CONVERGENT CHARACTERISTICS IN SYMPATRIC SPECIES: A POSSIBLE RELATION TO INTERSPECIFIC COMPETITION AND AGGRESSION

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Striking similarities in coloration, voice, or both have been described in mainly or partly sympatric species of territorial animals (for some recent studies see Bock 1963; Hall et al. 1966; Grant 1966). Such similarity may be much more widespread among higher vertebrates, but no overall explanation for its occurrence has been proposed.[1] In this paper it is suggested that the convergences between such species could promote (or arise as a secondary result of) a spatial separation of activities such as food-gathering. In the extreme case of complete separation, species pairs become interspecifically territorial.

The situation under discussion has the following attributes which must be firmly stated at this point so that other related phenomena may not be confused with it (see p. 225). (a) The species concerned may be congeneric, but are often more distantly related; "sibling species" are not involved. While various degrees of taxonomic relationship are exhibited, the ecological requirements of the species pairs are evidently very close. (b) These species are territorial, or at least show intrasexual aggressive behavior. The similarities in appearance affect only those characteristics involved in visual or vocal aggressive displays, such as plumage and song in birds. (c) These similarities are often less pronounced or even absent where the two species are allopatric. Sympatry is necessary for their maintenance.

THE HYPOTHESIS AND ENVIRONMENTAL CIRCUMSTANCES OF ITS OCCURRENCE

The various possibilities open to largely allopatric populations of related or ecologically-similar species which have come into second-

ary contact have been adequately summarized by Lack (1944), and by Orians and Willson (1964) with special reference to interspecific territoriality. These same possibilities also apply if a newly-arisen or closely-related species colonizes extensive parts or the complete range of a former conspecies, and they are independent of the extent of subsequent sympatry. Orians and Willson (1964) point out that interspecific territoriality can be an alternative to character displacement, hybridization, or differential habitat selection if one or more of the following conditions are met. The species (1) occupy simple habitats, (2) have stratified feeding habits, or (3) exploit the same food resources. I would like to restate the latter two conditions in a more general way and suggest that species which have specialized feeding methods or apparatus, or occur in associations with ecologically-similar species, as perhaps in the tropics (Klopfer and MacArthur 1962), are possible candidates for interspecific aggression and, hence, interspecific territoriality. Interspecific territoriality is used in a broad sense, i.e., some area is defended at some time between species (see Discussion for qualifications).

The current proposal may be stated as follows. Interspecific territoriality depends upon the recognition and exclusion of heterospecific as well as conspecific competitors. In some such cases natural selection has favored the convergence of those characters by which individuals defending territories are prompted to evict others from the defended area. These excluded individuals, usually of the same sex and species, now include convergently-similar members of another species. It is suggested that interspecific territoriality operates more efficiently, and that the recognition and thence exclusion of challengers of both species by a territory holder is facilitated if plumage, voice, or both are similar in the two species concerned. Intersexual recognition must not be affected; the maintenance of specific integrity is assured by the existence of certain species-

[1] Since this paper has been in press, M. Moynihan's "Social mimicry: Character convergence versus character displacement" appeared in Evolution 22:315–331. Although there is considerable overlap between the ideas presented here and in that paper, my emphasis and examples are largely different. Whereas Moynihan stresses convergence to facilitate gregariousness, I am concerned only with convergence to promote interspecific aggression.

specific cues in behavioral or morphological characteristics associated with courtship and mating. Such a system prevents actual or attempted hybridization which would be disadvantageous (e.g. if less fit intermediates invade those regions or habitats where the two species are in allopatry).

A convergence in appearance or voice could arise by the normal process of natural selection. This could happen after interspecific territoriality had already evolved. Alternatively, 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. Such an individual would leave more offspring in the population (if food is limiting and all other things being equal or nearly so) and his phenotype come to predominate. As this successful phenotype becomes more common in the population, encounters between them will increase, and thus a behavioral adjustment to territorial defense against opponents more similar to the second species will automatically follow. This convergence in plumage should continue until the two species are fully interspecifically territorial when the similarities in appearance may be extensive. Note that benefits from non-overlap in territory between close competitors are mutual, and the evolution of convergence would be speeded up by a selection on the second species to recognize and exclude converging individuals which resemble only approximately their conspecies.

We now look for circumstances which would bring a pair of species together in this way. In either of the following two rather fundamental situations (arrangements of species ranges and of their preferred habitats), interspecific competition might be severe enough to optimize interspecific territoriality with perhaps resulting convergence.

Case A. An environment varies smoothly for a particular set of conditions on which habitat selection is based. Two species can occupy the habitat, one along each half of the gradient, and coexist because of the range of different conditions. If either the difference

between the ends of the gradient or the geographic area encompassed by this habitat is small, or if historico-geographic circumstances limit colonization or speciation, a single species might occupy the whole gradient. But if two species are present, they meet in a band across the gradient where differential habitat selection is insufficient to separate their territories. This area of contact is a region of potential interspecific territoriality, provided any one of the three conditions listed on p. 223 exists.

Case B. Many habitats are patchy, where, for example, wet-dry contrasts associated with topography result in differential growth of vegetation. This can be approximated if the above habitat gradient is broken up into patches of various sizes which are juxtaposed in a haphazard fashion over the same area. The resulting habitat would be composed of quite discrete patches of two extreme types plus a range of intermediates, but under natural conditions patch types grade into one another and provide more habitat of an intermediate character. Again two species could coexist in this mosaic if the extremes are "sufficiently" different (see MacArthur 1965: 519–20). In areas where the habitat is closer to either extreme, only one species will occur. But in intermediate patches and where patches are large compared to territory size, with a gradient between adjacent types, a situation exists which is again conducive to interspecific territoriality, with the usual provisions stated above. If the patches are small compared to territory size but the species are able to weight their foraging time in favor of their preferred patch type ("coarse-grained" habitat), one species only will occur in areas where the proportion of either patch type is greater than some particular figure. When the patches occur in intermediate proportions, both species will be present and potentially will defend territories against each other.

It is supposed that the two species have fitnesses which vary with the habitat they occupy (fig. 1) and that there is at least some habitat type in which their fitnesses are intermediate and identical. Natural selection will favor a high degree of differential habitat selection or resolution, which tends to shorten the coincident portion of the gradients in figure 1. While maximum divergence in habitat preference is maintained over the area of sympatry, interspecific recognition, facilitated by convergence, is advantageous because fitnesses are maximized over the available habitat. It is worth noting that with-
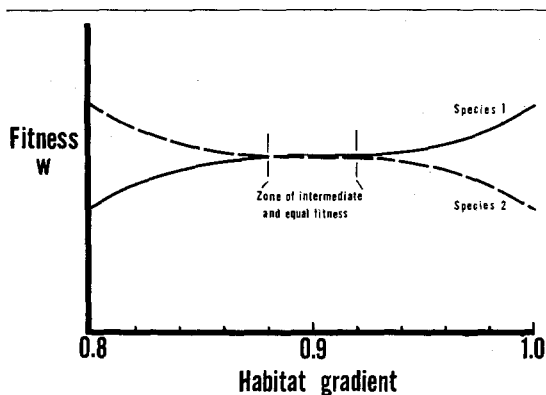
FIGURE 1. Variation in fitness with a habitat gradient which could result in character convergence between two ecologically-similar species. The abscissa represents variation in a habit selection cue which in intermediate habitat will not suffice to separate territories of the two species. Large geographic areas of intermediate habitat and imprecise habitat resolution by the two species magnify the effective zone of coincidence.

out the presence of habitat in which each species is competitively superior to the other, the situation cannot be a stable one. As with all cases of interspecific territoriality, it would be necessary for each species to have refuges which cannot be successfully invaded by the other. Without these, one of the two would surely have been eliminated before we had the chance to observe it.

