CHARACTER CONVERGENCE IN MEXICAN FINCHES

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The natural history literature contains many striking examples of sympatric species more similar in appearance than common ancestry or chance warrant. Recent papers by Moynihan (1968) and Cody (1969) summarized the relevant literature, termed this phenomenon "character convergence," and emphasized the mutual advantages to convergently similar species in gregarious and aggressive interactions respectively. In particular Cody (1969) suggested that convergence in appearance or voice may evolve as a response to selection for interspecific territoriality between ecologically similar species, as territories are defended by vocalization and/or visual displays.

The examples to support this hypothesis were few, because in most apparent cases of convergence attributable to this phenomenon the necessary field observations on interspecific territorial interactions were lacking. Species showing an apparent convergence where their ranges overlapped became, *ex hypothesi,* good candidates for interspecific territoriality. It will be shown that, in one such instance at least, the speculation was justified.

THE PREDICTION

Pipilo ocai, the collared towhee, is a large ground-feeding finch strikingly colored in green and chestnut, black and white. It is endemic to the mountains of southern Mexico. The chestnut-capped brush finch, *Atlapetes brunneinucha,* is a similarly sized bird of similar habits which ranges from Peru to southern Mexico. It is found more typically in forest than in the open scrub-type habitats of the towhee. These two species are remarkably similar in appearance (see Fig. 1 and color plate in Sibley, 1950). Sibley, who has studied the *P. ocai–P. erythrophthalmus* complex in Mexico (Sibley, 1950; Sibley and Sibley, 1964 and other papers between) remarks *in litt.* that the naive observer can easily confuse the two in the field, so great is the resemblance.

P. ocai and *A. brunneinucha* were offered as an example of character convergence by Cody (1960, p. 237). As viewed from Los Angeles, the two species appeared to have converged in appearance, and by hypothesis the convergence was expected to be associated with interspecific territoriality between them. No information on the relative disposition of their territories was then available. This report provides the necessary information; the two species are interspecifically territorial as predicted and as described below.

THE TEST

Between March 27 and April 4, 1969, we plotted the territories of four finch species at La Cumbre, at an elevation 9000 feet near Cerro San Felipe in Oaxaca, Mexico (see Sibley, 1950, for full description and photograph). We found *Pipilo ocai, P. erythrophthalmus, Atlapetes brunneinucha,* and *A. pileatus* to be common in the strip of scrubby habitat which separates the *Quercus* cloud forest from cleared land in this location. The territory maps of Figure 2 were drawn after we had accumulated sufficient observations on position and movements of paired individuals; we believe that these are accurate within at least a few feet. The almost linear nature of the habitat facilitated this task. All species were actively territorial; interactions within and between species were observed, singing intensity appeared high and nesting activities were underway. We found one *ocai* nest with eggs on March 30, and a newly-built *brunneinucha* nest on March 28.

