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*Evolution*, Vol. 17, No. 4. (Dec., 1963), pp. 449-459.

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# COMPETITION AND BLACKBIRD SOCIAL SYSTEMS

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Received November 1, 1962

The principle of competitive exclusion, variously known as Gause's Law, the Volterra–Gause Principle, or Grinnell's Axiom, has emerged as an important ecological generalization notwithstanding the reservations of some ecologists (Cole, 1960) and the active antagonism of others (Andrewartha and Birch, 1954). The evidence in support of competitive exclusion, derived from six main sources, strongly suggests that interspecific competition has had an important influence on the evolution of contemporary community structure despite the apparent relative abundance of resources with respect to the sizes of the populations utilizing them (Hutchinson, 1957). Unfortunately, most of the supporting evidence is indirect.

Closely related sympatric species have attracted the most attention, and whenever they have been carefully investigated, important ecological differences have been discovered (Lack, 1944, 1945, 1946; Carpenter, 1952; Diver, 1940; MacArthur, 1958; Gibb, 1954). However, since identical species are theoretically unlikely, differences are to be expected whether competition is manifest or not. This evidence would, therefore, be less convincing if it were not for evidence of the second type, namely, that closely related species may be more different morphologically and ecologically in areas of sympatry than in areas of allopatry (Lack, 1947, 1949; Vaurie, 1951; Brown and Wilson, 1956).

A third source of evidence is the structure of the incomplete communities of isolated mountains and remote islands, where those few species present nearly always occur in a wider range of habitats than in areas with a full faunal complement (Moreau, 1948; Lack and Southern, 1949; Crowell, 1962). Fourth, though the problems of defining the boundaries of arbitrary communities are formidable, Elton (1946) and Moreau (1948) found fewer closely related species occurring together than would be expected if species were randomly distributed. Fifth, studies of breeding bird censuses (MacArthur, 1957, 1960) have revealed a rather consistent logarithmic relationship between the relative abundances of species. MacArthur (1960) has shown that this distribution is to be expected if niches are contiguous and non-overlapping. No distributions are currently known that fit assumptions of either completely separated or completely overlapping niches. This implies that, for birds at least, food determines the abundance of all species since it is the only unsharable, completely utilizable resource (Hairston, 1959).

The sixth and last source of evidence is direct observation of interactions between species under natural conditions. Unfortunately, direct evidence of this sort is more difficult to obtain than indirect evidence, but in many bird species interactions can be observed readily, provided sufficient time is spent (e.g., Pitelka, 1951). Moreover, evidence from behavioral interactions is potentially of great theoretical interest since the utilization of some form of social organization to aid environmental exploitation and the development of complex behavior patterns to mediate population interactions are fundamental features of vertebrate evolution. The simple interaction of a population with its food supply as found in *Daphnia,* for example (Slobodkin, 1954), does not exist among birds and mammals. Moreover, it

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Evolution **17**: 449–459. December, 1963

is characteristic of many manifestations of social behavior, such as territoriality, that they usually result in each species depressing its own population more than the populations of other species, a vital condition of coexistence (MacArthur, 1958). In addition, the operation of a social system is consuming of both time and energy (Orians, 1961), since a territorial bird requires more food but has less time in which to obtain it than if it were not engaged in aggressive behavior.

The purpose of this paper is twofold. First, to present data on interactions between the Red-winged Blackbird (*Agelaius phoeniceus*) and the Tricolored Blackbird (*A. tricolor*) in California, and second, to develop from them a theoretical framework for thinking about the energetics of competition as an evolutionary factor in the establishment of sympatry. The data for this paper were gathered during intensive studies of social organization among the two blackbirds from 1958 to 1961. Orians worked in north-central and Collier in southern California, each in a wide variety of habitats, so that the observations reported here are probably representative of interactions between the species wherever they occur together. We shall refer to all aggressive encounters between the species as interactions, reserving until later a consideration of their competitive significance.

