

A CRITIQUE OF INTERSPECIFIC TERRITORIALITY AND CHARACTER CONVERGENCE

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Cody (1969) suggested that species may converge in appearance or voice because similarities increase interspecific aggressiveness, which leads to the individuals of two species maintaining mutually exclusive territories in a common habitat. The advantage of such behavior is that it results in the exclusion of food competitors within the individuals' territories. Thus, according to Cody, interspecific territoriality is adaptive. In 1971 I published an interpretation of observed cases of interspecific territoriality, in which I assumed that interspecific territoriality was aggression that evolved in intraspecific contexts but was misdirected toward individuals of other species which possessed similar features that normally stimulated intraspecific territorial aggression (Murray 1971). I argued that *mutual* interspecific territoriality is maladaptive for at least one of the species because the subordinate species would eventually be excluded from otherwise optimal habitat, but I did not exclude the possibility of the existence of cases of adaptive interspecific territoriality. The two hypotheses, then, seem contradictory. The first assumes that cases of mutual interspecific territoriality *are* adaptive, while the second assumes that they are not.

Some authors studying birds (Barlow et al. 1970, Brown and Orians 1970, Cheke 1971, Rohwer 1972, 1973, Kroodsmma 1973, Emlen et al. 1975), fishes (Myrberg and Thresher 1974), hermit crabs (Hazlett 1972 a, b), and flowers (Levin and Schaal 1970) have found Cody's hypothesis reasonable. It has appeared as an annual review article (Cody 1973) and as a portion of a book (Cody 1974), and has been described in at least two ecology textbooks (Ricklefs 1973, Smith 1974). Because Cody's hypothesis is widely accepted and is contradictory to my own, I wish to examine it and the evidence for it in some detail.

CODY'S CASES OF INTERSPECIFIC TERRITORIALITY

One criterion for evaluating a theory is the quality of the data presented as supporting evidence.

(1) Cody first discussed the similarities in color and pattern of the African bush-shrikes of the genera *Chlorophoneus* and *Malaconotus*

(which, as Cody noted, were merged into *Malaconotus* by Hall et al. 1966). Of this case Cody (1969: 227) wrote, "Convergence in advertising characters presupposes interspecific territoriality in some form or to some extent, but no evidence has been found in the literature to indicate that the species of the '*Chlorophoneus*' group are in fact interspecifically territorial with those of the '*Malaconotus*' group; rather, as this information is at present lacking, the inclusion of bush-shrikes in this paper amounts to a prediction that when these birds are better known they will be found to defend territories interspecifically across the groups."

(2) Concerning a pair of Asian woodpeckers Cody (1969: 231) wrote, "No one has reported interspecific territoriality between *Dinopium* and *Chrysocolaptes*, and until direct evidence is forthcoming the ultimate test of my hypothesis cannot be made."

(3) Concerning another pair of Asian woodpeckers Cody (1969: 231) wrote "That [*Meiglyptes*] *jugularis* and [*Hemicircus*] *cante* may be interspecifically territorial cannot be verified from published observations."

(4) Concerning another pair of Asian woodpeckers, *Micropternus brachyurus* and *Blythipicus pyrrhotis*, Cody (1969: 231) wrote, "Again [!] the similarities may be attributed to interspecific territoriality," but also again no references to such interspecific territoriality are reported. These species are not known to be sympatric (Short, in litt. 1975).

(5) Concerning the Central American woodpeckers, *Dryocopus lineatus* and *Phloeocastes melanoleucos*, Cody (1969: 232) wrote, "As such observations [of both species feeding in the same tree] are not dated in reference to the breeding season, they do not preclude the possibility of interspecific territoriality." Subsequent observations by Kilham (1972) showed that *D. lineatus* and *P. melanoleucos* differ in the time of their breeding seasons, in their nest sites, and in their foraging behavior and that when they come into contact their relationship is "peaceful." Karr (1971) also failed to find evidence of conflict between these species in central Panama.

