Holland	Pine wood	0	0	1	
			Mixed wood	0	0	2	Density buffered

TABLE 2 cont.

Species	Reference	Place	Habitat	Surplus Non-territorial Males	Females	Level	Comment
	Lack 1966	England	Broad-leaved woods	0	0	1	
Blue Tit	Kluyver and Tinbergen 1953	Holland	Pine wood	0	0	1	
			Mixed wood	0	0	2	Density buffered
	Lack 1966	England	Broad-leaved woods	0	0	1	
Coal Tit	Kluyver and Tinbergen 1953	Holland	Pine wood	0	0	1	
			Mixed wood	0	0	2	Density buffered
	Gibb 1960	England	Pines	0	0	1	
Chaffinch	Glas 1960	Holland	Pine wood	0	0	1	
			Mixed wood	0	0	2	Density buffered
Many passerines	Hensley and Cope 1951	Maine	Spruce woods	Many	Few	Males 3 Females 1	
Song Sparrow	Tompa 1964	B.C.	Shrubbery	4–8%	0	Males 3 Females 2	
Skylark	Delius 1965	England	Dunes	— 10% —		3	Mostly males (?)
Blackbird	Snow 1958	England	Botanic Garden	+	+	3	
	Ribaut 1964	Switzerland	Park	19%	8%	3	
House Wren	Kendeigh and Baldwin 1937	Ohio	Garden Orchard	15%	13%	3	
Australian Magpie	Carrick 1963	Australia	Savannah, pasture, woods	>50%	>50%	3	
Red Grouse	Jenkins 1963	Scotland	Heather	— + —		3	
Rock Ptarmigan	Watson 1965	Scotland	Tundra	— + —		3	
Partridge	Jenkins 1961*a, b*	England	Fields	— + —		3	
Red-winged Blackbird	Orians 1961	California	Marsh	+	—	Males 3	Polygynous

a role in determining the limit which was mediated by the territorial behavior of the birds. The complexity of the interaction between environment, condition and number of competing individuals, and behavior is again shown, and the danger of using stability of breeding density as a criterion is illustrated.

Yearly and regional variations in the degree of crowding necessary to prevent some individuals from holding territories should be expected, and the concept of a rigid maximum breeding density which is independent of the environment should be rejected. The use of the surplus as an indication of a limiting effect of territoriality frees one from reliance on stability of breeding density.

The only population that Lack (1966) admitted was probably limited by territorial behavior was that of the Tawny Owl studied in a British broad-leaved woodland by Southern (1959). In contrast, it will be apparent from a reading of my discussions of Levels 2 and 3 and from Table 2 that, using different criteria, I have accepted many cases of partial limitation by territoriality which were rejected by Lack; my assignment of a population to Level 2 or 3 indicates my belief that territorial behavior was participating in the limiting of breeding density in that population, either by forcing some individuals into poorer habitats or by preventing them from breeding altogether.

The conclusions of Lack and others on the importance of mortality in non-breeding seasons and on the unimportance of territorial behavior in setting breeding densities of titmice have been challenged by Smith (1967) on the basis of her study of survival and dispersal of Black-capped Chickadees. She emphasized the importance of determining precisely the time at which the major losses from the population occur and whether or not they coincide with the resurgence of territorial behavior in the spring and the resultant dispersal of winter flocks. At least some of the disagreement on this matter appears to be semantic.

Other behavioral, density-dependent effects.—In addition to the effect of territoriality of excluding some individuals from breeding, there are other consequences of behavior at high population densities which depress reproduction. There is evidence that density-dependent depression of reproductive success can arise from an increased frequency of agonistic encounters resulting from the compression of territories or overlapping of activity spaces and the presence of floaters continually attempting to set up new territories in defended areas. Depression of reproductive success at high population densities in natural populations of mammals is now well known (Christian, 1963), but it is rarely reported for birds. It was first reliably reported by Kluijver (1951, Kluyver, 1963) for the Great and Blue Tits. Lack (1958, 1966) demonstrated a reduction in clutch size at higher breeding densities in the Great, Blue, and Coal Tits. Perrins (1965:621) found a similar relationship in the Great Tit. Kluijver demonstrated that clutch size and the percentage of females attempting second broods were lower in the years of higher densities in his study areas. The effect was shown in comparisons between habitats in the same years and between years in the same habitats. Kluijver was inclined to attribute the effect essentially to an increased frequency of agonistic encounters at high population densities, but the food supply was not measured or controlled.

In a summary paper on the Australian Magpie, Carrick (1963) reported evidence for an effect of agonistic encounters on ovarian function. In this species oocyte development could be "inhibited by emotional factors, such as intrusion of a strange magpie of either sex into the territory, an undue amount of boundary fighting, or domination by another female of the same group" (p. 749). Inhibition of nesting in resident females because of the presence of non-territorial individuals was directly observed and said to have been confirmed experimentally. In the male, Carrick found that certain physical environmental stimuli were necessary for maturation of the testes but that age and "social status" determined how far development would proceed. Further suggestive evidence of a depressive effect of agonistic stimuli on gonadal function was provided in a report by Ficken et al (1960) in the Budgerigar (*Melopsittacus undulatus*). They demonstrated that the presence of a mirror in the cage inhibited ovarian but not testicular development. A neurobehavioral demonstration of the inhibitory effects of agonistic behavior on ovarian development was given by Phillips (1964) in the Mallard (*Anas platyrhynchos*): lesions in the medial archistriatum produced both reduction in agonistic behavior and disinhibition of ovarian follicle development in the same individuals.

A different side effect of behavior at high populations densities was observed by Kendeigh (1941:28–29) in the House Wren. As males competed aggressively for nest boxes (which were in excess of requirements) they cleaned out eggs and young of former owners; of 331 matings recorded, eggs were destroyed in 13 cases and young in five, resulting in about a five per cent loss from this cause. Kendeigh wrote, "Although there is considerable variation in this aggressive behavior, it tends to be most intense during years when the total house wren population on the area is highest" (p. 117).