## Comparative Social Organization

The widespread Redwing is sympatric with the Tricolor throughout the narrow range of the latter in the lowlands of California and adjacent Oregon and Baja California. Morphologically they are very similar, but the Tricolor has narrower and more pointed wings and a more slender bill, and the males have prominent white borders to the middle wing coverts. Behaviorally, however, the species are strikingly different (Orians, 1961; Orians and Christman, MS; Collier, MS). In California male Redwings defend moderately large territories of 500–30,000 square feet, usually in marshes, within which several females establish subterritories and build nests. The males take no part in the construction of the nest or incubation and normally do not feed the nestlings until after they have fledged, if at all. The females gather food partly on the territory and partly on the adjacent dry land, the pattern of exploitation varying with the vegetation types involved.

In contrast, the nomadic Tricolor is the most highly colonial of North American passerines. Colonies of less than 50 nests are rare, and in favorable habitat, such as the Californian rice fields, they may be as large as 200,000 nests (Neff, 1937). Territories average about 35 square feet in area but are difficult to measure accurately in congested areas. One to three females construct nests within these small territories. The males do not assist in nest building or incubation and may leave the marsh while the females are on the eggs. However, once the eggs hatch, the males take an active role in the feeding of the young. No food is gathered on the small territories and the radius of exploitation around a large colony may extend as far as four miles and include more than 30 square miles of utilized land.

## Study Areas

Observations were concentrated at several localities in north-central and southern California (fig. 1). Extensive field work was carried out at Lake Sherwood, an artificial body of water (formed in 1905) in the Santa Monica Mountains located 25 miles east of Ventura, Ventura County, at an elevation of 955 feet. At its western end is a marsh about five acres in extent, divided into north–south halves by an east–west land bank. The northern half is occupied by bulrushes (*Scirpus*), the southern half by cattails (*Typha*). The quarter-acre Hidden Valley Marsh, 200 yards distant, is separated from the northwest corner of Lake Sherwood by a low ridge. Blackbirds nest in both areas. Another area of concentrated field work was the East Park Reservoir, located in the North Coast Ranges of Colusa County

FIG. 1. Blackbird study areas.

at an elevation of 1,200 feet. It is also an artificial body of water whose level fluctuates markedly during the year, as the water is used for irrigation in the Sacramento Valley. It is surrounded by heavily grazed blue oak parkland–chaparral, and, at the south end, by wheat and alfalfa fields. The Haskell Ranch marsh, eight miles southeast of Marysville, Yuba County, is surrounded chiefly by irrigated pastures and owes its existence to runoff water from these pastures. Observations were also made in others areas in the Sacramento and San Joaquin valleys and in southern California.

## INFLUENCE OF ENVIRONMENTAL CONDITIONS ON BREEDING SUCCESS

If the effects of interactions between the species are to be understood, they must be separated from the influence of environmental fluctuations upon reproductive success. It has been shown (Orians, 1961) that the colonial system of the Tricolored Blackbird is more demanding of energy than the territorial system of the Redwing, primarily because of the enormous amount of energy expended in flying back and forth from the distant feeding areas when gathering food for the young. From this it follows that the Tricolor requires rich food supplies which can be obtained rapidly once the feeding ground is reached. Therefore, this species has an unpredictable breeding distribution and has poorer reproductive success than the Redwing in unfavorable years.

Of the years of this study, 1958 was very wet, with heavy rains continuing into April in all areas of the state. In contrast, 1959, 1960, and 1961 were drought years (table 1). Adequate spring rains did not occur on any of the study areas in 1959. No rain fell at Lake Sherwood between February 21 and April 25. In 1960 spring rains were well distributed in northern California, but the southern part of the

TABLE 1. *Monthly precipitation and seasonal totals for study areas in north-central and southern California*