(6) Concerning the North American woodpeckers, *Dryocopus pileatus* and *Campephilus*

principalis, Cody (1969: 233) wrote, "From information in Tanner's (1942) monograph on the Ivory-bill, the question of interspecific territoriality could not be resolved (one instance of apparent interspecific aggression was observed), but it appears that territories do in fact overlap somewhat between the two species (Tanner, pers. comm.)."

Cody (1969: 233) summarized the results of his survey of convergence and interspecific territoriality in woodpeckers, "Although interspecific territoriality has not been established for the above species pairs, it is commonly found in woodpeckers generally, e.g., for breeding *Centurus aurifrons*, *C. carolinus*, and *C. uropygialis* (Selander and Giller 1959, 1963), for wintering *Centurus carolinus*, *Melanerpes erythrocephalus*, and *Dendrocopos pubescens* (Kilham 1958), for wintering *Melanerpes formicivorus* and *Asyndesmus lewis* over acorn stores (Carl Bock, pers. comm.), and for *Picus viridis*, *Dendrocopos major*, and *D. minor* over nest sites (Howard 1920)." One can only speculate why Cody did not test his theory of convergence in appearance and voice resulting from advantages gained by interspecific territoriality against these reported cases of interspecific territoriality. It is of interest that *Centurus aurifrons* and *C. carolinus* are sibling species that are virtually allopatric, coming into contact only near Austin, Texas (Selander and Giller 1959). Their similarity is almost certainly the result of common ancestry rather than the result of convergence that promotes interspecific aggression with potential competitors. The case of interspecific territoriality between *C. aurifrons* and *C. uropygialis* is a casual speculation (Selander and Giller 1963: 242). Even if interspecific territoriality is confirmed, these species are allopatric (Selander and Giller 1963: 259) and closely related, forming a superspecies with *C. carolinus* (Mayr and Short 1970).

Interspecific territoriality between the Red-bellied Woodpecker, Red-headed Woodpecker, and Downy Woodpecker, between the Acorn Woodpecker and Lewis's Woodpecker, and between the Green Woodpecker and the Greater Spotted and Lesser Spotted woodpeckers seems to indicate that woodpeckers which differ strikingly in plumage, voice, and behavior can be interspecifically territorial.

Further, Kilham (1958) reported that the Red-headed Woodpeckers were intensely and persistently aggressive toward Blue Jays (*Cyanocitta cristata*) and Tufted Titmice (*Parus*

bicolor), both competitors for acorns; they behaved similarly toward Starlings (*Sturnus vulgaris*), competitors for holes in trees, indicating the capacity of woodpeckers to be interspecifically territorial against birds of different appearance and behavior.

Finally, the interpretation of the woodpecker cases depends upon one's conception of their phylogenetic relationships. Cody (1969) separated the woodpeckers into two groups of genera, the "logcocks" (*Meiglyptes*, *Micropternus*, *Dinopium*, and *Dryocopus*) and the "ivory-bills" (*Hemicircus*, *Blythipicus*, *Chrysocolaptes*, *Campephilus*, and *Phloeoceastes*), following the classification in Peters (1948). He cited but did not discuss the implications of Bock's (1963) arguments for grouping *Micropternus* with *Blythipicus*, *Dinopium* with *Chrysocolaptes*, and *Dryocopus* with *Campephilus* (= *Phloeoceastes*). Goodwin (1968) also considered *Dinopium* and *Chrysocolaptes* closely related and went so far as to merge the New World *Dryocopus* and *Phloeoceastes* into *Campephilus*. Short (1973) has described vocalizations and other displays that indicate a close relationship between *Meiglyptes* and *Hemicircus* and, again, between *Dinopium* and *Chrysocolaptes*.

If the woodpecker relationships are as described by Bock (1963), Goodwin (1968), and Short (1973), then the similarities of the woodpeckers cited by Cody are probably the result of close relationship rather than of selection for similarities that promote interspecific aggression, which has yet to be reported.