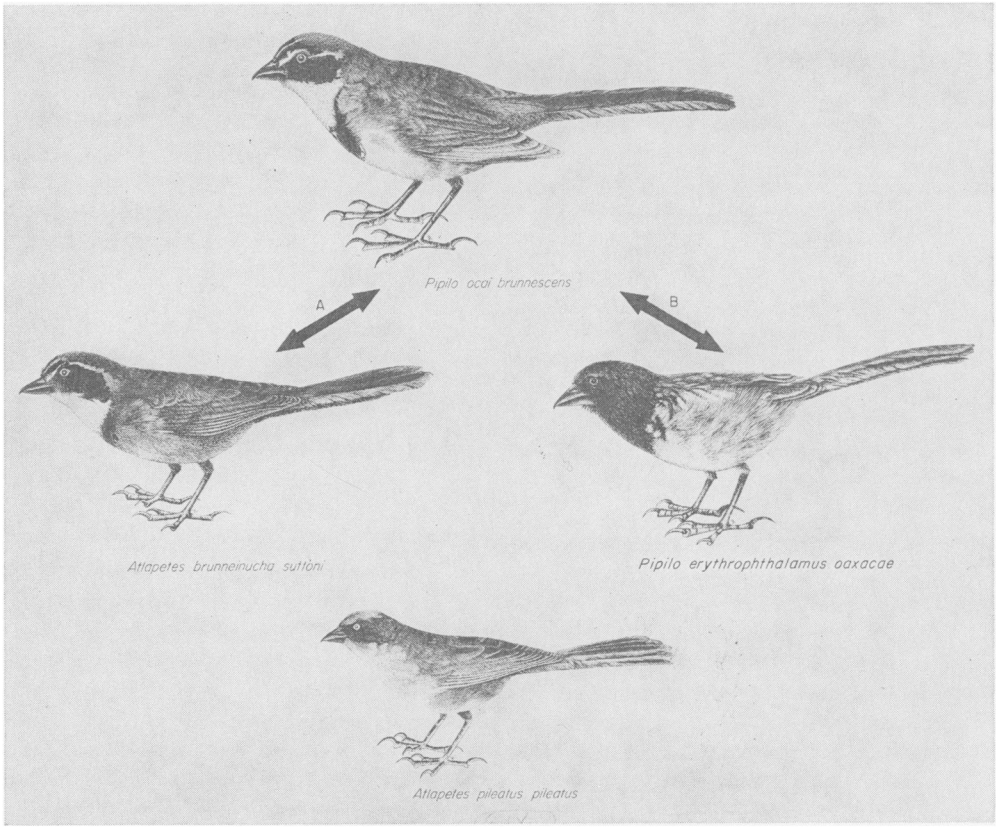

FIG. 1. Drawings of the four species of finches studied. The pair indicated by arrow *A* are convergent in appearance; the pair indicated by arrow *B* have similar songs.

THE RESULTS

The information gathered on territory sizes and interspecific overlaps is summarized in Table 1. Pairs of species will be discussed separately and remarks on the possible evolution of the present system will follow.

P. ocai–A. brunneinucha.—Eleven pairs of *ocai* were censused, including eight complete territories; these together occupied 55.1% of the total area surveyed. Six *brunneinucha* territories, five complete, were mapped to total 26.5% of the study area. The territory maps clearly show that *ocai* and *brunneinucha* behave virtually as a single species in dividing up the habitat. In several instances the territories of the two species abut, in others there is marginal overlap. Only 1.8% of *ocai*-occupied habitat was also occupied by *brunneinucha*; this overlap comprises 3.7% of the *brunneinucha* territories. Intraspecific overlaps in *ocai* amount to a larger figure (4.7%). If *brunneinucha* territories were distributed at random within the study area without regard to the position of *ocai* pairs, overlaps of 55.1% (relative to *brunneinucha*, or 26.5% relative to *ocai*) would be expected. The observed overlap figures differ significantly from these.

The spacing information alone does not eliminate the possibility that *ocai* and *brunneinucha* are merely selecting distinct habitat types within the study area, but the following observations are decisive. The *ocai* pair O_8 abutted *brunneinucha* B_3 on the south until March 29. On March 30