| | Precipitation in inches | | | | | | |
|---|---|---|---|---|---|---|---|
| | Lake Sherwood | | | | Sacramento | | |
| Month | 1957–1958 | 1958–1959 | 1959–1960 | 1960–1961 | 1957–1958 | 1958–1959 | 1959–1960 |
| September | none | 0.16 | 0.10 | none | 1.35 | 0.12 | 1.54 |
| October | 1.33 | 0.02 | 0.02 | none | 1.35 | 0.42 | T |
| November | 0.40 | 0.44 | none | 4.15 | 0.33 | 0.16 | 0.01 |
| December | 6.30 | 0.13 | 1.96 | 0.16 | 3.07 | 0.72 | 1.28 |
| January | 3.13 | 3.22 | 3.92 | 1.54 | 5.38 | 4.62 | 3.25 |
| February | 8.64 | 4.65 | 2.06 | none | 9.13 | 3.64 | 2.91 |
| March | 7.39 | none | 0.38 | 0.54 | 5.93 | 0.46 | 1.62 |
| April | 6.89 | 0.52 | 2.26 | 0.34 | 4.41 | 0.30 | 1.26 |
| May | 0.05 | none | none | 0.02 | 0.72 | T | 0.41 |
| Seasonal total | 34.13 | 9.14 | 10.70 | 6.75 | 32.37 | 10.44 | 12.28 |
| Long-term average | | 19.04 inches | | | | 16.32 inches | |

state remained abnormally dry. Nearly all of the spring rain at Lake Sherwood fell during a heavy storm April 27.

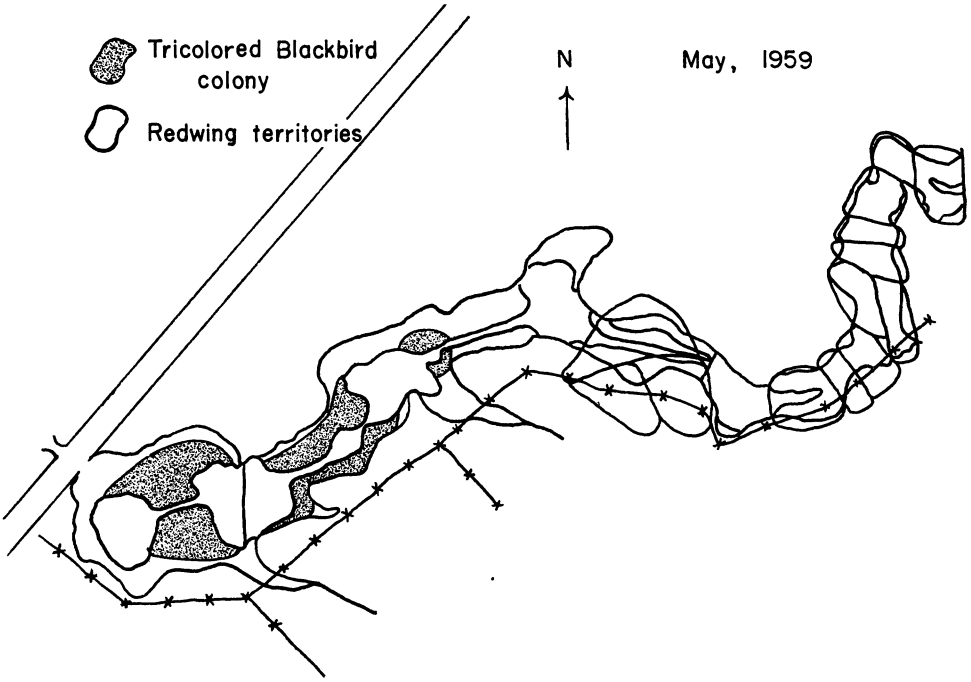
Response of Tricolors to drought is of three main types: failure to breed, desertion, and poor nesting success. At Lake Sherwood in 1960, the second year of the drought, about 400 Tricolors established territories on March 27 and engaged in territorial and reproductive behavior for two days. However, by March 30, all signs of breeding behavior had ceased, and two weeks later the marsh was completely deserted. Redwings, however, bred successfully in the marsh that year. In 1959, about 150 Tricolors moved into the Hidden Valley Marsh April 2, and 65 nests were started. However, it was evident by April 10 that the number of birds was sharply dropping and only 20 nests were completed. Eggs were laid in only 7, and young hatched in only 3 nests. A similar situation was observed at the East Park Reservoir in 1959. Several thousand birds were present when the colony started April 20, and complete clutches were laid in most nests, but in early May desertions began. On May 7, there were actively incubated eggs in only one-fourth of the nests, and by May 16, only 15 females were feeding young. Redwing breeding was successful that year, but fewer young were fledged per nest than in the wetter spring of 1960 (Orians, 1961). The season of 1960–1961 was the driest on record for Lake Sherwood. Grain crops withered before the plants exceeded a height of ten inches and Tricolored Blackbirds made no attempt to breed either at Lake Sherwood or other breeding areas in the Los Angeles region. Massive desertion of full clutches and poor survival of fledglings (also correlated with poor environmental conditions) characterized the two fall colonies in the Sacramento Valley in 1959 (Orians, 1960).