(7) Cody's seventh case was the reported interspecific territoriality and similarity of songs of the two closely-related wren species, *Thryothorus felix* and *T. sinaloa* in Mexico (Grant 1966). Because I believed that interspecific territoriality had not been sufficiently documented, I did not consider this case in my earlier analysis of interspecific territoriality (Murray 1971). Grant studied populations of unmarked birds for one week and produced a map showing non-overlapping territories. Although he was unable to distinguish the songs of the two species, the caption to his figure (Grant 1966: 268) stated, "Each bird seen or heard was recorded." I am reluctant to accept this evidence for interspecific territoriality because of my own experience with populations of individually color-marked sparrows (Murray 1969), warblers (Murray and Gill 1976), and a thrush (work in progress). For example, Blue-winged Warblers (*Vermivora pinus*) and

Golden-winged Warblers (*V. chrysoptera*) tend to sing from different perches even though their territories overlap extensively (Ficken and Ficken 1968, Gill and Murray 1972, Murray and Gill 1976). A brief survey of unmarked birds could lead one to believe that they were interspecifically territorial.

Although Cody (1969: 235) considered the similarity of the songs of the wrens "An indisputable case of vocal convergence," Grant (1972) emphasized that there was no evidence for convergence. Grant considered the similarity of songs to be the result of a lack of divergence. In fact, the songs may not be as similar as Grant reported. Both Davis (1972) and Edwards (1972) described distinctively different songs for *T. felix* and *T. sinaloa*, and J. W. Hardy (pers. comm.), who has tape-recorded both species' songs in western Mexico, identifies Grant's (1966: 269) audiospectrograms of the two species' songs as belonging to the same species, *T. sinaloa*.

(8) The next case discussed by Cody is an undoubted case of mutual interspecific territoriality, between the Eastern and Western meadowlarks (*Sturnella magna* and *S. neglecta*, respectively) as reported by Lanyon (1956, 1957). Cody (1969: 235-236) suggested that where these species are sympatric their primary songs have converged: "Throughout most of the zone of sympatry the phenomenon of 'hybrid song' has been recorded (Lanyon 1957: 23; J. Zimmerman, pers. comm.; and myself for Kansas), in which it becomes exceedingly difficult to determine whether the vocalist is *magna* or *neglecta*." Cody implied that "hybrid song" is common, but other authors have found "hybrid song" rare. Lanyon (1957) cited several published references to "hybrid song" and bivalent repertoires, but he found no cases of "hybrid song" and only three cases of bivalent song in four years' study in the northcentral United States. He has never found a case of "hybrid" song in later research throughout the zone of overlap (Lanyon, in litt. 1975). And in two years' field work in the central and southern Great Plains Rohwer (1972) found "hybrid" or intermediate meadowlark songs "extremely rare."

Rohwer (1973), however, reported convergence in appearance of these species, which he attributed to selection for interspecific communication signals associated with interspecific territoriality. Rohwer measured the size of the black V and the brightness, purity, and dominant wavelength of yellow breast of both males and females. Although only six

of the 16 comparisons between sympatric and non-sympatric populations of Eastern and Western meadowlarks showed statistically significant differences, all differences were in the direction of convergence. Because five of the significant differences were in male comparisons and because these characters seemed to be associated with male aggressive display, Rohwer thought the convergence was caused by selection for signals related to interspecific aggression. Yet, Rohwer has not demonstrated that the small differences measured by his planimeter and reflectance spectrophotometer are detectable by the birds or that these differences in any way enhance interspecific aggression. Inasmuch as all changes in both species, including even the females, which are not aggressive, are towards convergence, I think the parsimonious interpretation is that both species are responding to their common physical environment.