The results of these selective forces can appear somewhat paradoxical. Where two species meet there is selection for maximal divergence in habitat preference and intersexual recognition signs, and perhaps for divergence in general ecological characteristics, but simultaneously there is selection for convergence in intersexual recognition and aggression-promoting stimuli. Where the species do not meet, intersexual symbolism may converge and vice versa for that within the sexes. A documented example will illustrate all of these interesting nuances.

Several types of selective pressure can cause unrelated sympatric species to look alike. Mimicry can be distinguished from convergence, as described in this paper, by the local distributions, relative abundances, and difference in ecology of the species involved. Various phenotypic characteristics may change in direct or indirect response to climate. These changes are generalized in the so-called eco-geographic laws, such as Allen's, Bergman's, and, in particular, Gloger's Rules (Rensch 1960; Mayr 1963). In these cases latitudinal

or other clines in mean temperatures or inter-habitat differences in such factors as humidity are thought to be responsible for general and parallel gradients in body size, approximate pigmentation, or the relative lengths of appendages. For potential prey species a resemblance in body coloration to the substrate, or some other type of crypsis, might be selected for, and produce parallel variation in related or unrelated species which occupy similar niches and have similar predators. When such phenotypic variations affect plumage coloration it is necessary to distinguish between the selective forces involved so that cases of the convergence here hypothesized might not be misidentified or overlooked. Also, Moynihan (1960) has described interspecific plumage similarities which may help to promote gregariousness in mixed species feeding flocks.

Similar difficulties exist with vocal characteristics. While the relations between variables associated with song (such as frequency average and range, pattern, and wavelength) and the configuration of the habitat are not yet known quantitatively (but see Ficken and Ficken 1962), consistencies in these relations can be recognized by any keen ear. For instance, the similarity between the songs of bird species resident in the needlerush and saltgrass marshes of coastal eastern North America is striking. The species involved (Red-winged Blackbird, *Agelaius phoeniceus*; Seaside Sparrow, *Ammospiza maritima*; Sharp-tailed Sparrow, *Ammospiza caudacuta*; and Long-billed Marsh Wren, *Telmatodytes palustris*) are members of three different families, but at least part of the songs of all of them have a low-pitched "buzzy" passage of wide frequency range, which presumably "carries" well and does not become distorted by this type of vegetation. While species differences in songs must normally exist, the "carrying" and distortion-free qualities of a song must be under selective pressure. Therefore, at any point in a habitat potentially or actually occupied by several species, these particular selective pressures would be identical or nearly so (varying slightly with the position of the vocalist in the vegetation). In fact, convergence brought about by habitat configuration and physical conditions associated with latitude, altitude, and other factors of climate and topography is readily distinguished from that which has arisen, according to this hypothesis, as a result of the sympatry of pairs of species so similar in their ecology that they have become interspecifically territorial where they meet and overlap. Of importance here is the steep

TABLE 1.   Examples of actual or potential interspecific territoriality[a].

Type of Convergence	Pairs of species which[b]:		
	occupy simple habitats	are food specialists	contact many similar species
None obvious	Ammodramus bairdii- A. savannarum[c] (grasslands, Case A[d]) Agelaius phoenicieus- A. tricolor (marshes, ? Case B)	Centurus aurifrons- C. uropygialis (trunk arthropods, Case A) Calypte anna- Selasphorus sasin (nectar feeders, Case B)	Parus atricapillus- P. carolinensis (tree insectivores where many warblers are present, Case A) Sylvia atricapilla- S. borin (common family in England, Case B)
Appearance	Some subspecies of the salamanders Plethodon jordani- Desmognathus ochro- phaeus (both terrestrial, Case A and/or B)	Numerous species from pairs of woodpecker genera of the "logcock" and "ivory-bill" groups (trunk arthropods, in tropical forests, Case B)	Pairs of bush-shrike spp. of the groups Malaconotus and "Chlorophoneus" (tropical savannah species, Case B)
Voice	Sturnella magna- S. neglecta (?) (grasslands, Case A)	The wrens Thryothorus sinaloa and T. felix (tropical dry scrub habitat, feed on insects in low thick tangles, Case B)	

[a] References are included in Orians and Willson (1964) and this paper.
[b] This classification scheme is somewhat arbitrary, but the best apparent fits are made.
[c] An unpublished observation by Cody.
[d] Case A, species mainly allopatric; Case B, species mainly sympatric. See text for further qualification.

and discontinuous variation which these species often exhibit where they become allopatric. Also the precision with which the convergent species resemble each other, but only in territorial defense characters, assists in making the distinction.

DETAILED EXAMPLES OF CONVERGENCE RELATED TO TERRITORIALITY

CONVERGENCE IN APPEARANCE

Some territorial animals, particularly birds, are known to exclude conspecific individuals from their territories by reacting aggressively to general or specific parts of color patterns. Such characters could be influenced by natural selection in interspecific interactions over territory. Some probable examples are listed in table 1 and discussed below.

African bush-shrikes of the genera "Chlorophoneus" and "Malaconotus" were recently united in the genus Malaconotus by Hall et al. (1966). Much has been published on the polymorphism found in some of the species of this "supergenus," and most recently Hall et al. (1966) demonstrated that sympatric populations comprised of a single species from each "group" (an old genus) exhibit remarkable similarity in appearance. Moreover in some pairs of species these populations vary in parallel over the range of their sympatry. This 1966 paper also gives a description and color

illustration of the species involved and information on their distributions and color phases. It will suffice to say here that the species within a group are almost completely allopatric, geographically or altitudinally, but that the two groups as a whole are largely sympatric. There are lowland, montane forest, and savannah species in each group, so that any small area will hold a single species from each group. All species of both groups have similarly colored upperparts. What is so striking, as Hall et al. successfully showed, is that in any pair of sympatric species, one from each group, the color of the underparts, a breast band (if any), certain head markings, and markings on the wings and tail are virtually identical, while these characteristics vary in color throughout the groups as a whole. These authors discuss, as have others before them, the possibility of balanced polymorphism operating in the genus, but Owen (1967) criticizes this interpretation on a number of grounds and the fact that local populations seem to be monomorphic precludes this. The evolution of the parallelisms is ascribed to the coincidence of selection pressures for coloration in a local environment, which pressures presumably change with the environment across the geographic ranges of the species involved. Galbraith (in Hall et al. 1966) includes among these selection pressures those by predators for crypsis, warning coloration,

or both; he further suggests that mimicry by the slimmer *"Chlorophoneus"* species of *"Malaconotus"* species may account in part for the similarities and their parallel variation. Significantly the selective advantage of a common warning coloration in interspecific territory holders is mentioned, but not stressed (Hall et al. 1966:180). The possibility that such a convergence in plumage colors and patterns could arise under the agency of visual selection by the birds themselves, to facilitate interspecific territoriality, is, according to my hypothesis, the key to the convergence and parallelism in *Malaconotus*.

The differences in plumage among different populations within a species, as suggested in the above reference, must be due to local (different) pigments and patterns, but the precision with which a pair of species resemble each other indicates that further selective forces are involved. After all, species other than these bush-shrikes occupy similar niches and are exposed to similar physical and organic environments in the same habitats, but do not closely or approximately resemble the bush-shrikes. A Batesian mimicry hypothesis also seems to be an inadequate explanation for the convergence, as it appears unlikely that *"Malaconotus"* is a sufficiently formidable or undesirable prey item to have evolved a warning coloration (presumably directed to raptorial birds and snakes) and consequently that it would be of little benefit to *"Chlorophoneus"* to imitate the larger bird.