## INTERACTIONS

*Prenesting situation.*—Since the Tricolored Blackbird is a nomadic species, the situation prior to the start of nesting varies considerably. In some localities both species roost in the nesting marsh months before breeding begins, while in other localities the Tricolors may appear suddenly in marshes from which they have been absent for months. Neither species consistently breeds earlier than the other, but since male Redwings establish and maintain territories up to several months prior to the commencement of nest building, Redwing territories are always occupied at the time the Tricolors start breeding.

Certain sites regularly used by colonies of Tricolors are avoided by Redwings during the period of territory establishment, but it is difficult to be certain that those areas are in fact suitable for Redwings. It has become apparent to us that the Redwing is primarily a species of the edges of marshes and that large expanses of unbroken cattails in California are normally occupied only on the periphery. Thus, the failure of Redwings to occupy the site of the Tricolor colony at the Capitol Outing Club in Colusa County (Orians, 1961), and the large bulrush section of the main marsh at Lake Sherwood, may have nothing to do with the presence of Tricolors.

However, there remains one case which is difficult to dismiss on these grounds. The Haskell Ranch, Yuba County, has been the site of a large Tricolor colony for at least eight years and probably much longer. The colony has always been located in the southwest half of the marsh though its extent varies considerably (figs. 2 and 3). Redwings do not establish territories in that portion of the marsh even prior to the arrival of the Tricolors, despite the fact that the marsh is nowhere broad in extent and is surrounded by similar irrigated pastures its entire length. It is difficult to know how an avoidance of Tricolor areas by Redwings prior to the arrival of the Tricolors could be selected for and maintained in the Redwing population. Even if adult Redwings with previous experience avoided these areas, birds from other areas and individuals breeding for the first time would presumably settle



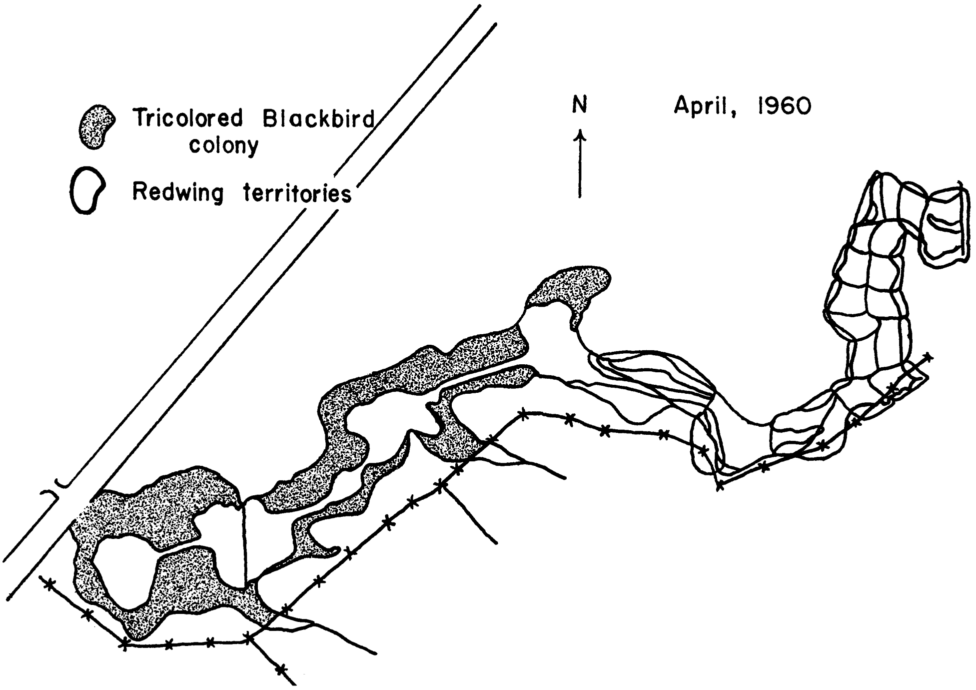


FIG. 2. Location of Redwing territories and Tricolored Blackbird colony at the Haskell Ranch, Yuba Co., California in 1959.