An effect of high population density on parental behavior may be indicated in certain upland game birds. Jenkins (1961*a*, 1961*b*) found an inverse correlation in the Partridge (*Perdix perdix*) between frequency of agonistic interaction and chick survival. In Red Grouse it was shown that chick survival was correlated with general physiological condition of the adults (as reflected in body weight, incidence and severity of parasitism, and summer survival), persistence of the parents with the nest and the brood, and frequency of distraction display (Jenkins, 1963; Jenkins et al, 1963). It seems possible that an unusually high frequency of agonistic encounters in the Partridge might have been detrimental to general health or hormone balance thus reducing the effectiveness of parental behavior. Density-dependent depressions of population density have been reported for several other species, but the mechanisms are unclear.

In any consideration of reproductive success as a function of agonistic behavior it is necessary to make sure that the food supply is controlled. Although compression of territories and creation of a surplus increases the frequency of agonistic encounters, it also reduces the share of the food supply available to each territory holder. Perrins (1963, 1965) in a study of the Great Tit demonstrated that weight of nestlings and survival for the first three months of life in an area where the density was 0.43 pairs per acre were higher than in nestlings from an area with a density of 1.3 pairs per acre. He considered it likely that this difference was due to the amount of food available during the development of the young; however, the less likely possibility of an effect of agonistic behavior on the frequency of feeding the young was not excluded by his data, and he has cautiously reserved judgement on the role of the food supply in this case.

The importance of isolation for the breeding of some species of birds in captivity is well known to aviculturists; crowding or the presence of other birds in these species somehow inhibits reproduction. Extreme crowding in poultry (*Gallus domesticus*) is thought to affect adrenal function (Siegel, 1959, 1960). Subordinate dominance status in a group of the same species, regardless of density, seems to depress testis function (Flickinger, 1966). Whether or not such endocrine effects are of widespread significance in mediating behavioral effects on reproduction or mortality in natural populations re-

TABLE 3
CRITICAL PERIODS FOR POST-BREEDING LOSSES IN EUROPEAN TIT POPULATIONS, WITH SPECIAL REFERENCE TO GIBB'S (1960, 1962*a*) STUDY OF COAL TITS

	Phase I	Phase II
Principal Characteristic	Dispersal	Death from food shortage
Season	Autumn (Spring)	Late winter
Agonistic Behavior	Territory defense	Rank-dominance
Food Supply	Not critical	Critical

mains to be determined. Only in the Australian Magpie (Carrick, 1963) is there evidence of the importance of endocrine effects in a natural population.

High densities do not necessarily cause low reproductive success in natural populations. For example, the dense population of Song Sparrows studied by Tompa (1962, 1964) and the dense population of European Blackbirds in the Oxford Botanic Garden studied by Snow (1958) both maintained high levels of production relative to other populations of the same species despite unusually high densities of breeders. On the other hand, a dense population of European Blackbirds studied by Ribaut (1964) had such poor reproductive success that the maintenance of the high population density probably depended on immigration from other areas.

Although the density-dependent behavioral effects on reproduction referred to above share in the regulation of population density, they have not been shown in any species to be the primary factors responsible for population declines from high levels (Lack, 1966).

EFFECTS ON MORTALITY

In certain populations of titmice (Kluijver, 1951; Lack, 1955, 1958, 1964, 1966; Gibb, 1960, 1962*a*; Perrins, 1963) and probably other species the principal fluctuations in breeding density are effected by mortality in the non-breeding seasons (but see Smith, 1967, for a contradictory interpretation). The possibility exists, consequently, that territoriality may have a greater effect on population fluctuations in some species through its effects on mortality in summer, autumn, and winter than through its effects on reproduction. The effects of territorial ownership may persist through the year in some resident species in the form of dominance in the home area even though boundaries may not be defended, as has been demonstrated in a number of species including the Great Tit (references in Brown, 1963*b*).

That survival is enhanced by territorial ownership in a number of resident species is suggested (but not proven) by the high rate of loss from populations of marked individuals lacking territories (e.g. Black-capped Chickadee, Smith, 1967). The food value of the territory is important to winter survival. In Kluijver's (1951) study, Great Tits holding breeding territories in the pine wood but wintering in the mixed wood, where the winter food supply was richer, suffered a higher mortality rate than individuals whose breeding territories coincided with their wintering areas in the same mixed wood. The higher rate of survival of the latter birds might be attributed to their probable dominance at food sources over the individuals from the pine wood.

It is convenient to consider post-breeding losses (after the post-juvenal molt) as occurring in two phases as summarized in Table 2. These may be demonstrated in the data from Gibb's (1960) study of a Coal Tit population. The first phase consists of *dispersal*; it occurs mainly in autumn (but also in spring) and may result in either a loss or a gain in particular local populations. The number in the whole population of the species is, however, unaffected by dispersal alone.

The bulk of dispersal takes place before competition for food has become critical (but not in Perrins' study). In the four years of Gibb's study the percentage of birds disappearing from the population varied only from 46 to 53 in this phase (July through September). It is noteworthy that the number of emigrants was not density-dependent (Gibb, 1960, 1962*a*).

The second phase occurs primarily during the late winter. It consists of the actual death of individuals due directly or indirectly to food shortage and accompanied by severe competition for food. The percentage of birds disappearing for Coal Tits during this phase, from October through March, varied greatly, from 34 to 77 per cent and was inversely correlated with the level of the food stock at the end of winter.

The role of territoriality differs in the two phases. In the first, territoriality reduces the population in one area by shunting the surplus into vacant territories and other areas but causes no loss to the species. This process sets the stage for the second phase. In the second phase, in which the behavioral effect is expressed as dominance resulting from territorial ownership rather than as strict territoriality, losses are due to death, and their magnitude is directly correlated with food scarcity. Because the second phase is irreversible and more sensitive to the degree of overpopulation, it is more efficient as a regulator. In fact, if the second phase were not to occur, the effect of the first phase might be largely nullified when the birds returned in the spring to breed in the vicinity where they were hatched.

The first phase probably enables a higher number of tits to survive the second phase, and it determines which individual tits will survive, namely those holding fall territories in favorable habitats and consequently remaining dominant there in contests for food during the winter when competition and individual selection are intense. Although we may conclude that the limiting effect of autumn territoriality exists for tit populations, fluctuations in the number of survivors of the winter are governed primarily by the food supply.