Convergence in advertizing 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. This hypothesis also supposes that there are subhabitats, such as the savannahs which are inhabited by *M. blanchoti* and *"C." sulphureopectus,* which are occupied respectively by just one species of the convergently similar pair. On the distributional map of these two species in Hall et al. (1966:163) are marked what presumably are collecting localities or sight records where one or both species have been found. It seems significant that in the great majority of these localities only one species occurs, perhaps indicating a patchy distribution of two sub-habitats and of the two species which occupy them.

In general *"Malaconotus"* is comprised of larger species with heavier bills than those of the *"Chlorophoneus"* group. While both *blanchoti* and *sulphureopectus* are found in the trees of open savannahs, Chapin (1954:42) finds that *blanchoti* frequents only the lower trees. This indicates that the two species may, on an average, have dissimilar vertical feeding ranges, as is evidenced also by stomach contents of the two species and, indirectly, by the proportionately larger bill size of *blanchoti.* Where both species occur in the bush-veld of Kenya and Uganda, Jackson (1938) finds that the relative abundances of the two species vary over this region, and his notes indicate a difference in foraging height and food items between the two. Therefore it seems reasonable to suppose that in a savannah with trees of a fairly uniform but intermediate height (between the heights preferred by the two species when foraging) competition between the two species would be severe enough to make interspecific territoriality advantageous. The occurrence of patches of savannah which are of either low or high trees, or a mixture of two such types, would then account for the persistence in savannahs of both species of bush-shrike.

It is possible to speculate that the differences in eye color between sympatric species may prevent hybridizations, as might also the group-specific differences in voice. Those of *sulphureopectus* are given as "cheery whistles," while those of *blanchoti* have a "strange hollow" quality (Chapin 1954; verified in part by Jackson 1938). For this case to fit the requirements of the Case B convergence above, nothing further need be supposed about the evolution of the two groups than was discussed by Hall et al. (1966:172–3).

Another striking sequence of parallels occurs between members of two different branches of the woodpecker family Picidae. I am grateful to Mr. Charles Rogers of Princeton University for bringing this remarkable case to my attention, and I follow his terminology by calling one group of genera "logcocks" and the other "ivory-bills," after the North American representatives. The logcock genera appear as a group early in the list of genera of the subfamily Picinae, while the five genera of ivory-bills mentioned below end this list (Peters 1948). Between the two groups there are certain fundamental differences in morphology and behavior, including the structure of the bill; arrangement of the tail feathers; the

TABLE 2. Comparison of "logcock" and "ivory-bill" woodpecker genera.

	Logcocks	Ivory-bills
Genera involved:	*Meiglyptes, Micropternus, Dinopium, Dryocopus.*	*Hemicercus, Blythipicus, Chrysocolaptes, Campephilus, Phloeoceastes.*
Taxonomic characteristics:	Outer hind toe shorter than outer front toe.	Not so.
	First toe reduced, vestigial or absent.	All four-toed.
	Gonys comparatively short.	Gonys much longer.
	In closed tail, retrices fold under middle pair.	Second pair of retrices permanently abreast of mid-pair.
Other morphological features:	Usually with red or black malar stripe.	No malar stripe.
	Bill dark, often black.	Bill pale, whitish, or horn.
	Always the smaller of a logcock-ivory-bill pair of species.	Length averages over 11% more, and bill averages 43% longer.
Behavioral characteristics:	Voice a laugh or yaffle, often flicker-like.	Voice usually a harsh scream.
	Uses first toe, if present, directed posteriorly on the inside.	First toe rotated to lie outside and perpendicular to body, or even further forward to a position adjacent to the fourth.
	Drumming, a steady roll —*Dryocopus*	Drums a "double-rap" —*Phloeoceastes.*
Ecological characteristics:	Drier, more open forests.	Moist, denser forests.
	Forages more on ground, lower in trees.	Forages higher, on the average.
	Ants and termites prominent in diet.	Not nearly so prominent.
	Clutch size 20% larger.	Clutch size smaller in spite of the average higher altitude.

number, length, and orientation of the toes; the voice; habitat preference; and various plumage characteristics. Moreover, generalizations can be made pertaining to life history and other ecological properties. These comparisons are contained in table 2. Bock and Miller (1959) and Bock (1963) have already drawn attention to the fact that certain pairs of genera, one from each of the two different groups of woodpeckers, contain species which are startlingly similar in appearance (frontispiece). Usually two species are involved in these convergent similarities, but sometimes two or more congeneric species occur within the geographic range of the species from the second genus and are presumable geographic replacements (see the *Dinopium-Chrysocolaptes* case beyond). I believe that some species in these pairs of genera can be referred to a Case B convergence between food specialists. The frontispiece illustrates most of the species concerned and the range maps of the lesser-known southeast Asian species are given in figures 2–4.

The similarity between these pairs (or trios) of woodpecker species, which are individually described below, has been commented upon by almost every author on the birds of the

areas they inhabit.[2] The enigma of the strong superficial resemblances has been mentioned time after time, but no explanation has been forthcoming except the recent suggestion by Bock (1963) that the true taxonomic affinities of these woodpeckers lie across rather than within the traditionally separate logcock and ivory-bill groups. If these cases can correctly be ascribed to the convergence described above, it is not difficult to suggest species-specific recognition marks which could prevent hybridization. Two of the most consistent differences between the two groups are the divergent bill coloration (black as opposed to yellowish) and the presence of a red or other malar stripe in the logcocks. Both of these characters appear to figure prominently in courtship behavior. Many authors have reported fencing and mutual grasping of bills between courting pairs of the better known members of both logcocks and ivory-bills (Allen and Kellogg 1937; Tanner 1942; others

[2] Recent notes on these woodpecker pairs by D. Goodwin [1968. Bull. Brit. Mus. (Nat. Hist.), Zoology. 17 (1):1–44] attribute the similarities in most cases to selection resulting from similar habitats and ecologies, and in others to a hypothesized close taxonomic relation.
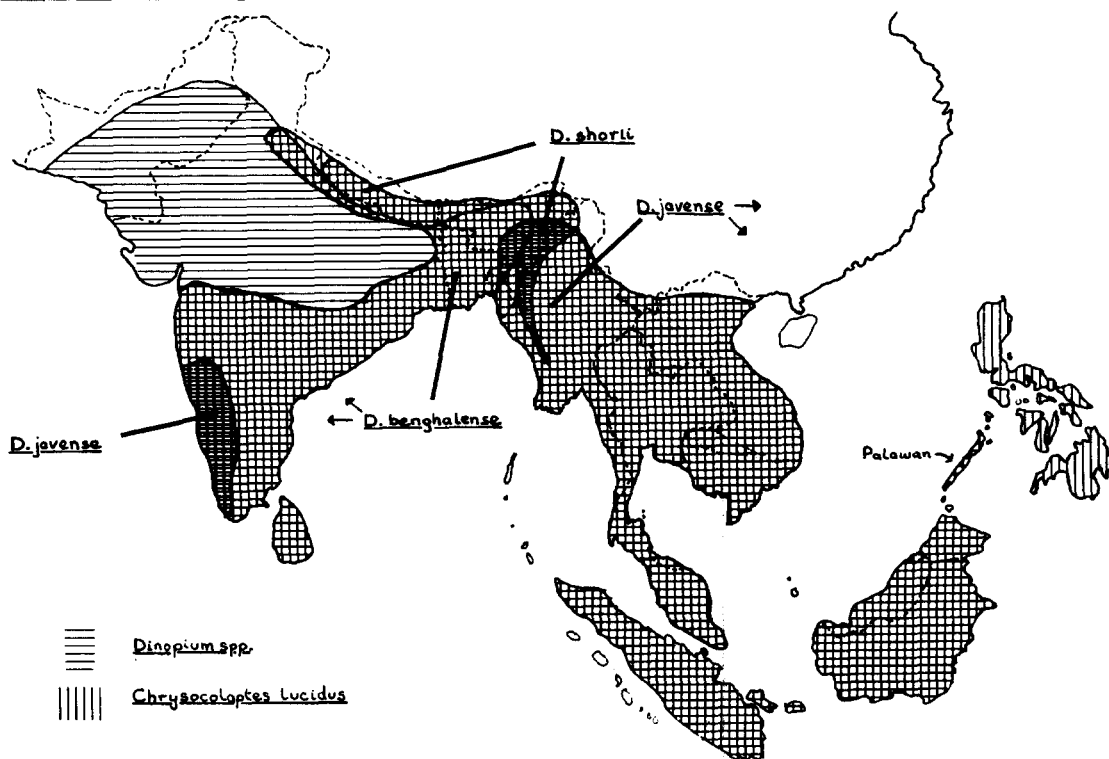
FIGURE 2. Range map of convergently-similar species of the genera *Dinopium* and *Chrysocolaptes*. Occurring in the same area, in addition to those shown here, are three species of these two genera which differ in appearance, moderately (*D. rafflesi*) or distinctly (*C. festivus* and *C. vallidus*).