(9) The final case considered in detail by Cody (1969) concerned the similarity between certain populations of the salamanders *Plethodon jordani* and *Desmognathus ochrophaeus*. Again, there are no references to interspecific aggression or even to intraspecific territoriality. Historically this case has been considered to be one of mimicry (Dunn 1927 and following workers), a possibility that Cody considered and rejected. However, Brodie and Howard (1973) restudied these populations in the field and laboratory, conducted further experiments on mimicry, and concluded that mimicry of *P. jordani* by *D. ochrophaeus* is the best interpretation of their similarities. They found no evidence of either intra- or interspecific territoriality.

These are the nine cases that Cody presented in detail. *No case unambiguously links interspecific territoriality and convergence.* Indeed interspecific territoriality is *unreported* in seven of the nine cases. And the similarities may be a consequence of close relationship rather than convergence in all but the salamanders, which is an apparent case of mimicry.

THE MEXICAN FINCHES

Cody and Brown (1970) observed interspecific territoriality between *Pipilo ocai* and *Atlapetes brunneinucha* and between *P. ocai* and *P. erythrophthalmus* during nine days' field work on Cerro San Felipe, Oaxaca, Mexico. In the first case the two species bear a striking resemblance to each other. This resemblance has been noticed by others

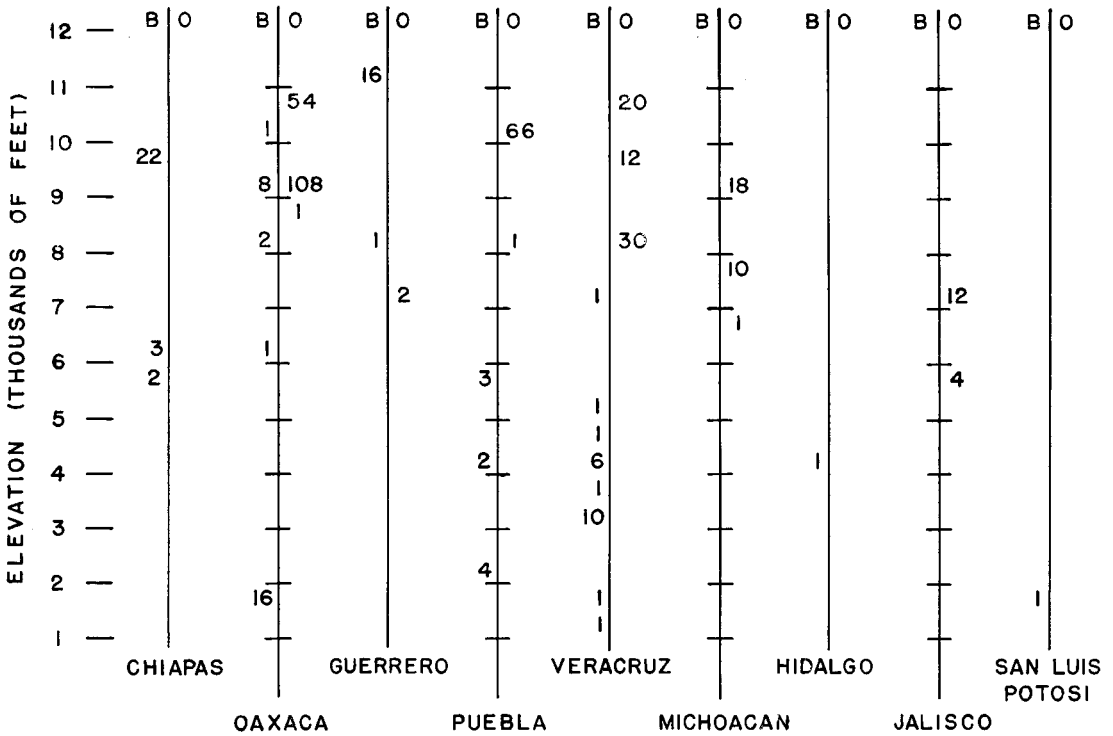


FIGURE 1. Distribution of *Atlapetes brunneinucha* (B) and *Pipilo ocai* (O) in Mexico. The number of specimens is given for each species in each state at 500' intervals. Data for *P. ocai* are from Sibley (1950), Sibley and West (1958), and Sibley and Sibley (1964). Data for *A. brunneinucha* are from specimens at the Moore Laboratory of Zoology, National Museum of Natural History, American Museum of Natural History, University of California Museum of Vertebrate Zoology, California Academy of Sciences, and Carnegie Museum.