It is clear for these populations that territoriality affects but does not regulate the number of birds which survives the winter and sets up breeding territories the next spring. The primary effects of territoriality and dominance are first to disperse the population more equitably in relation to the food supply and second to ensure that the vigor of the survivors of the winter is not damaged by the competition for food during the winter.

In the Red Grouse population studied by Jenkins, Watson and Miller (1963; and Jenkins, 1963) the situation differs from that for the titmice in that the number that survived the winter generally exceeded the number of territories. Therefore, a fraction of the population of potential breeders was regularly deprived of the opportunity to breed through lack of territories. The number of breeding territories was established in the fall and varied yearly with the general vigor of the cocks (as indicated by their weight, incidence and severity of parasitism, and summer survival rate). In years when the physiological condition of the cocks was good more of them were able to meet the strain of holding territories than in years when it was bad. The condition of the birds appeared to be related to the quality and quantity of their food, heather, which was apparently determined by the weather. In Red Grouse the *general level* of the breeding population appears to be limited *jointly* by the *territorial behavior of the species and the food supply,* while the yearly *fluctuations* in breeding density appear to be caused by factors affecting the *food supply.*

CONTROL OF THE SURPLUS

The usual fate of potential breeders in excess of those which actually breed varies with the species. The alternatives for a non-territorial individual whether in spring or fall are to stay in an area known to be desirable but fully occupied, and perhaps eventually to fill a vacancy should it arise, or to emigrate and perhaps find a territory elsewhere. The strategies normally employed by surplus individuals facing this choice in different species determine the fates of the potential surpluses.

Especially among permanent residents which show autumn territoriality and some degree of place-dependent dominance in winter hierarchies, emigration of the non-territorial or low ranking individuals may become necessary for their survival long before the breeding season. These are typically species in which "irruptions" may sometimes occur and the amount of migration varies greatly from year to year.

The result of these migrations may be that a potential surplus of breeding birds is disposed of even before it has a chance to reach the breeding season; those individuals which might have become non-breeding floaters had they survived are eliminated through a combination of unfavorable environmental conditions and virtual exclusion from those environmental requisites which would have enabled their survival had they not been pre-empted by the territorial or dominant individuals.

For the Old World tit populations which have been studied, a breeding surplus seems not to be present mainly because it does not survive until the breeding season and because the territories of tits are compressible within the limits of the population densities which normally survive the winter. In the Red Grouse population of Jenkins (1963: 698–9) heavy mortality of surplus individuals occurred during and following times of dispersal. In spring and summer, surplus birds were seen in marginal areas and seemed to be more susceptible to infections by nematode worms, *Trichostrongylus tenuis* Eberth, than were territory owners. In this species the surplus appeared to have a significantly higher mortality than the breeders.

It is clear that single-factor explanations of such cases are inadmissible. It is primarily the *interaction* of aggressive behavior (manifested as territoriality, dominance, or both), food supply, and weather conditions which *limits* these populations. Furthermore, *fluctuations* in density seem to be attributable to the *interaction* between food supply and weather conditions, rather than to territorial behavior, which, if it varies at all, varies as a function of the first two variables and numbers.

In some other species the non-breeders survive well enough to constitute a fair proportion of the population during the breeding season. Such surplus individuals may either exist separately where survival is assured but successful nesting is nearly impossible, as in the Australian Magpie (Carrick, 1963), Great Reed Warbler (*Acrocephalus arundinaceus*) (Kluyver, 1955), and Red-winged Starling (*Onychognathus morio*) (Rowan, 1966) or they may mix with breeding individuals in weakly defended or neutral areas in or near occupied territories, as in the House Wren (Kendeigh, 1941), Skylark (Delius, 1965), and other passerines. Surpluses which exist separately from the breeding population seem on the basis of presently available data to be larger than those which mix with the breeding population. Perhaps this is because the surplus individuals in the former case need not compete directly with territory holders for the essentials of survival, whereas in the latter they must. This would enhance survival in both surplus and breeding birds.

If all utilizable habitats are just filled and the rates of recruitment and immigration exactly balance the rates of mortality and emigration, there will be no surplus. But if this balance is tipped slightly on the positive side a surplus will tend to accumulate. Although territoriality might in some species limit breeding density, it places no direct limitation on the density of floaters. Consequently, it cannot be said to "limit the population"—a frequent oversimplification in the literature.

The size of the surplus, or the density of floaters, N_F, is determined by the number added to the population each year in excess of the number needed to maintain the fixed upper limit of density of territory holders, a, and by the rate of survival of the surplus individuals, s. When the density of breeders, N_B, is taken as one, then for a given year the increment above replacement equals the reproductive rate per breeder (to maturity) minus the mortality rate, m, per breeder (exclusive of emigration and immigration),

$$a = rN_B - mN_B = r - m$$

Over n years N_F equals the excess from the preceding year, a, plus the survivors from the excesses produced in previous years.

$$N_F = a + as + as^2 + \ldots + as^{n-1}$$

As a geometric progression this equation can be stated in the following form:

$$N_F = a\left(\frac{1-s^n}{1-s}\right)$$

Since s can only be a fraction between 0 and 1, s^n approaches zero as n approaches infinity. Consequently, in the limit $s^n = 0$,

$$N_F = \frac{a}{1-s}$$

Survival rate is here assumed for simplification to be relatively independent of age after maturity. That this is a reasonable general assumption for birds on the basis of the available evidence was tentatively supported by Lack (1954), Farner (1955), and Meunier (1960), who reviewed survival rates in birds. An exception to this generalization was shown by Berndt and Sternberg (1963) for the Pied Flycatcher but questioned by Lack (1966).

The relationship between survival rate of the surplus individuals and the size of the surplus is shown in Figure 1. It may be seen that the problem of control of a surplus should tend to be much more severe in longer-lived species than in those with a high mortality rate. For two hypothetical species each with an a of 10 per cent, average survival rates of 0.6 and 0.8 would yield surpluses of 25 and 50 per cent of the breeding populations respectively. Thus, a small difference in survival rate of the surplus individuals could make a large difference in the size of the surplus.