in Bent 1939). Noble's (1936) experiments have shown how important moustachial stripes are for inter- and intrasexual recognition in the flicker (*Colaptes auratus*). Further remarks which apply to species pairs in general follow the descriptions of the individual cases. Whereas the more specific references on these woodpeckers are cited in the body of the paper, numerous general sources were consulted in the construction of table 2 and figures 2–4 as well as for information used in the discussions. These references are appended to the end of the paper.

Dinopium-Chrysocolaptes. The ranges of three species of the logcock genus *Dinopium* and one species of the ivory-bill genus *Chrysocolaptes* are shown in figure 2. *D. benghalense* (five subspecies) inhabits West Pakistan through India and Ceylon to western Burma; *D. javense* extends the range of the genus from Bengal to Indo-China and Malaysia, with *D. j. everetti* reaching the Palawan group of the Philippine Islands. *D. shorii* occurs in the Himalayas and *D. rafflesi* in the Tenasserim mountain range in southern Burma. These latter species are separated altitudinally from the first two, and, where a race of *D. javense*

occurs in the humid regions of southwest India sympatrically with *D. benghalense*, the two species are separated by habitat (deciduous vs. evergreen forest, Ali 1953). *C. lucidus* extends from Bombay across India and Ceylon through the whole of the Indo-Malaysian region to the Philippines. Thus *Dinopium* is mainly sympatric with *Chrysocolaptes* but extends further west and not so far east (it is absent from the main group of the Philippine Islands). Any one location in this vast area produces two heterogeneric species which are difficult to separate in the field. An exceedingly accurate plumage convergence affects the color of the crown, crest, mantle, tail and wings, underparts, and lower back. In north India *D. shorii* is likewise convergently similar to *D. benghalense* and *C. lucidus* in these characteristics, but apparently *D. rafflesi* is not involved in this complex (its upperparts are slightly different).

The *Dinopium-Chrysocolaptes* case is interesting because it provides a means of testing several features of the convergence concept. First, by hypothesis, convergence can evolve only where species of the two genera meet; selection for similarity cannot operate on a
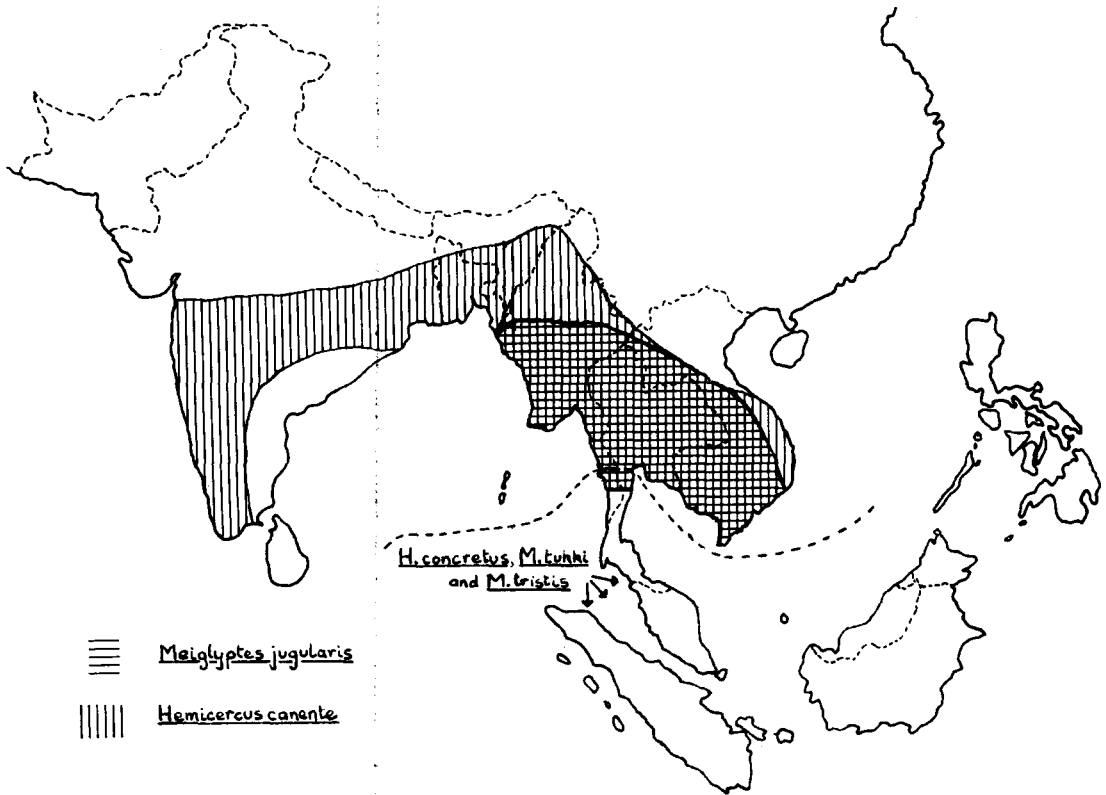
FIGURE 3.   Range map of convergently-similar species of *Hemicercus* and *Meiglyptes*. The three additional species which occur south and east from peninsular Siam do not resemble each other.

species where it occurs alone. There are two opportunities here to test this. Of the *Dinopium* species mentioned, the only populations which do not come into contact with *Chrysocolaptes* are those of northwest India, the subspecies *D. b. dilutum* and part of *D. b. benghalense*. These are the only two races of all three *Dinopium* species which lack a crimson rump, a feature possessed by all of the *C. lucidus* subspecies. Towards the south, within the range of *C. lucidus* in west-central and southwest India, *D. j. malabaricum* and at least some individuals of *D. b. tehminae* all possess crimson rumps and have other features in common with *lucidus*, such as crimson crests, golden upper backs and wings, and black tails (frontispiece: 8). From this point south to southern Ceylon *D. benghalense* and *C. lucidus* vary in parallel in the color of their wings and mantles, these being red in more humid and yellow in drier parts of this range (frontispiece: 9, 13). The abrupt loss of crimson rumps in *Dinopium* subspecies as soon as they lose contact with *Chrysocolaptes* also provides a useful counter-argument to suggestions that the above parallelism is caused solely by coincident selection pressures of habitat or climate gradients.