FIG. 3. Location of Redwing territories and Tricolored Blackbird colony at the Haskell Ranch, Yuba Co., California in 1960.

there, particularly since territories are known to be in short supply (Orians, 1961). Perhaps these areas are unsuitable for Redwings in some undetected manner.

*Colony establishment period.*—Interactions between Redwings and Tricolors are most common at the time colonies are formed. At the East Park Reservoir, in 1959, Redwing territories, established during February and March, occupied the entire marsh. A large flock of several thousand Tricolors roosted there nightly but they were completely absent during the day until the first week of April when they began to shift from site to site, as if prospecting for the best location for the colony, before leaving in the morning. These shifting flocks were continually attacked by the resident male Redwings, but without success, even though aggression was actually never countered or resisted.

Suddenly, on April 21, the Tricolors remained all day, the colony site was established, and by afternoon nest building was under way. Aggression by male Redwings whose territories were invaded was intense but ineffectual and gradually subsided. During the period of territory occupation by the Tricolors these male Redwings were still present on their territories, but they stopped singing and were no longer aggressive. When mass desertion of Tricolors took place during the first week of May, the male Redwings again resumed singing and became aggressive towards those few female Tricolors still incubating. However, the female Redwings had deserted these territories, leaving unfinished nests behind them, and no new nestings were attempted.

At Hidden Valley Marsh in 1959, there were 16 male Redwings defending territories. However, the intermittent presence of Tricolors disrupted the system and by the time the Tricolors began to breed, nine of the Redwings had deserted their territories leaving seven holding territories on the periphery of the marsh while the Tricolors occupied the center (fig. 4). The remaining peripheral male Redwings harassed incubating female Tricolors and birds of both sexes returning to feed young. Even though the Tricolors were largely unsuccessful, no additional Redwing territories were established later in the season.

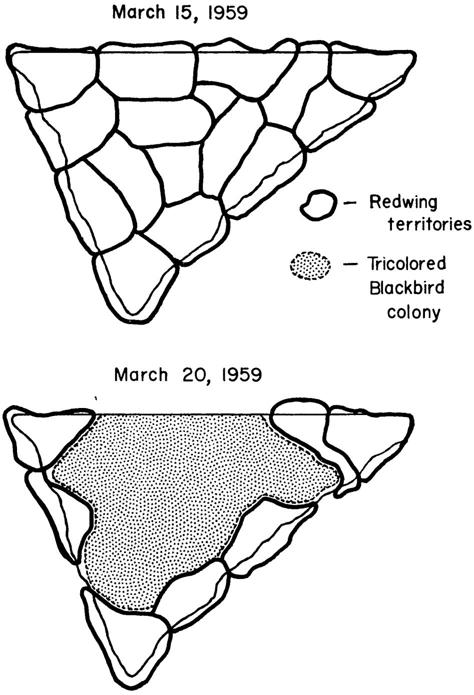


FIG. 4. Interactions between Redwing and Tricolored blackbirds at the Hidden Valley Marsh, Ventura Co., California in 1959.

When the Tricolor colony at Lake Sherwood was established in 1958, Redwings already had young in some of their nests. Dead and mutilated nestlings were found in several nests soon after the Tricolors took over the area. They may have been pecked by the Tricolors, but there is no direct evidence for this.

We have additional evidence from colonies less well studied that invasion of a marsh by Tricolors may result in nest desertion by Redwings. In early May, 1959, thousands of Tricolors began nesting in a marsh five miles southeast of Marysville, Yuba County. We had not visited the area prior to the establishment of the colony, but deserted Redwing nests with eggs were found in several parts of the colony. Territorial male Redwings remained only on the fringes of the colony and only a few broods of young were successfully reared, whereas nesting success in adjacent marshes, with no Tricolors, was normal. In 1960, the entire marsh was occupied by Redwings, and there was no large Tricolor colony. At Lake Sherwood in 1957, incubating female Tricolors were harassed by immature male Redwings when the latter came to roost in the evenings. Many fights were observed, but no cases of actual nest destruction were discovered.