Since larger species tend to have longer life expectancies, we can predict that the problem of a surplus will be exaggerated in those species. The surprisingly large surplus of non-breeding "flock" birds in the Australian Magpie, up to 183 per cent of the breeding population (in winter) (Carrick, 1963), becomes somewhat more understandable in view of the (presumed) high survival rate of the species, and in particular of the non-breeding birds. On the other hand, the production of a considerable surplus by a small, short-lived passerine is likely to be due more to reproductive excess.

THE SURPLUS AS A SELECTIVE FORCE

When territorial behavior together with other factors results in the continual existence of a surplus population of one or both sexes over a long period of time, the surplus becomes a predictable feature of the environment of the population and the possibility of

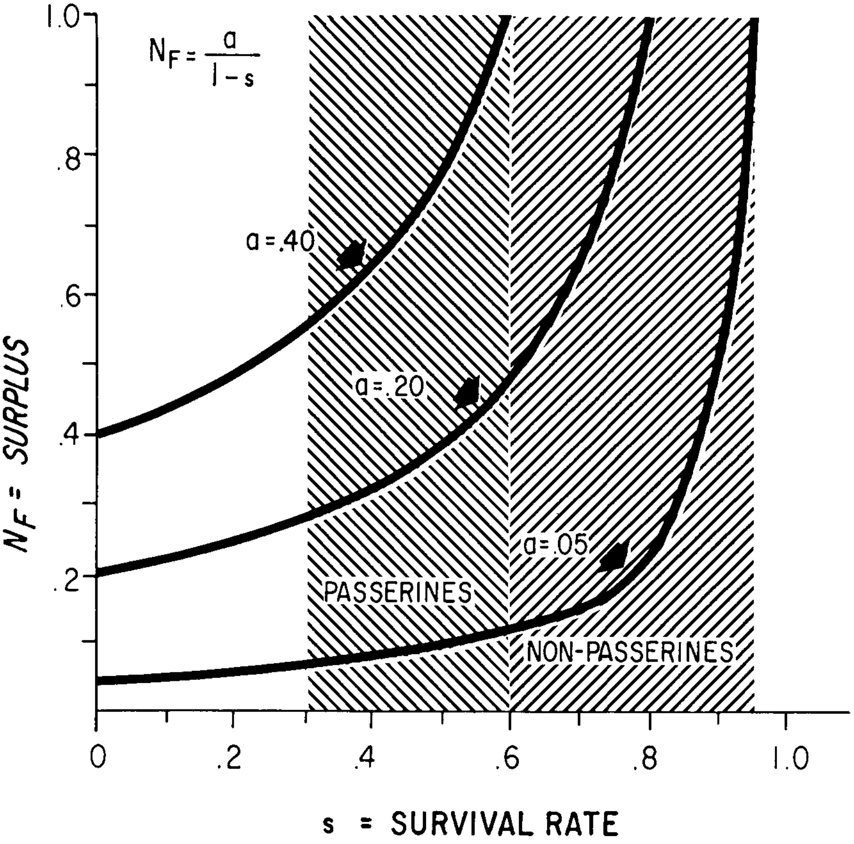

Fig. 1. Curves showing the size of the predicted surplus, N_F, in relation to mean survival rate, s, of the surplus for various amounts of excess of population gains over losses, a. Both N_F and a are expressed as proportions of mean breeding density, which is taken as 1.0. The approximate ranges for adult survival rates of temperate zone passerines and non-passerines are from Lack (1954:91–92), and are merely suggestive; game birds are excluded.

evolutionary adaptation to it emerges. Some of the phenomena which might be interpreted as adaptations to a persistent surplus will now be considered. Circumstances which cause some individuals to attempt breeding in habitats where success is unlikely should have similar evolutionary effects.

Adaptations which might have the secondary effect of reducing the surplus seem to belong to the "last resort" type. They are adaptations to an environment which is less favorable than the previous one in the sense that the chances of being prevented from breeding are higher. Individuals with the highest net reproductive rates will still be selected for, but the selected rates will be lower than before. Delayed maturation, emigrations, lower clutch sizes, group territoriality, year around territoriality, polygyny, smaller territories, and related phenomena may in some cases be so interpreted.

Polygyny.—When any tendency toward polygyny exists, its evolution should be favored by a surplus of potential breeders of both sexes. Consequently, polygyny in some species might be considered as an adaptation of females to the persistence of a surplus. As Verner (1964) and Verner and Willson (1966) have mentioned, in a species in which the female chooses her mate, when a female can leave more offspring by mating with an already mated male in a "good" territory than by mating with an unmated one in a "poor" territory or lacking one, this will favor genetic predisposition in the female toward polygyny. For example, in the Great Reed Warbler some males set up territories in areas where it is impossible for the female to build a proper nest, while other males in suitable habitat for nesting are polygynous (Kluyver, 1955); females who choose polygyny with a male in suitable habitat for nest building will leave more offspring than those choosing monogamy with a male in unsuitable habitat.

When polygynous males also leave more offspring than monogamous ones, then polygyny will be favored in both sexes. Under these conditions there is also selection on the females for their ability to choose males who attract the greatest number of successful females (Fisher, 1929).

The common factor in these situations seems to be that of exclusion of some males from breeding. As population density increases, more males are excluded from breeding, more females are available per territorial male, and the greater is the reward to a successful polygynous male. Shortage of nest space in a colony, or of good habitat for nest building (Great Reed Warbler), or heterogeneity in the distribution of food resources among territories of males may increase the differential between desirable and undesirable males to the females, thus in effect increasing the surplus and increasing the evolutionary advantages of polygyny for the successful breeders.

Delayed maturation.—Delayed maturation may in some cases also be interpreted as an evolutionary adaptation to a persistent surplus or to the conditions which cause it. As noted by Lack (1954), Orians (1961), and Selander (1965), the relationship between age of first breeding and body size is not consistent since large or moderate sized species of ducks and gallinaceous birds may breed in their first year while many smaller species do not breed until subsequent years. Orians (1961:308) has noted that slow maturation rates are characteristic of species in which breeding sites are limited and has written, "Probably these are all species which are ineffectively controlled between breeding seasons so that surpluses of breeding birds are regularly present." Following Selander's (1965) modification of Lack's (1954) explanation, one can interpret a large surplus as decreasing the probability that a first year male can mate and rear young successfully; consequently, it should be less advantageous for him to take the risks associated with the attempt. That first-year male American Redstarts (*Setophaga ruticilla*) are less successful than adults in mating and nesting was shown by Ficken and Ficken (1967).