Of the seven subspecies of *C. lucidus* in the Philippines, only one (*C. l. erythrocephalus*) comes into contact with *Dinopium*. This race meets *D. j. everetti* on Balabac, Palawan, and Calamianes. As do all other races of this species, *D. j. everetti* has golden wings (frontispiece: 14). Only *erythrocephalus* of the *C. lucidus* races in the Philippines is golden-winged (frontispiece: 10); the other six have wings which are red (e.g. *C. l. xanthocephalus*, frontispiece: 11) or intermediate in color.

There is a second aspect of the current hypothesis which can be tested with these species in the Philippines. Species-specific recognition marks are necessary to prevent hybridization when the female makes her selection of a mate, and circumstantial evidence was given previously suggesting that bill color, or a malar stripe, or both might be such a cue in woodpeckers. Natural selection should favor the divergence of bill color between *Dinopium* and *Chrysocolaptes* where they meet, but bill color might well vary in a species which occurs alone in an area or converge to resemble that of the second species of the pair. This is, in fact, just what is observed here. The bill colors of *D. j. everetti*

and *C. l. erythrocephalus* in the Palawan group are black and whitish-yellow respectively (Hachisuka 1932), colors typical for the two groups in sympatry. However, in the other six subspecies of *C. lucidus* on islands which *D. javense* has failed to colonize, bills are black or dark in color (*C. l. xanthocephalus,* frontispiece: 11). Thus the factor which selects for the ivory-colored bill in *C. l. erythrocephalus* is absent from the other islands. This strongly suggests that the presence of *Dinopium* is that factor.

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. However, there is indirect evidence for very strong competition between members of the genera, indicating that two such species cannot simultaneously occupy the same uniform piece of woodland. This again may be deduced from their distribution in the Philippines. *D. j. everetti* on the Palawan group is reported to be common in forests, scattered woodlands, and in the plains (Hachisuka 1932). *C. l. erythrocephalus* is strictly confined to the forest here, and is said to be uncommon. But on the rest of the Philippine Islands, which have not been reached by *Dinopium,* *C. lucidus* is common and is found both in second growth and in forest habitat. The application of character convergence does not preclude the possibility that *C. lucidus* also undergoes a character displacement in ecological and associate morphological characteristics where it meets the smaller *D. j. everetti,* for culmen length in this race is seven per cent greater than the average for the other six races in the islands. The more restricted habitat occupancy has already been described; this must represent a selection for increased habitat subdivision to reduce the ecological proximity to *Dinopium* by using only those habitats in which it is at least as efficient as *Dinopium,* the thick forests. In summary, where the two species occur together there is convergence in the plumage characteristics by which males presumably recognize each other and divergence in the habitat which is occupied, in bill size, and in species-specific cues by which females presumably recognize a male of their own species. When one species occurs alone the reverse is true.

Meiglyptes-Hemicercus. *Hemicercus canente* of the ivory-bill group ranges across lower India through Burma and Thailand to Vietnam. This tiny woodpecker is sympatric with the logcock *Meiglyptes jugularis* in the eastern part of this area (fig. 3). In their black-and-buff patterned plumage these two woodpeckers are virtually identical (frontispiece: 1, 2); the most obvious difference between them is the red malar stripe on the logcock. *M. jugularis* is replaced by *M. tristis* and *M. tukki,* and *H. canente* by *H. concretus* in Malaysia, although there is some overlap with each of the former in southern Tenasserim. The three more southerly species differ considerably in appearance from each other and from the aforementioned two; for unknown reasons no convergence has affected them. That *jugularis* and *canente* may be interspecifically territorial cannot be verified from published observations. *Jugularis* may feed lower on trees and be commoner in more open forest, but the similarity of their habitat and feeding methods remains extensive (Delacour and Jabouille 1931; Deignan 1945; Smythies 1953).

Micropternus-Blythipicus. *Micropternus brachyurus,* a logcock, is present over most of India, Southeast Asia, and the Malay peninsula to southern China. It is sympatric with the ivory-bill *Blythipicus pyrrhotis* from northeast India through Indochina to Malaya (fig. 4). The two species are both medium-sized woodpeckers, barred rufous and black, and both possess red marking around the head (frontispiece: 3, 4). These consist of a crimson crescent under the eye on the lores and side of the head in *M. brachyurus* and a scarlet band on the nape and ear coverts in *B. pyrrhotis.* As with all of these woodpecker pairs, there are some altitudinal, habitat, and food habit differences between these two species, but these do not appear to be very extensive. Again the similarities may be attributed to interspecific territoriality. The distinguishing red plumage marks on a dull background give every indication of being inter- as well as intraspecific recognition signals rather than characters which are similarly influenced by the physical environment. The mutual possession by these two species of so similar a sign cannot be coincidence. The near-convergence to a common "message" recalls the often approximate and always very superficial resemblances between Batesian mimics and models in insects, but by hypothesis, selection by the individuals themselves is acting simultaneously on both species to produce the resemblance.

Dryocopus-Phloeoceastes. *Dryocopus lineatus* and *Phloeoceastes guatemalensis,* large powerful woodpeckers of the logcock and ivory-bill groups, respectively, are sympatric from México to western Panamá. *P. melanoleucos* replaces *guatemalensis* from the Canal
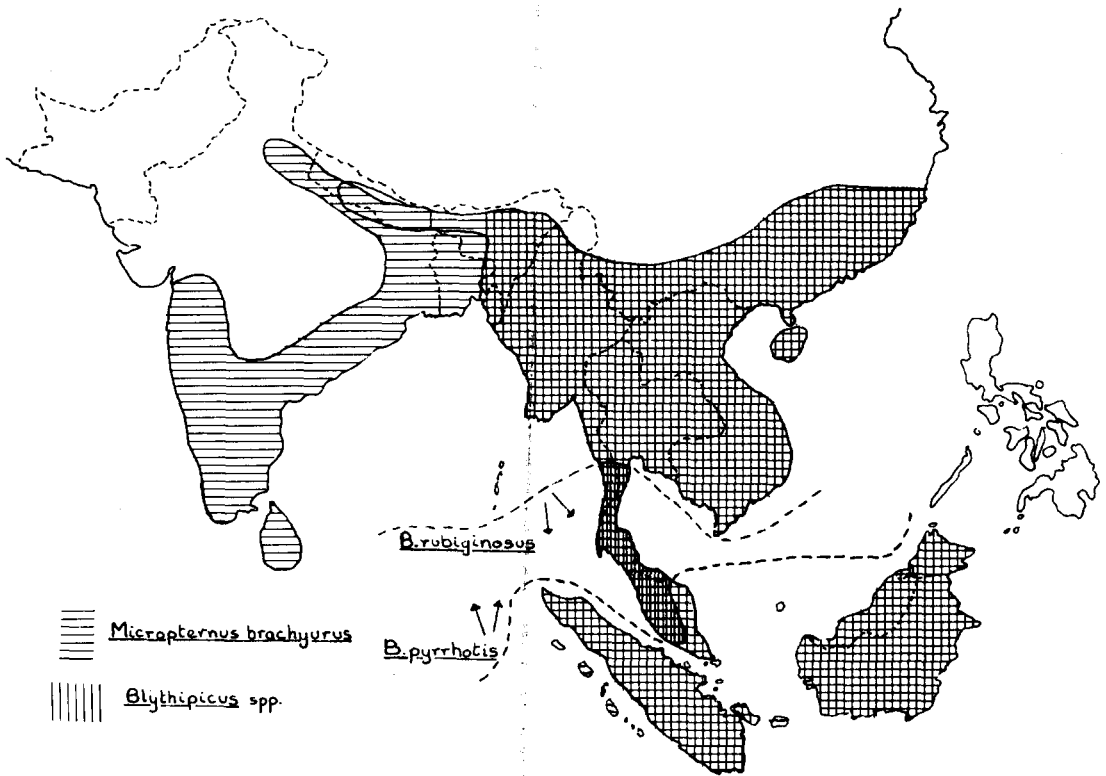
FIGURE 4. Range map of *Micropternus brachyurus* and two species of *Blythipicus*. *M. brachyurus* and *B. pyrrhotis* are both barred black and brown above, but *B. rubiginosus*, while retaining the red head markings of the above two, lacks this barring and has a uniformly brown back.