and attributed to either close relationship (Short 1971) or parallelism (Wetmore 1943, Sibley 1950), although their exact relationship is not known (Parkes 1954). That this resemblance can be considered "convergence" that enhances interspecific territoriality, as suggested by Cody and Brown, seems unlikely because, although *P. ocai*'s geographic range is almost entirely included within *A. brunneinucha*'s much more extensive range, the two species normally occur at different elevations (fig. 1) and in different habitats (Blake 1953, A. R. Phillips in litt.), contrary to Cody and Brown's (1970: 309) statement that "within the range of sympatry the altitudinal distribution of *brunneinucha* virtually coincides with that of *ocai*. . ." They seem to meet in numbers only in Oaxaca, in particular on Cerro San Felipe. The extent of contact seems too small to account for convergence of plumage, whose advantage is stimulation of interspecific aggression. This case fits the pattern of interspecific territoriality I presented earlier (Murray 1971), being an example of interspecific territoriality between

species normally occupying different habitats within an area of sympatry.

The second case of interspecific territoriality involves the resemblance of songs of *P. ocai* and *P. erythrophthalmus*. A problem here is whether the two forms are in fact species. Although *P. ocai* and *P. erythrophthalmus* interbreed extensively in central Mexico, Sibley (1950) recognized the two forms as distinct species because at Cerro San Felipe no interbreeding was detectable. Mayr (in Mayr and Short 1970) also considered them different species. However, Short (1969, and in Mayr and Short 1970) preferred to consider them conspecific because the extent of interbreeding and introgression greatly exceeds the extent of coexistence without interbreeding. If the two forms are conspecific, then, by definition, their mutual aggression cannot be interspecific territoriality. But even if considered conspecific the two populations at Cerro San Felipe have certainly achieved reproductive isolation, and some may consider their aggression *there* to be interspecific territoriality. Surely, it is not intraspecific ter-

itoriality. The point, however, is that whatever taxonomic rank one gives the two Cerro San Felipe populations, they are clearly closely related. The similarities between *P. ocai* and *P. erythrophthalmus* that stimulate the mutual aggression seem more likely attributable to recent common ancestry than to convergence.

OTHER CASES

Cody (1969, 1973, 1974) referred to other cases of actual or alleged interspecific territoriality or convergence. The actual cases are discussed in the next section of this paper. The alleged cases include unpublished or incompletely published observations of Cody and others. To evaluate each of these cases as evidence for or against one theory or another seems to depend upon the publication of details. For instance, Cody (1973, 1974) referred to an abstract by Ferry and Deschaintre, in the abstracts of the Fourteenth International Ornithological Congress, which I have not seen. Evidently, in a narrow zone of sympatry the Melodious and Icterine warblers (*Hippolais polyglotta* and *H. icterina*, respectively) are interspecifically territorial and have similar songs. Further investigation of this case by Ferry and Deschaintre (1974) resulted in the conclusion (p. 307), "En somme, nous admettons que, dans le cas de nos contrefaisants et comme le dit Murray (1971), 'interspecific territoriality is misdirected intraspecific territoriality'."

Evaluation of particular cases should await detailed reporting.

ACTUAL CASES OF INTER-SPECIFIC TERRITORIALITY

A second criterion for evaluating a theory is its generality. Cody did not claim generality, and thus the fact that he did not discuss all known cases of interspecific territoriality is in itself of no great consequence. Nevertheless, consideration of these cases will help in understanding interspecific territoriality in general, and this understanding may allow us to evaluate the theory.