In a population at equilibrium ($s + m = 1$) the number of young, N_Y, which must be fledged yearly to just replace annual losses to the breeding population, N_B, depends on the rate of survival after fledging, s, and the age at first breeding, b, in the following manner:

$$N_Y = \frac{(1 - s)\, N_B}{s^b}$$

With the use of this equation it can be seen that the loss in reproductive potential due to evolution of delayed maturity, although large in species with low survival rates, is much less severe in species with high survival rates. For example, if breeding were delayed from the first breeding season to the second in a species with a survival rate of $s = 0.2$, each pair in order to just replace annual losses to the breeding population would have to fledge five times as many young as it would if the pair bred in its first year; when $s = 0.5$, then twice as many; and when $s = 0.8$, only one third more. Adaptation to the existence of a surplus by means of delayed maturation is, consequently, more likely in a species having a high rate of survival.

Group territoriality.—In some permanent resident species, especially those that defend Type A territories all year, first year birds sometimes linger in the territories of their parents and help in nest building, nest defense against other species, and feeding the young (Skutch, 1935, 1961). Such species seem to be preadapted for the evolution of group territories. The additional selective force necessary for group territories to evolve from a simple family group (as opposed to evolving from a colony) might well be provided by a surplus in the following way. As the density of competitors for territories increases, the probability of an individual's being excluded from the breeding population rises. Consequently, for most males more energy must be expended in competition for territory at high breeding densities. This added cost might be offset by allowing subordinates, which would normally be excluded, to participate in territorial defense and other family affairs (except mating). In small family groups the presence of additional members probably would help in maintaining territories even though the principal burden would rest on the dominant male. Subordinate birds would aid in detecting intruders, and by sheer numbers and noise would contribute psychologically to driving them out. Dominance of large groups over smaller ones was noted by Robinson (1956) in *Gymnorhina dorsalis* and by Power (1966) in the defense of nest holes by parakeets. That large numbers of less aggressive individuals by simple persistence can successfully overcome the resistance of single aggressive males was observed by Orians and Collier (1963) when Tricolored Blackbirds (*Agelaius tricolor*) successfully founded a colony on the territories previously owned by Red-winged Blackbirds. Furthermore, the aid of earlier offspring in caring for later ones should lessen the cost of "aggressive neglect" (Hutchinson and MacArthur, 1959; Ripley, 1961) on the part of the dominant male. That intraspecific aggressive neglect can reduce reproductive efficiency was illustrated in the Red-winged Starling when young in the nest "starved to death" during a protracted territorial battle (Rowan, 1966: 400).

The probability of an individual's eventually gaining the opportunity of successful breeding, if the surplus is large and persistent enough, may be greater if it remains within the family group awaiting the demise of its elders (as do young males in the Superb Blue Wren (*Malurus cyaneus*) Rowley, 1965), than if it forsakes all claims to its old territory and attempts to establish a new one in the face of uniformly fierce defense (Selander, 1964). Under conditions where the chances of infiltrating another group or establishing a new territory in a suitable habitat are remote, an individual can still contribute to raising the frequency of its genes in the population even without actually breeding. Since its siblings are genetically more closely related to it than are the offspring of competing families it can help to increase the frequency of its genes in successive generations by aiding its parents even if it is denied the opportunity to breed itself (Hamilton, 1964). A demonstration of this in the Superb Blue Wren was given by Rowley; groups with helper males produced 1.9 fledglings per adult annually, while groups without helpers produced only 1.2.

Under such Level 3 conditions there is probably intense competition between groups, with each group tending to enlarge its territory at the expense of its neighbors. Those groups which maintain themselves in successive generations, expand, and take over the areas of other groups, either by fission and expansion of the successful groups or by infiltration of emigrants into other groups, are the most successful in terms of gene frequencies in the population. Consequently, the fate of the individual and of its genes in such cases depends on the fate of its group (especially its kin).

The evolution of behavioral and other traits involving conferral of benefits on close relatives has been called kin selection (Smith, 1964; Brown, 1966). A mathematical theory by which the evolution of such social traits can be described, along lines consistent with theories based on individual fitness, has been given by Hamilton (1964). Briefly, the hypothesis that I have developed is that in a species which is preadapted by the occasional participation of young birds in the care of subsequent broods, kin selection for this and related traits within the family becomes intensified through the persistent presence of a large surplus of potential breeders and the environmental conditions which lead to the surplus. This would act to increase the role of the young in the family, to lengthen their stay with the parents, and to increase the tolerance of the parents for such a relationship. The added birds would then participate not only in territorial defense, but also in foraging, predator detection, and, in some cases, care of the young. Social organizations with communal cooperation in nest building but retaining internal territories, such as certain "lodge builders" (Crook, 1965) require different explanations.

A number of species with group territories have been studied, the three species of Crotophaginae (Davis, 1942), two of the three species of Australian magpies (*Gymnorhina dorsalis*, Robinson, 1956; *G. tibicen*, Carrick, 1963), the Superb Blue Wren (Rowley, 1965), and one of the communal species of American jays (*Aphelocoma ultramarina*) (Brown, 1963*a*). A number of other species are known to have group territories, for example, the Jungle Babbler (*Turdoides striatus*) (Andrews and Naik, 1965), and certain Galapagos mockingbirds (*Nesomimus macdonaldi*) (Hatch, 1966); further references may be found in Wynne-Edwards (1962), Davis (1942), and Crook (1965). Of these only for *Gymnorhina tibicen* has it been established that an actual surplus exists for a long period of time. This point and the related phenomenon of delayed maturation require further attention.

Whether or not individuals in these groups tend to be close relatives, which is required by theory, is not known with certainty, except for *Malurus*; the long-term banding studies which would be necessary to settle the question have not been done. In some primate species with group territorial defense it is known from observation of marked individuals that members of troops defending a territory do tend to be closely related (Washburn, Jay, and Lancaster, 1965).