Zone east through Panamá over the northern half of South America, and is also sympatric with *D. lineatus*. Sympatric species again are virtually identical (Sutton 1951) and differ mainly in head pattern and the malar stripe (frontispiece: 5–7). Here particular emphasis is placed on the importance of the malar stripe, for in these three species, together with the *Hemicercus-Meiglyptes* pair above, the convergence in appearance extends to the bill color. In the pair of species west and north of the Canal Zone, the bill color in each is ivory-white, but in *P. melanoleucos* and the several *lineatus* subspecies sympatric with it, bills are dark in color.

A general preference in *lineatus* for drier, more open areas is evident. Even so, both species can occur together in a small area when they occupy the same habitat, and have been observed feeding on the same tree. As such observations are not dated in reference to the breeding season, they do not preclude the possibility of interspecific territoriality. There is substantial evidence suggesting that the forest habitat is patchy for the species pairs, for in any one locality (see, e.g., Dickey and Van Rossem 1938; Slud 1960; Miller 1963;

Alvarez del Toro 1964) there is a tendency for one species to be common and the other rare. *D. lineatus* and *P. melanoleucos* both occur on Barro Colorado Island in the Panamá Canal Zone where, according to Sturgis (1928), they both occupy "old forest." But in a census of a 12-acre patch of mature forest on the island, MacArthur et al. (1966) found only one of these species, *lineatus*, although the other bird was present elsewhere in the forest. G. Orians (pers. comm.) has taken five breeding censuses in Costa Rican localities where these two species are sympatric. His data show that the two species meet only in "edge" areas intermediate between different forest types. Slight differences in habitat preference between the two species (wetter and denser as opposed to drier and more open forest) would certainly be conducive to interspecific territoriality in forests intermediate in these characteristics.

Dryocopus-Campephilus. The North American Pileated Woodpecker or logcock, *Dryocopus pileatus,* and the Ivory-billed Woodpecker, *Campephilus principalis,* were once sympatric (before 1800) from Illinois to southern Florida, but now both subspecies of *prin-*

cipalis are almost extinct. The two species also occurred in allopatry, for *C. principalis* is absent from the great forest tracts of northern and western North America inhabited by *D. p. picinus* and *D. p. abieticola,* and no *pileatus* has reached Cuba where *C. p. bairdii* is found. The Pileated and Ivory-billed Woodpeckers are quite similar in their general coloration; both are largely solid black with white on the wings and neck, and the males of both species are red-crested. While the distribution of the white markings, the bill color, and the malar stripe in the logcock make the two species quite distinct, they are far more alike than similarities in their habitat and taxonomy warrant. For instance, *pileatus* is much closer in appearance to *principalis* than it is to the congeneric *D. martius,* the logcock replacement in Europe, which lacks white markings and interestingly, because of the absence of an ivory-bill there, has a pale bill.

Both species in allopatry occupy all types of heavy forest, or used to in the case of *C. p. bairdii,* which was widespread in the lowlands of Cuba but is now restricted to montane pine forests. Where the species are now sympatric in Louisiana (*D. p. pileatus* and *C. p. principalis*) Tanner (1942) reports no habitat difference. In fact ivory-bills preferred habitat where Pileated Woodpeckers were also very common. Competition is obviously severe between the two species, as there is a 51 per cent overlap between them in scaling vs. digging behavior, and 60 per cent overlap in the proportions of tree species on which they forage. 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.). In view of the drastic reduction in range of the Ivory-bill from former times it could be that no selective pressure has maintained in *pileatus* a behavioral reaction to the plumage pattern of *principalis* because of lack of contact between the two. A divergence in some characters is apparent in the sympatric races of the species, as was shown above for woodpeckers on Palawan. *D. p. pileatus* and *C. p. principalis* have total length/culmen length ratios of 8.25 and 6.66, respectively, whereas the corresponding figures for *D. p. abieticola* and *C. p. bairdii* are 7.40 and 7.18. On the whole this seems a less convincing case of possible character convergence. With the imminent extinction of *principalis* the best test

for my hypothesis will be to look not for interspecific territoriality but for a divergence in the plumage patterns in *D. pileatus* in those areas once occupied by *C. principalis.* A possible change in bill color (lighter) would be predicted.

The overall picture which emerges of the logcock-ivory-bill woodpecker groups can be summarized as follows. Bock and Miller (1959) believe that the ivory-bills are an offshoot from the older and less specialized logcock line. As with the African bush-shrikes, it would seem that one of the groups, presumably the latter, already occupied more or less its present range when the ivory-bill line diverged in isolation and subsequently expanded into approximately the same area. The ivory-bills probably evolved in a dense wet forest habitat and thus were able to outcompete the logcocks wherever this habitat was occupied by the latter; in intermediate habitat the two are evenly matched. In this way average habitat differences were further developed between the two groups. Woodpeckers are generally regarded as food specialists in that they exploit a narrow range in the spectrum of food resources and use a highly specialized feeding apparatus. Consequently there must be less opportunity for territorial overlap through divergence in food requirements than, for instance, in insectivorous foliage gleaners. Some North American woodpeckers occupy habitats where no other woodpecker is present. Where two species do occur, there is usually a large size difference which may allow the exploitation of differently sized trunks and branches. 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 Boch, pers. comm.), and for *Picus viridis, Dendrocopos major,* and *D. minor* over nest sites (Howard 1920). Bock (1963), referring to the similarity between members of some of the above species pairs, states that "the complexity of these color patterns precludes any reasonable possibility of their rising independently in three pairs of genera; no known selection forces could explain such a pattern of convergence." He is forced to conclude that the true affinities of the species lie across the logcock-ivory-bill lines, i.e. between similar-

appearing pairs, and that the typical morphological features of the groups have arisen separately in each of the respective genera. The hypothesis presented in this paper at least suggests a way in which natural selection could achieve the observed convergences, without invoking, on the basis of superficial characteristics, rather unlikely close relationships between members of the convergent pairs.

Plethodon-Desmognathus. Convergence should not be restricted to birds, but could occur in any animals which are territorial. On these grounds some mammals, amphibia, and reptiles could qualify as candidates for the phenomenon. In many territorial mammals, defense of territory is by means of olfactory signs, and any character convergence in such signs as advertized by different species will be difficult to recognize. Among the Amphibia a remarkable similarity between two species in different genera can be cited as an example of aggression-associated convergence. *Plethodon jordani* and *Desmognathus ochrophaeus* present a situation which has puzzled herpetologists for many years. These species belong to different groups (genus or several genera), the woodland and dusky salamanders, respectively, of the same family Plethodontidae. A northern subspecies, *D. o. ochrophaeus*, lives in the Appalachian Mountains from New York to Tennessee, while the other subspecies, *D. o. carolinensis*, occupies the more eastern ranges of the same chain from Virginia to Georgia. *P. jordani* has about seven subspecies which occur mainly as discontinuous populations in the Great Smoky Mountains and on different Blue Ridge Mountains (Conant 1958; also see this reference for color illustrations, range maps, and general descriptions).