*Nesting period.*—Normally, by the time the nestling Tricolors hatch, the period of interaction is over unless Tricolor colonies have become very small due to desertions and/or failures. By the time the Tricolor eggs hatched at the East Park Reservoir in 1959, only five females and no males remained in that part of the colony which had been most intensively studied. Females returning to the nests with food were vigorously attacked by the male Redwings and, while this did not completely prevent their feeding the young, the delay was at times considerable. Furthermore, whenever one of the Tricolors attempted to gather food at the edge of the marsh, she was chased by the male Redwing in whose territory she foraged. This completely prevented the Tricolors from foraging adjacent to the marsh in the areas in which female Redwings gathered food. The probable result was a reduction in the rate of food delivery to the nestlings.

During the afternoon of May 16, one of the Tricolor nests was destroyed. A male Redwing was observed behaving strangely near the nest site, disappearing into the cattails near it while uttering the guttural notes normally given when attacking other birds. When visited a few minutes later, the nest was empty and the nestlings could not be found in the dense vegetation. Whether the Redwing actually tossed them out or whether he had been attracted by some predator, such as a snake, could not be determined. At Lake Sherwood in 1959, when the Tricolor colony was reduced to a few active nests, the females also had difficulty in returning to incubate and feed the young because of Redwing aggression.

The almost constant aggressive interactions between Redwings and Tricolors in the field wherever colonies of the latter are bounded by territories of the former thus have conspicuous adverse effects upon the reproductive success of one or the other of the species. Which species suffers depends upon the particular situation, but the behavior of the two species is remarkably and consistently different. The Redwing exhibits strong territorial aggression towards Tricolors, but field observations clearly indicate that mistaken identification is not involved. These attacks are unsuccessful not because of their low intensity but because of the numbers of Tricolors involved. Individual Redwings are always dominant to individual Tricolors, but attacks by single Redwings on flocks of Tricolors are ineffectual. When repeated attacks on the Tricolors fail, the male Redwings respond either by continuing to occupy the territory but ceasing to display there, or by completely deserting the area. Females also desert and no successful Redwing nest has been found by us in a Tricolor colony except at its very edge. On the other hand, it is possible that Redwings may actually destroy Tricolor nests if the number of Tricolors is greatly reduced. In this situation attacks upon those few remaining Tricolors are successful.

In contrast, the Tricolors normally exhibit no signs of interspecific aggression; the possible case of nest destruction at Lake Sherwood in 1958 is perhaps an exception. Rather, the birds merely fly a few feet and land again, only to be chased again by the male Redwing. But while some birds are being evicted, others move in to take their place so that despite lack of overt resistance by individuals, continued occupation of the desired site by the population is maintained if there are enough birds.

## DISCUSSION

Since the interactions between the two species of blackbirds have such striking effects upon their reproductive success, it is to be expected that the existence of such interactions through time has had an influence upon the evolution of their social behavior. The Tricolored Blackbird probably evolved in California at a time when the pancontinental Redwing population was split into at least two groups, perhaps by Pleistocene glaciation, but possibly earlier. There has been a long period when both species have coexisted in California, during which time the Redwing has developed several well-marked races, including those in which there has been character displacement in the male plumage from that of the Tricolor. On the other hand, there is little to suggest that the major features of social organization of either species have been substantially altered by interspecific contacts. The colonial system of the Tricolored Blackbird appears to be well adapted to the alternating flood and drought conditions prevailing in the lowlands of California and probably was established in approximately its present form when the Redwing reinvaded the area (Orians, 1961). It is possible, however, in view of the success of Redwing aggression when the number of Tricolors is small, that continued interspecific contacts have served to reinforce the advantages inherent in close synchrony in Tricolor colonies. In general, however, data support the conclusion that the different social systems have evolved in response to ecological conditions independently of interspecific contacts (Orians, 1961).