In addition to the cases involving (a) the Red-bellied and Golden-fronted woodpeckers (Selander and Giller 1959) and (b) the Eastern and Western meadowlarks (Lanyon 1956, 1957), already discussed above, other cases that seem adequately described (Murray 1971) involve (c) the Dusky Flycatcher (*Empidonax oberholseri*) and the Gray Flycatcher (*E. wrightii*) reported by Johnson (1963, 1966), (d) the Black-winged Red

Bishop (*Euplectes hordeacea*) and Zanzibar Red Bishop (*E. nigroventris*) reported by Fuggles-Couchman (1943), (e) several species of bishops (*Euplectes*) and whydahs (*Coliuspasser*, sometimes considered congeneric with *Euplectes*) reported by Lack (1935), Moreau and Moreau (1938), Emlen (1957), and Ruwet (1964), (f) the Red-winged Blackbird (*Agelaius phoeniceus*) and the Tricolored Blackbird (*A. tricolor*) reported by Orians (1961) and Orians and Collier (1963), (g) the Redwinged Blackbird and the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) reported by Linsdale (1938), Fautin (1940), Orians and Willson (1964), and Miller (1968), and (h) the Sedge Warbler (*Acrocephalus schoenobaenus*) and the Reed Warbler (*A. scirpaceus*) reported by Brown and Davies (1949) and later by Catchpole (1972). Finally, (i) Murray (1969, 1971) has interpreted the non-territorial behavior of the Sharp-tailed Sparrow (*Ammodramus caudacuta*) and the sporadic aggression of the Le Conte's Sparrow (*Ammodramus leconteii*) toward the Sharp-tailed Sparrow to be the consequences of selection against mutual interspecific territoriality, which had occurred in the past.

A pattern in this diversity of situations can be discerned. Cases of *mutual* interspecific territoriality occur between species that either are largely allopatric (cases a and b) or occupy different habitats in areas of sympatry (cases c, d, e, h). Species that are widely sympatric and occupy the same habitats either differ in their intra- and interspecific territorial behavior (cases f and i) or they are quite different in appearance (case g). This pattern indicates that *mutual* interspecific territoriality in widely sympatric species extensively occupying the same habitat is rare, if it occurs at all. I therefore suggested that *mutual* interspecific territoriality is disadvantageous for one of the species and should not be selected for (Murray 1971). This conclusion is contrary to the assumption of the "convergence" hypothesis that mutual interspecific territoriality is advantageous.

THE "CONVERGENCE" HYPOTHESIS

There are other reasons for finding the "convergence" hypothesis less than satisfying. Of particular concern is the fact that the predictions of the "convergence" hypothesis are explicitly contrary to those of the Competitive Exclusion Principle. As Cody wrote, "To many ecologists the idea that selection may actually favor increased similarity between

species in character value until they eventually coincide is contrainuitive and contradictory to what has been since the fifties a blanket application of the so-called 'Volterra-Gause' principle" (Cody 1973: 190; paraphrased in Cody 1974: 216). For one to accept the "convergence" hypothesis, then, one must reject the Competitive Exclusion Principle as a principle, applying it to certain competitive situations and not to others. Earlier authors (Wynne-Edwards 1962, Hamilton 1964) had recognized that if cases of mutual interspecific territoriality between species occupying the same habitat were stable and had evolved by natural selection, then they contradicted the Competitive Exclusion Principle. Challenging currently held principles is surely respectable scientific activity, but in this case there is no substantial body of fact to support the challenge. At the same time, an enormous amount of observation seems to be consistent with the predictions of the Competitive Exclusion Principle, including one interpretation of the documented cases of interspecific territoriality (Murray 1971).