Where *P. jordani* (subsp. *jordani*) is sympatric with *D. o. carolinensis* in the Great Smokies, both have red cheek patches, including almost all of *jordani* and 24 per cent of *carolinensis* (Hairston 1949). In the Nantohola Mountains of southwestern North Carolina *carolinensis* occurs in the same habitat as *P. j. shermani*. This race of *P. jordani* has bright red legs, and here *carolinensis* also has red legs (Bishop 1947; Martof and Rose 1963). Not only do the salamanders have the red color and its position in common, but they are also "amazingly similar in general body coloration" (Martof and Rose 1963). The altitudinal range of *carolinensis* on these mountains is roughly from 2400–6700 ft, while *P. jordani* is found only above 3000 ft and is apparently replaced by *P. glutinosus* (no red cheeks) at lower elevations. The incidence of the red

or reddish cheek patch in *D. o. ochrophaeus* falls from 24 per cent above 5400 ft to 5 per cent below 3000 ft (Hairston 1949; Martof and Rose 1963); some individuals have both red cheeks and red legs.

Mimicry has been suggested as a possible explanation for this striking convergence. The supposed model, *jordani*, is known to secrete slime, which may have some protection value from predators. Although Dunn (1927) favored this interpretation, others have voiced either a lack of conviction (Huheey and Brandon 1961) or very strong doubts (Orr 1967). Huheey (1960) reviewed several possible explanations for the interspecific similarities but discounted or omitted interspecific relations other than mimicry. After some quite inadequate experiments to test the mimicry hypothesis, using a sparrow hawk, shrike, and garter snake as reluctant predators, he tentatively favored this interpretation. Later (Huheey 1966) genetic drift was invoked to account for the lack of correlation between the incidence of the red cheek pattern and physical attributes of the habitat. Subsequently Orr (1967) has retested the same hypothesis with all likely and some unlikely predators (snake, shrew, other salamanders). No trace of preferential selection or different palatability was shown between red-cheeked and "non-mimetic" *D. o. ochrophaeus* and the red-cheeked "model" *P. jordani*. Orr concludes that some explanation other than mimicry will have to be sought to account for the similarities. The current hypothesis provides such an alternative.

But are salamanders territorial, as the application of aggressive convergence to this situation presupposes? There are few references in the literature to any such behavior in this group of animals, but aggression between males has been recorded in *Amphiuma*, *Ambystoma*, *Triturus* (Evans and Abramson 1958, who also cite references to the first two genera), *Plethodon jordani* and *P. glutinosus* (Hutchinson 1959; Organ 1960), and *Desmognathus*, including *D. o. carolinensis* (Organ 1961). Fortunately these few observations include just those species which now concern us, and this is perhaps not a coincidence. No aggression (biting) between males and females has been recorded, and the interactions between males are apparently in response to visual stimuli. As Organ (1960) remarks, this aggression would tend to space out males and can thus be loosely described as territoriality. The significance of a general red

coloration in courtship has also been reported (Organ 1960). It remains to be tested whether males of *Plethodon jordani* and *D. o. ochrophaeus* are interspecifically aggressive. A mechanism to prevent hybridization between the two species perhaps exists in the elaborate species-specific ceremony of courtship and the deposition of the spermatophore.

D. ochrophaeus is at the terrestrial extreme in a gradient of dusky salamander species, going from mostly aquatic to mostly terrestrial in habit. So in areas where both species occur, *D. ochrophaeus* is ecologically the closest of its group to a strictly terrestrial woodland salamander of the *Plethodon* group, and hence these two species are the two most likely to compete for habitat resources. In summary, then, all of the necessary ingredients (from male aggression provoked by visual recognition to convergence in potential competitors of color patterns only in areas of sympatry) are present in the case of these salamanders for an interpretation of character convergence to be forwarded.

CONVERGENCE IN VOICE

Birds exclude conspecific individuals from their territories by song or other vocalizations as well as by reactions to plumage, and this characteristic may also become convergently similar in competing species. An indisputable case of vocal convergence occurs between two Mexican wren species of the genus *Thryothorus*, the Happy Wren (*T. felix*) and the Sinaloa Wren (*T. sinaloa*). On the Pacific slope of northern México these two wrens are sympatric from southern Sinaloa to northern Guerrero (Friedmann et al. 1950). While *felix* extends further southeast, *sinaloa* appears to be replaced by *T. pleurostictus* beyond the latter point. Grant (1966) finds that the two species are interspecifically territorial in Jalisco and Nayarit. Furthermore, both species gave versions of two songs which sounded identical to him, and the published sonographs are virtually indistinguishable. That convergence is actually involved here is further evidenced by a divergence in the song of *T. felix* where it occurs on the Tres Marias Islands from which *sinaloa* is absent. Hybridization apparently does not occur (Grant 1966), and may be prevented by differences in plumage, particularly face and head patterns. The case becomes even more convincing when it is known that these head and face patterns converge in allopatry between the island race of *T. felix* on the Tres Marias and the mainland *T. s. sinaloa* (Grant 1965, 1966).

Wren species generally have similar foraging behaviors and often coexist by having different habitat preferences, at least in temperate species. In intermediate habitats, species are often interspecifically territorial (Orians and Willson 1964; Grant 1966). Where *T. felix* and *T. sinaloa* are sympatric there is a broad ecologic overlap between them, but from the literature one gains the impression that slight (average) differences in habitat and altitudinal range (*felix* is commoner at higher elevations) permit coexistence and the survival of both species. Grant (1966) found the two species in the same habitat in his study areas, and presumably this habitat was intermediate between the slightly distinct preferences of the wrens. Thus interspecific territoriality would be indicated a priori for these species from what is known of wren coexistence in temperate habitats and from conditions on p. 224 of this paper. The distribution and ecology of these wrens conform well with the Case B situation of my hypothesis, in which a patchy habitat is occupied by two broadly-overlapping species which must become interspecifically territorial in intermediate habitat.

The last two species to be discussed strongly suggest a Case A character convergence in voice. Eastern and Western Meadowlarks (*Sturnella magna* and *S. neglecta*) have extensive areas of sympatry in the central United States, and in this region are interspecifically territorial (Lanyon 1957). These two species occupy a simple grassland habitat and select territories on the basis of vegetation height and density, both of which roughly increase in magnitude from west to east across North America (Cody 1968a). The values of these habitat variables where the two species are sympatric will be intermediate between typical mean values encountered by each species, and will presumably be insufficient in places to separate the territories of the species. In variable topography the Western Meadowlark occupies higher and drier terrain (Lanyon 1957, in Wisconsin), which has lower values of vegetation height and density, and the Eastern Meadowlark the lower and wetter fields, with higher values in these indices. My own studies (Cody 1968a) support these data quantitatively. Even so, the two species meet and defend territories against each other in intermediate fields.

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*. These species are normally very easily identified by their different songs; the instances of vocal convergence occur only where the two species meet and are interspecifically territorial. This intermediate song was originally interpreted as a result of hybridization, but Lanyon finds that interbreeding is extremely rare between the species (see also Szijj 1963 and Lanyon 1966) and is apparently prevented by distinctive species-specific call notes, on which the females base their choice of the appropriate mate.