Since aggressive behavior must entail disadvantages as well as advantages, the level of aggression which evolves must be a compromise between their relative importance. The expenditure of excessive amounts of time and energy would result in increased mortality and neglect of offspring, which would be uncompensated if all necessary environmental requisites could be provided by a lesser time and energy expenditure. On the other hand, an insufficient expenditure of time and energy could seriously impair the reproductive output if, as a result, some requisites were in short supply. The particular spacing system which evolves will therefore depend upon many variables, among them the ecology of the species, its previous history, and the nature of the environment which it exploits.

Whereas territorial aggression is usually restricted to conspecific individuals, species which are ecologically very different may defend mutually exclusive territories when they come into contact. However, natural selection should quickly act to eliminate interspecific aggression *no matter what the degree of divergence in species-specific characters,* because a mutation causing its possessor to ignore individuals of the other species would immediately save a great deal of time and energy without concurrent disadvantages. Conversely, if ecological divergence has not been sufficient for the species to be truly compatible, selection should favor the continuance of interspecific aggression, again no matter what the degree of differences in species-specific characters. Interspecific aggression is by no means restricted to those species which are morphologically similar, nor are similar species necessarily interspecifically territorial. A review of interspecific territoriality in birds as related to the age of the species groups, structural diversity of vegetation, and methods of exploitation will be given elsewhere (Orians and Willson, in prep.).

On this view, certain problems currently considered in the literature on speciation and isolating mechanisms can be given at least partial resolution. For example, ornithologists have questioned whether species coexist because of plumage differences evolved after contact or whether these plumage differences, evolved during their allopatric evolutionary histories, permit the sympatry (Hamilton, 1962). We suggest that the problem of sympatry is basically independent of the degree of divergence in species-specific plumage patterns although the possibility of further divergence in such plumage patterns following the establishment of sympatry is not thereby discounted. In fact, the character displacement in male Redwing plumage is attributable to this cause. Ecological compatibility, the prime requirement for sympatry, is relatively independent of species-specific plumage patterns, but rather is strongly influenced by such behavioral attributes as feeding behavior which vary remarkably in morphologically similar species (Hartley, 1953; MacArthur, 1958).

Similarly we suggest that the strong segregation of congeneric species into different habitats where they are sympatric is primarily related to the inability of the species to achieve ecological sympatry rather than to the problems of hybridization and ethological isolation. To deny access to suitable habitats for one's self and offspring to achieve ethological isolation is highly disadvantageous and should at best be only temporary. Failure to achieve sympatry may result from swamping of peripheral adaptations by gene flow from the center of range of the species (Hamilton, 1962; Mayr, 1954; Snow, 1954), or because the environment is structurally too simple to afford opportunities for alternate patterns of exploitation.

However, divergence of ecological as well as species-specific plumage characters is to be expected following the establishment of sympatry provided peripheral adaptations are not completely swamped. In the zone of sympatry there will be strong selective advantage to any individuals which are ecologically more divergent from their congener because of their lesser competitive impact. By this means divergence in excess of that required to make interspecific aggression energetically disadvantageous is possible and likely.

Behavioral patterns are important in species interactions because they may decrease the incidence of misidentification and may result in different foraging techniques and hence important ecological differences. In the case of the Redwing and Tricolored blackbirds the impact of behavior is not primarily upon foraging technique, which appears to be identical in the two species, but upon the places in which the individuals are foraging. Whereas Redwings are primarily restricted to feeding areas within 300 yards of their nests, Tricolors regularly forage as far as four miles from the nesting colony.

*Evolution of interspecific aggression in blackbirds.*—If we postulate that the essential differences between Redwings and Tricolors were in existence at the time contact between the species was established, it follows that territorial aggression was initially low in Tricolors. In view of the impact of interspecific aggression it might be argued that selection should have favored the evolution of increased aggression towards Redwings. However, it has been noted that aggression by Redwings is successful only when Tricolor colonies have been seriously reduced for other reasons, at which time reproductive success of the remaining individuals may be low in any case. Moreover, under normal circumstances non-aggressive resistance by Tricolors is completely effective because of the overwhelming influence of numbers. A similar relationship between Noddy and Sooty terns on the Seychelles Islands has been reported by Vesey-Fitzgerald (1941), but his observations were fragmentary. A mathematical model for such relationships has been developed (Hutchinson, 1947) but good substantiating field evidence has not previously been available.