In the Australian magpies (*Gymnorhina* spp.) (Robinson, 1956; Carrick, 1963), the joining of a flock by an outsider is known, as is the staying of birds hatched by the group and their eventual reproduction within the group. Since the more successful groups should tend to produce more young than there will be places available, it is to be predicted that some birds would leave the more successful groups and perhaps eventually find their way into the less successful ones. Despite this predicted mixing, however, there should in this system be a greater amount of inbreeding than would occur in the more usual pair-territory system.

There has been no adequate evolutionary interpretation of group territories by earlier authors. Davis (1942) discussed the evolution of communal nesting in the Crotophaginae but did not stipulate the ecological conditions favoring group territorial defense per se. Crook (1965), in discussing certain cases of communal social organizations, stressed the assistance in finding food, which in his view might be critical at times of food scarcity. This is probably involved but it cannot be the critical factor. In *Gymnorhina dorsalis*, a prime example of a communal species, the males are conspicuously aggressive within the group and they rarely participate in nest building, incubation, or feeding of the nestlings (Robinson, 1956:289). Non-breeding immature birds do not seem to contribute significantly in feeding the young (op. cit.:295), although they occasionally help in certain regions. In *Malurus cyaneus* multi-male groups raised 42 per cent more independent young than did pairs, but the difference was due mainly to the incubation period rather than to the period when the young were being fed (Rowley, 1965). Consequently, communal food-finding does not seem likely to be serviceable as a general explanation for the evolution of group territoriality.

THE EVOLUTION OF TERRITORIAL BEHAVIOR

The prevention-of-overpopulation hypothesis.—Kalela (1954) and Wynne-Edwards (1959, 1962, 1963) have advanced the hypothesis that territorial behavior has evolved because of its limiting effects on population densities by preventing overpopulation and the resulting destruction of food populations. Howard (1920), Meise (1930), and earlier authors (cited by Wynne-Edwards, 1962) also considered control of population density to be an important property of territorial behavior. For a fair evaluation of this hypothesis it would be necessary to consider also various alternative hypotheses together with the evidence relevant to each. Space does not permit such a procedure, but it is desirable at this point at least to consider whether or not the available data on populations are consistent with the hypothesis. More recent hypotheses will then be considered.

The data seem sufficient to conclude that territorial behavior tends to spread a population relatively evenly over its available habitat at Levels 1 and 2, with higher densities in the richer habitats than the poorer ones. Local "overpopulation" due to chance and to unusual attractiveness of certain habitats would consequently be less than if there were no other means whereby the population could achieve the same dispersion pattern. However, other means are possible, judging from their existence in other species (Lack, 1954); and the hypothesis of Wynne-Edwards does not adequately explain why these other means did not evolve in the now territorial species.

The critical point for the overpopulation hypothesis is met with Level 3 populations, for it is at this level that individuals are prevented from breeding altogether. Surpluses of significant size involving females have only rarely been demonstrated; and in some of these cases there is doubt that the surplus was caused entirely by territoriality. The better demonstrations of surpluses mainly involve habitats altered by man. The prevention-of-overpopulation hypothesis for the evolution of territoriality is only weakly supported by this rather small amount of reliable evidence.

Other criticisms of Wynne-Edwards' theory regarding territoriality have been advanced (Smith, 1964; Brown, 1964; Crook, 1965; Williams, 1966; Lack, 1966; Wiens, 1966.) These arguments, in my opinion, quite convincingly eliminate the prevention-of-overpopulation hypothesis from serious consideration as the major force selecting for territorial behavior. They may be summarized as follows:

1. Community Complexity. Population regulation is never completely under the control of the species by itself but depends in a complex way on interactions between members of the ecological community. Evolutionary adaptations tending to favor one species at the expense of a predator-, prey-, or competitor-species can lead to a "counter-adaptation" in other species. Consequently, the evolution of population regula-

tory mechanisms cannot be conceived of as occurring wholly within the gene pool of the species concerned, for it must also involve evolution and zoogeographic change in other species. Community complexity is important for the stability of the populations of the member species (MacArthur, 1955, and others).

2. Avian Food Habits. Most bird species are not restricted to a single food species but can switch from one to another when one becomes scarce, thus tending to relieve heavily utilized species from further destruction when low densities are reached. Great diversity in diet has been revealed by food-habits studies in many birds. The concept of "specific search images" and the data which support it are consistent with this interpretation (L. Tinbergen, 1960; L. Tinbergen and Klomp, 1960; Mook, Mook, and Heikens, 1960; Gibb, 1962*b*). The sudden appearance and disappearance of some plant and invertebrate foods, such as weed seeds and insects, helps to protect them from overexploitation, for example, the periodic cicadas (Lloyd and Dybas, 1966). Some food species actually depend on being eaten for dispersal, the hard pits of certain fruits, for example. Birds *in the reproductive season* may actually harvest only a small proportion of the populations of many insect species. In the studies discussed by Lack (1966:288) bird predation typically took a relatively small percentage of the populations of insect food species which were the main ones fed to nestlings, and birds were not the principal predators on the insect species utilized by the birds as food.

3. Alternative Means of Population Regulation. The more conventional views of population regulation, which rely on density-dependent mortality often involving the food supply and predation, have been comprehensively reviewed by Lack (1954, 1966), but received little attention from Wynne-Edwards (1962). Although Lack might have erred in underestimating the role of behavior in population regulation, there seems to be no reason to completely replace the conventional interpretation with one based mainly on behavior.

4. Slowness of Interpopulation Selection. Interpopulation selection is too slow and inefficient to be effective when compared to "inter-individual" selection. Genetic change in the frequencies of types of populations requires either extinction of established populations or colonization, whereas genetic change in types of individuals requires only the conception or death of an individual (in birds).

Extinction of a bird population *through over-exploitation* of its food supply seems never to have been observed or recorded in nature, nor has the extinction of a regular food species through overexploitation by birds been observed to my knowledge. In the absence of proof that interpopulation selection for prevention of overpopulation actually occurs today, one would have to assume that such selection is no longer important and that the traits concerned evolved long ago—a convenient, if lame, excuse for lack of evidence.