The isolating barrier between the species is efficiently maintained if, as Lanyon believes, the call notes are inflexibly inherited. A complicating factor is that the song is apparently learned, which could in itself account for individuals with songs possessing characteristics of both species. This in effect would act as "short cut" to convergence (which could not, of course, be involved in convergent appearance). In this case an equivalent substitute for the evolution of convergent characteristics is the evolution of learned rather than inherited song. Apart from these intermediate songs, cases have been recorded (Lanyon 1957) of a male singing "typical" songs of both species, sometimes consecutively. This would accomplish the same end as an intermediate song, namely the discouragement and exclusion of other males of both species.

DISCUSSION

In many of the above cases the interspecific territoriality aspect remains to be tested. It is predicted that some sort of aggression will exist between convergently-similar species. Such an interaction could either wholly or partially separate species spatially, or perhaps effect some temporal sequence of resource utilization. This latter variation on the more usual spatial separation of activities has been shown by Leyhausen and Wolff (1959) to operate with feral cats. Moynihan (1963) has described a similar situation in nectivorous Andean birds, involving three species of *Diglossa* and one of *Conirostrum*. The same food plants are used by these birds, but with a temporal displacement, which appears to be facilitated or regulated either by similar vocalizations between species, by similar appearance, or both.

Since many examples of interspecific territoriality are known, why are cases of this type of convergence not more abundant and obvious? First, it is quite possible that inter-

specifically territorial pairs of species which are generally similar in appearance have actually converged somewhat, but not to an extent sufficiently striking to catch our attention. In this context perhaps several of the above examples could be elaborated. For example, while *P. jordani* does not occur within the range of *D. o. ochrophaeus*, *P. c. cinereus* does. Both of these subspecies have a red mid-dorsal stripe for which the latter displays an interesting polymorphism (Williams et al. 1968). *Blythipicus rubiginosus* (see fig. 4) is certainly not as close in appearance to *M. brachyurus* as is *B. pyrrhotis*, but nevertheless their similarities warrant attention.

Second, strong competition between species, a prerequisite to interspecific territoriality, is most likely to occur between closely related species, and such species are already likely to be similar in appearance and voice. Convergence to greater similarity might not be favored; selection may merely prevent any divergence. The interspecifically territorial Plain and Bridled Titmice (*Parus inornatus* and *P. wollweberi*) studied by Dixon (1950) may be an example of this.

Third, any convergence which takes place in regions of sympatry must affect individuals breeding in regions of allopatry, by emigration and dispersal. The convergent phenotype may quite conceivably be at a selective disadvantage in allopatric populations. This could be sufficient not only to prevent its establishment where the competitor is not encountered, but to impair its fitness where the species are sympatric. Thus convergence may be rather less likely in extensively allopatric pairs of species (and of course strongly competing species are often separated in their geographic ranges). Convergence, however, need not be limited to the area of sympatry of the species involved, although this is the zone where selection maintains the similarities. If there are no attendant disadvantages, the characteristics in their convergent form might occur uniformly throughout a species range, even in those areas where the two species do not meet. Such monomorphic pairs of species are correspondingly more difficult to detect.

Here mention should be made of the North American hummingbirds. These tend to be taxonomically uniform over large areas, perhaps due to strong migratory tendencies (only 2 of 15 species are divided into subspecies in the area). The males are brightly colored and interspecifically quite distinct, but the females are uniformly drab. In fact the females of species such as Black-chinned, Costa's, and

Anna's Hummingbirds (*Archilochus alexandri, Calypte costae,* and *C. anna*), are impossible to separate in the field with certainty. Furthermore, the females defend separate territories from the males in which to raise young. It is tempting to suggest that their uniformity is a product of selection for interspecific territoriality, especially as the above-named species are closest in habitat preference. However, it has been shown that such similarity in appearance is not essential for the interspecific territoriality known to exist between both males and females of many hummingbird species (Cody 1968b). The situation parallels that in some butterflies, in which the males are distinct and non-mimetic but the females of several species mimic a single model.

A fourth possibility is the danger of hybridization between the convergent species. This is particularly important because plumage and song often play a substantial role in the isolating mechanisms of closely related species of birds. Elaboration of these dangers is beyond the realm of this paper. Finally, there is the fact that territoriality has been widely studied only among higher vertebrates, and only in a minute portion of the existing species. I would expect the list of examples to be much longer if, for instance, neotropical bird species had been as intensively studied as those of North America. In many poorly-known species and situations for which even less evidence for this type of convergence phenomenon can be accumulated than for the more detailed examples above, existing data suggest that the phenomenon may indeed be widespread.

Pipilo ocai and *Atlapetes brunneinucha* are both mainly ground-foraging finches narrowly sympatric in central México. They appear so similar in the color of the back, cap, eyestripe, cheeks, breast, breastband, and flanks that trained observers may initially confuse them in the field (Charles Sibley, pers. comm.). More anecdotally, several other neotropical finches of the genera *Saltator, Lysurus,* and *Arremon* also possess many features of the same color pattern. In grass fields in Panamá, three species of the genera *Oryzoborus, Sporophila,* and *Volatinia* may be found. All males are black with more or less white markings on the wing. These are, at least in some combinations, interspecifically territorial, but the situation is complicated by polymorphism in the second genus (Neil Smith, pers. comm.). Philip Regal (pers. comm.) has described the similarity between adult male salamanders *Chiropterotriton demidiata* and juvenile *C. multidentata* as a situation which would lend

itself to the interpretation favored here. It is interesting that the colorful markings of salamanders in general are brightest in the juvenile individuals, which are the population members which Test (1954) reports as most aggressive in another amphibian, the frog *Phylobates*. Lorenz (1966:Ch. 2) describes the same progression from colorful aggressive youth to peaceable but plain adulthood in coral fish. He also describes the interspecific aggression between a blue triggerfish and other species which either were the same in coloration or had the same shape and form as the aggressor. Whereas Lorenz interprets this activity as behavior released by inappropriate or merely accidentally effective stimuli (no other triggerfish of the species were present), the current hypothesis can assign selective advantages to releasers such as the appearance of competitors which approximately resemble each other. Perhaps a more subtle habitat division is exercised in behaviorly sophisticated adults, whereas the younger stages develop in closer proximity to others of different species. For instance, with forest Amphibia various species differing in spatial location during adulthood might all have to utilize for egg-laying water pools caught between buttress roots or in epiphytes. Thus the young would be found in close association in an uncomplicated and non-divisible environment and it could be to their advantage to act ecologically as a single species.

SUMMARY

There exist between some pairs of sympatric species similarities in appearance or voice which seem much more exact than can be accounted for by common ancestry or response to similar ecological gradients. The convergent similarities affect only characters which are used by animals for territorial defense, namely color patterns and voice, and are either absent or reduced when the same species occur in allopatry. It is suggested that the similarities arise because they permit the recognition of competitors and facilitate the development of interspecific territoriality. The convergence can thus be economically advantageous in some circumstances and its evolution can be accounted for by the normal process of natural selection. Arrangements of species' ranges and habitat preferences conducive to interspecific territoriality are discussed.

Hybridization between these species is prevented by the maintenance of species-specific

recognition cues which enable females to select a male of their own species. Whereas characters by which individuals exclude others of the same sex from their territories converge in areas of sympatry, these specific recognition cues can converge in areas of allopatry. Species pairs or groups which can be referred to this type of convergence are discussed in those aspects of their biology pertinent to the hypothesis. Convergence in appearance is exemplified by different evolutionary lines of African bush-shrikes, woodpeckers, and salamanders, while vocal convergence may occur between meadowlarks in North America and between Mexican wrens.

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The following is a list of general references which were consulted for information on woodpecker distributions and ecology. They were not cited in the paper, but were used, in addition to those which appear in the above bibliography, to construct table 2, the range maps in figures 2–4, and as sources on appearance and habits.

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