The Redwing, on the other hand, because of its strongly territorial system, would initially have been aggressive to Tricolors as well as other members of its own species. Because of the devastating impact of a large Tricolor colony upon the reproductive activities of the Redwings whose territories they invade, selection should favor the continuance of this interspecific aggression. If the size and location of Tricolor colonies were more predictable from year to year, it would be expected that avoidance on the part of Redwings of traditional sites of Tricolor colonies would evolve. Since this is apparently not possible, Redwings continue to occupy all suitable areas and remain aggressive to Tricolors attempting to take over their territories, despite the low degree of success of such aggression.

Since most objections to competitive exclusion as a factor of importance in nature are based upon the indirect nature of most of the supporting evidence, it is vital that direct evidence bearing upon the problem be gathered whenever possible. If by careful observation competitive interactions cannot be demonstrated, theories relegating the importance of competition to the past could rightly be viewed with greater skepticism. But we suggest that such evidence will be easily obtained in many bird groups. Moreover, if competition has been important in determining the structure of natural communities, it should be demonstrable today. In all sexually reproducing species enormous amounts of new variability are produced each generation, the extremes being continually selected against. Moreover, in nature many bird species enter the breeding season with larger populations than the usual habitats can support. Given these facts, it should be impossible to completely avoid competition by specializations to habitat, and continued interactions are to be expected among closely related species wherever they come into contact.

## SUMMARY

Evidence for competitive exclusion, largely indirect, is supplemented by observations of interactions between the closely related Redwing and Tricolored blackbirds which differ strikingly in their social organization and, where they are sympatric in California, interact strongly. Male Redwings establish territories early in the winter in California so that marshes are usually fully occupied at the time the nomadic Tricolors start to establish their breeding colonies. Nesting success in both species is influenced by amount and distribution of rainfall during the winter and spring, but the Tricolor, because of the greater demands of its system, suffers more acutely in drought years.

When large numbers of Tricolors move into a marsh inhabited by Redwings, there is strong aggression on the part of the male Redwings, but through superior numbers, Tricolors are successful without offering any counteraggression. Redwings either desert their territories, or if they remain on them, cease defending them. No successful Redwing nests have been found within large Tricolor colonies. Redwing aggression is successful against Tricolors only when the numbers of the latter are small, thus providing evidence in support of Hutchinson's model.

The evolutionary consequences of aggressive interactions are considered in the light of the probable action of natural selection upon time and energy expenditure. Levels of aggression are assumed to evolve as a compromise between the pattern of spacing which provides maximum reproductive success through the securing of the nest sites, mates, and food supplies, and the increasingly large expenditure of time and energy needed to maintain the system. Interspecific territoriality is to be expected when two species come into contact, but if they are ecologically compatible, selection should eliminate interspecific aggression. Conversely, in the absence of sufficient ecological divergence, continuance of interspecific aggression is likely. The Redwing and Tricolored blackbird have diverged primarily through their social systems which permit different spatial utilization of environmental resources in heterogeneous environments. Observations of direct interactions are of particular importance since most of the evidence for competitive exclusion is indirect.

## ACKNOWLEDGMENTS

The work of Orians in north-central California was supported by a National

Science Foundation Graduate Fellowship for the academic years 1958–1960. Travel expenses were in part defrayed by a grant from The Museum of Vertebrate Zoology. Collier was supported by a Frank M. Chapman Memorial Grant from the American Museum of Natural History during 1957 and by a National Institute of Health Predoctoral Fellowship (E-9555) for the academic years 1959–1961. Costs of travel were borne by the Department of Zoology, University of California, Los Angeles. We wish to thank Frank A. Pitelka and Thomas R. Howell under whose guidance our work was carried out and Nicholas E. Collias and Alan J. Kohn who offered valuable suggestions during the preparation of the manuscript.

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