5. Required Dispersion of Populations. Interpopulation selection requires a large series of almost completely isolated populations—a degree of isolation which is the exception rather than the rule on continents. Although the division of populations into demes is a concept which applies well to some bird species, the degree of isolation of these demes required for the successful operation of inter-demic selection for population regulation in opposition to strong individual selection would be rare except on oceanic islands. The degree of isolation necessary for effective interpopulation selection should be greater than that needed for genetic drift to be significant. In most continental species, despite the well known Ortstreue, there would seem to be enough interchange between local populations to allow superior genotypes to flow more rapidly through

a species than they could be defeated by interpopulation selection. For example, Berndt (1960) in a study of the Pied Flycatcher showed that 10 per cent of the recovered adult females which had been ringed as nestlings were found breeding 19 to 235 km from the hatching site.

6. Origin Unexplained. Interpopulation selection can theoretically explain the continuance of a character but cannot easily explain its origin within a population. For simple traits mutation or genetic drift might suffice, but for a highly complex trait such as territorial behavior, involving display, fighting, avoidance, releasers, and appropriate responses to key stimuli, a constructive evolutionary force such as is supplied by individual selection is required.

7. Resistance to Individual Selection Unexplained. Wynne-Edwards (1963) regarded population regulatory mechanisms such as territoriality as so deeply tied in with the biology of the species as to effectively resist the forces of change imposed by individual selection. A comparison was drawn to the mesoderm and coelom. Yet social organizations in birds are anything but conservative; great diversity is well known even in closely related groups, e.g. the genera *Agelaius* (Orians, 1961) and *Aphelocoma* (Brown, 1963*a*), families Icteridae, Ploceidae (Crook, 1964, 1965). The evident diversity in avian social organizations even in species of recent evolutionary origin is proof that the behavioral traits on which the various organizations are based are subject to relatively rapid evolutionary change. Neither can the various types of social organizations be considered homologous in different species as the mesoderm and coelom are.

8. Diversity of Territorial Systems Unexplained. Although many types of social organization are known in birds, the hypothesis of their evolution via interpopulation selection for prevention of overpopulation does not adequately explain why a particular kind of organization is found in a particular species. In contrast, this aspect is relatively easily explained through recourse to individual selection (Brown, 1964).

9. Adequacy of Individual Selection. It was reasoned by Wynne-Edwards (1962, 1963) that since territorial behavior was an adaptation for population control (in his view), it could not have evolved by individual selection. Most authors have based their theories on individual selection, and it is difficult to see why individual selection should now be thought of as working against the evolution of territorial behavior, without being given a more persuasive argument (see below).

A role for interpopulation selection in the evolution of social organizations cannot be completely ruled out by the above considerations. The balance of evidence suggests that individual selection is much more powerful and faster than interpopulation selection in the evolution of avian social organizations, but a minor, complementary role for the latter, especially at the species level, should not be excluded as a possibility. More quantitative approaches to the problem than are now available would seem to be necessary to substantiate even this hypothetical complementary role in nature. Lacking the necessary, sophisticated quantitative studies, the case for interpopulation selection in the evolution of avian social organizations is exceedingly weak at present.

Basic questions.—A part of the confusion in the literature on territorial behavior stems from confusion in statement of the basic questions. Rather than ask about the "functions" of territoriality (Hinde, 1956; Tinbergen, 1957; Lack, 1966), it would be more to the point to state directly that our primary interest is in the evolutionary origin, development, and maintenance of territoriality and that we approach this problem through a study of the effects of territorial behavior on gene frequencies. One of the dangers in speaking of the "functions" of territory is that the mechanisms of selection by which a particular function might act on the gene pool of the species are often left vague and unspecified. Thus, Tinbergen (1957) in an article on "The Functions of Territory" has stressed the role of territorial behavior in dispersion. Although dispersion is a population phenomenon and not easily explained on the basis of Darwinian natural selection except as a secondary consequence of some other primary benefit to an individual, no attempt was made by him to overcome this difficulty, probably because he had not addressed himself directly to the actual evolutionary mechanism involved, but rather to the vague concept of function.

Wynne-Edwards (1963) while supporting the role of territoriality in dispersion, took the logical next step in this line of reasoning and proposed a selective mechanism based on what he called intergroup selection, which might better have been termed "interpopulation selection" so as not to confuse it with kin selection (Brown, 1966). It is useless to ask whether territoriality is good for the species, good for the population, or good for the individual, and to reason from the answer how territoriality might have evolved. The answers to these questions might be yes or no in all three cases depending on one's personal inclination. More important is the question of relative fitness (in the sense of population genetics) of territorial and non-territorial individuals in specified environments. It is clear from the data on surpluses and from behavioral observations that a clear difference in fitness often exists, since non-territorial individuals simply cannot reproduce under Level 3 conditions and since those holding poor territories (Level 2) must also be a disadvantage. Behavior of this sort, which raises one individual's fitness at the expense of another, has been termed "selfish behavior" and can be treated theoretically in the context described by Hamilton (1964:15). In this sort of treatment the idea of "function" need not be considered at all.

The fitness differential between territorial and non-territorial individuals is so great and so widespread—in potentially every territorial species—that we are justified in seeking a general theory for the evolution of territorial behavior based on individual selection. Such a general theory has been proposed and examples of its power to explain diverse territorial systems have been given (Brown, 1964). Its essence is that for territorial behavior to evolve in respect to a given object, be it mating priority, living space, foraging area, or nesting site, 1) a situation must exist in which there can be aggressive competition for that object, 2) territorial individuals must be more successful than non-territorial individuals in acquiring that object, and 3) the successful acquisition of the object of territorial behavior must raise the overall fitness of successful individuals over that of unsuccessful ones. Competition for these objects is not merely "conventional" or "symbolic"; it is real.

The consequences to an individual bird of failure to obtain a territory, regardless of its type, are usually so obvious—failure to breed, or to live—that differences in fitness between individuals with and without territories are readily demonstrable or imaginable in virtually every territorial species. The selection pressures which might cause territorial behavior to evolve by acting on individual genotypes are thus both readily apparent and powerful.