Next, consider the "convergence" hypothesis: "increased similarity could evolve concurrently with a decreasing territorial overlap between two species and actually promote a behavioral response which separates territories to economic advantage. Suppose a mutation in a male of one territorial species causes a change in plumage coloration which results in a closer resemblance to males of an ecologically-similar second species. This change could result in its partial exclusion from the territories of this strong competitor, and this exclusion would be advantageous because the food density to which the individual is then exposed would be increased" (Cody 1969: 224).

This hypothesis explicitly assumes that an advantage of interspecific territoriality is in reducing competition for food. Yet in several proved cases of interspecific territoriality (e.g., the Redwinged and Tricolored blackbirds, Orians 1961, Orians and Collier 1963; the Sedge and Reed warblers, Catchpole 1972) much of the food is gathered outside the territories. In other cases, the birds do not normally occupy the same habitat but are interspecifically territorial where their habitats abut (e.g., Gray and Dusky flycatchers, Johnson 1963, 1966; the Black-winged Red Bishop and Zanzibar Red Bishop, Fuggles-Couchman 1943, Moreau and Moreau 1938).

The "convergence" hypothesis further as-

sumes that the degree of territorial exclusion depends upon the degree of similarity, but, as noted above, completely exclusive interspecific territoriality occurs between dissimilar species (e.g., some species of *Euplectes* and *Coliuspasser*, Emlen 1957, Ruwet 1964). And the Red-headed Woodpecker is persistently aggressive toward intruding Red-bellied Woodpeckers, Downy Woodpeckers, Blue Jays, Tufted Titmice, and Starlings (Kilham 1958). It seems that if interspecific aggression leading to exclusion of competitors were advantageous, interspecific territoriality should evolve regardless of dissimilarities in the appearances or voices of the species involved.

Finally, it is not clear how the exclusion of individuals from otherwise suitable portions of a species' habitat necessarily results in the exposure of those individuals to greater food density. It seems at least equally possible that exclusion from suitable portions of the habitat could result in those individuals occupying less suitable areas with lesser food densities. Numerous reports, summarized by Hinde (1956) and Brown (1969), indicate that within species some individuals are forced to occupy marginal areas because of intraspecific territoriality. Interspecific territoriality probably has the same consequences; individuals of the subordinate species are forced to occupy marginal areas and thus presumably reproduce less successfully.

SUMMARY

The hypothesis that species converge in appearance or voice because such convergence enhances mutual interspecific territoriality that results in the exclusion of food competitors is examined. The cases presented in support of this "convergence" hypothesis do not link any case of convergence with any case of interspecific territoriality; hence, the hypothesis does not explain any real situation, much less a substantial body of fact. There exist cases of interspecific territoriality that are unexplained by the "convergence" hypothesis. These known cases indicate that mutual interspecific territoriality between species extensively coexisting in the same habitat is rare. They also indicate that interspecific territoriality occurs between species which occupy different habitats, forage outside their territories, and differ in appearance, voice, or both. Finally, the predictions of the "convergence" hypothesis are contrary to the predictions of the Competitive Exclusion Principle.

ACKNOWLEDGMENTS

I thank all those persons who have assisted me in preparing this paper. I am particularly grateful to J. W. Hardy, J. R. Jehl, Jr., M. Gochfeld, W. Shields, and F. B. Gill for reading and commenting on one or more drafts of this paper. I have also benefitted from comments on portions of this paper by W. E. Lanyon, K. C. Parkes, A. R. Phillips, S. A. Rohwer, and L. L. Short. L. C. Binford (California Academy of Sciences), J. W. Hardy (then at the Moore Laboratory of Zoology at Occidental College), L. Baptista and Elizabeth Thompson (Moore Laboratory of Zoology), N. K. Johnson (University of California Museum of Vertebrate Zoology), and K. C. Parkes (Carnegie Museum) kindly forwarded information on specimens at their institutions. D. Amadon (American Museum of Natural History), R. W. Storer (University of Michigan Museum of Zoology), and R. L. Zusi (National Museum of Natural History) allowed me to examine specimens in their care.

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