Crook's hypotheses.—In a recent review of social organization in birds Crook (1965) mentioned some ideas relevant to the evolution of territorial behavior. In his view, ". . . the primary reason for territorialism remains the need for individual food exploitation." (p. 204). In territorial species, individuals who competed successfully for territories were supposed to raise more young than gregarious types 1) because their manner of feeding would be made more efficient by absence of interference from other conspecific individuals, 2) because over-exploitation of their private realm would be prevented, and 3) because their nests would be more protected from predators because of their uniform dispersion.

A number of objections may be raised. Crook wrote that success in foraging in one group of territorial species "depends on a combination of stealth (cryptic approach), speed and skill", and he went on to suppose that "the solitary nature of these species is an adaptation to their mode of food exploitation" (p. 195). It is not clear to me that hummingbirds, Ospreys, and kingfishers use much "stealth" in foraging, nor that they require solitude for effective finding of food. The advantage of solitude even to the most sensitive species would seem to be slight; even if intraspecific solitude were achieved, interspecific interruptions would remain. Given the same number of individuals and the same area of uniform habitat, it is difficult to understand why there would not be more interference with foraging under a territorial system than in a system of dispersion based simply on food abundance, perhaps with the addition of a slight tendency to avoid conspecifics. Such a small increase in foraging efficiency seems hardy worth the effort of territorial defense.

In my opinion, it is only when the demand for certain food resources exceeds the supply (Levels 2 and 3) that it becomes economical in terms of time and energy to fight and threaten for them, provided that they can be feasibly defended (Brown, 1964).

Crook was impressed by the correlation between the uniform dispersion of nests and their "crypticity"; consequently, he invoked predation as another factor favoring the evolution of territorial behavior, as has Lack (1966:279). But this correlation may have another explanation. If territoriality has already evolved because of selection pressures other than predation, then the nest may or may not be cryptic depending on the predation to which it is subsequently exposed. Lacking the protection offered by colonial nesting, it is logical that nests of territorial species would tend to be more protected or cryptic; similarly, colonial nests need not be so cryptic because of the protection afforded by the colony site and the behavior of the colonists.

Crook's approach seems to have been to consider groups of species with specified types of foraging habits and to speculate on how territorial behavior in the nesting season might be more beneficial to them than gregarious behavior. This method of approach is dangerous because it does not directly consider the problem of fitness differentials between individuals of different behaviors within one system; rather, it tends to compare whole systems, e.g. the territorial versus the gregarious. When the great difference in fitness between territorial and non-territorial individuals in an already territorial species is considered, it seems unnecessary to compare systems in seeking possible selection pressures leading to and reinforcing territorial behavior. It is desirable, however, to seek the ecological factors which make it profitable in terms of time and energy to defend territories with various qualities. Exemplary studies of this type have been carried out by Orians (1961), Verner (1964), and Willson (1966).

In a colonial species it is again instructive to consider the difference in fitness between territorial and non-territorial individuals. The territorial individual would gain nothing in most species through a greater isolation of its nest or defense of a feeding territory, for in most colonial species the food is distant from the nest site and is not economically defensible either because it is too mobile (swifts, swallows, seabirds) or so transient that its continual presence is unreliable and not worth the evolutionary gamble of territorial behavior (Orians, 1961; Brown, 1964; Crook, 1965).

Conclusion.—The consideration of the effects of territorial behavior on populations at different density levels, which has been attempted in this paper, reveals the importance of population density in relation to the selection pressures acting on territorial and non-territorial individuals. It is necessary to consider different types of social organization not only under ideal conditions, but also under conditions of severe competition. At Levels 2 and 3, where some individuals are led to choose inferior territories or not to attempt breeding at all, the relative fitness of territorial and non-territorial individuals is especially clear. Regardless of what the hypothetical properties of a superior territory in a particular species may be, they will have to be "worth fighting for" if they are to provide an adequate explanation for the evolution of territorial behavior.

SUMMARY

In examining the factual evidence on which the concept of population regulation through territorial behavior is based it was found desirable to differentiate between three critical population densities. The effect of territorial behavior on limitation of reproductive success should differ at each level. At the lowest density, Level 1, territory sizes should not be limited by competition for territories and no individuals should be prevented from nesting in good habitats. At middle densities, Level 2, some individuals should be excluded from the better habitats but should establish territories in poorer habitats. This may under certain conditions create the "buffer effect". At the highest densities, Level 3, some individuals should be prevented from breeding and would form a breeding surplus or reserve which might exist as a floating population in and around occupied territories or on separate ground.

The evidence supporting these hypothetical actions of territorial behavior on reproduction is found to be mostly behavioral and especially weak at the population level. The widespread importance of a buffer effect in population control has not been substantiated; the evidence is at present sparse and inconsistent. The prevention of *females* from breeding by territorial behavior has only very rarely been demonstrated in significant numbers. Surpluses involving primarily males are known in several species. In future population studies more attention should be paid to determining the magnitude and persistence of the surplus, especially in females. When a surplus exists, removal of the breeding population would be desirable to show that the surplus individuals would breed if allowed to establish themselves on territories. Although the hypothesis of population regulation through territorial behavior is a tempting one, too few critical studies on it have been done to conclude now that it is of widespread importance in limiting reproduction of avian populations; and, in any case, such a limit will be determined not by territorial behavior alone but by complex interactions between the environment, the number of birds competing for territories, and territorial behavior.

Territorial behavior probably also influences populations in some species by increasing the emigration and mortality rates of individuals unsuccessful in finding territories.

The size of the surplus depends on the excess of gains over losses and should be especially sensitive to variations in survival rates between species.

The surplus and the conditions which tend to create it are considered as a link in the control of population density both through behavioral effects influencing reproduction, mortality, and dispersal and through natural selection acting on individuals. The surplus and conditions which create it are conceived as selective forces. Some of the hypothesized evolutionary consequences are lowered reproductive rates, polygyny, delayed maturation, and group territoriality.

The hypothesis of the evolution of territoriality via individual selection resulting from

aggressive competition is reaffirmed, and the hypothesis based on interpopulation (group) selection for prevention of overpopulation is rejected.

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ADDENDUM

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