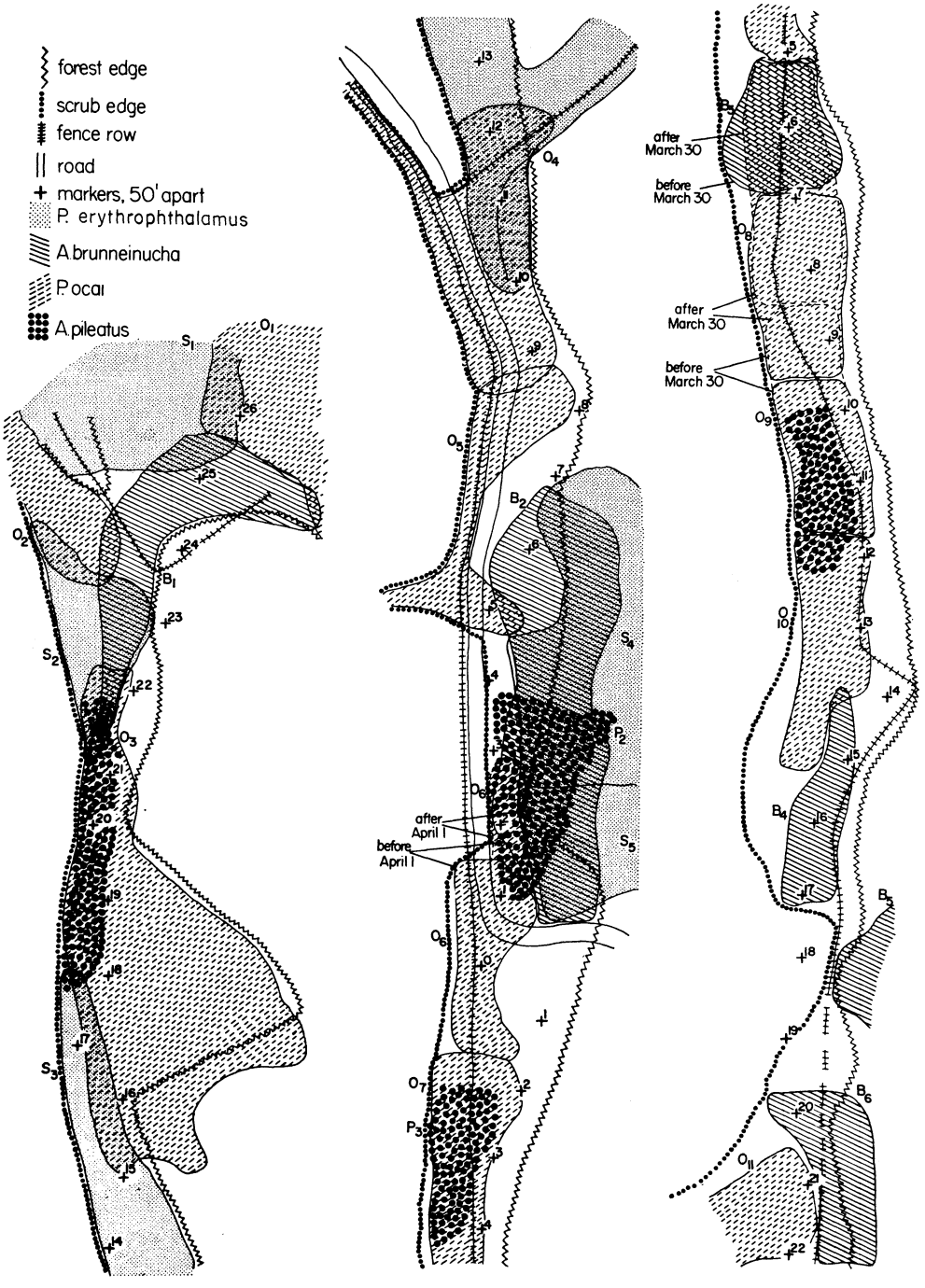

FIG. 2. A map of the territories of the four species of finches in a strip of scrub between forest and an open field. This map was used to compute the areas given in Table 1.

TABLE 1. *Territory sizes and overlaps among four finch species at La Cumbre, Oaxaca, Mexico.*

of	with	*ocai*	*erythroph-thalmus*	*brunnei-nucha*	*pileatus*	no. species pairs	Proportion[2] area occupied	Average[3] territory size
P. ocai	E[1]		0.344	0.265	0.112	11(8)[4]	0.551	9620
	O	0.047	0.176	0.018	0.116			
P. erythroph-thalmus	E	0.551[5]		0.265	0.112	5(1)	0.344	11400
	O	0.160	0.0	0.292	0.088			
A. brunnei-nucha	E	0.551	0.344		0.112	6(5)	0.265	8420
	O	0.037	0.379	0.0	0.137			
A. pileatus	E	0.551	0.344	0.265		4(4)	0.112	4640
	O	0.585	0.269	0.324	0.0			

[1] For between-species overlaps *E* is the proportion of the total area occupied by the species in the row above, and *O* is the observed proportion of the area occupied by the species in the column to the left also occupied by the species in the row above.

[2] The total area occupied by the four species is 165,960 ft^2.

[3] Units are ft^2. Only complete territories used, except for *erythrophthalmus*, where parts are included.

[4] Number of pairs censused, followed in brackets by the number of complete territories mapped.

[5] The boxed overlaps, and no others, differ significantly from those expected from independent territory disposition ($P \ll .005$), indicating interspecific territoriality.

the *brunneinucha* were no longer present, and the O_8 had shifted to occupy the former *brunneinucha* territory, in addition to about half of their previous holdings (see text table; units: sq. ft.). The *ocai* pair O_9 had also expanded north to occupy the southern part of the former O_8 territory. There was apparently nothing about the habitat in the B_3 territory which was unattractive to *ocai*. Prior to the move all three species occupied territories much smaller than average in size, although we place little weight on this (see below).

Species	Before	After	Date
B_3	5500	0	March 30
O_8	7420	8820	
O_9	5620	7980	
B_2	18340	17000	April 1
O_6	5060	6420	

A second incident showing the acceptability of known *brunneinucha* habitat to *ocai* occurred April 1. During the early morning O_6 extended its territory north into the contiguous B_2 area. The move was accompanied by continuous singing and overt above-ground movement from *ocai*; B_2 retreated with much agitation and vocalization. The new border was the scene of unusual vocal activity for several hours, after which the change became established. Other border contacts between *ocai* and *brunneinucha* were occasionally observed, when both species became momentarily arborial and excessively noisy, a noticable behavior in such normally retiring and ground-haunting species; in this manner they approached their common boundary and maintained the display for some minutes. Presumably territory limits are defined in this way.

P. ocai–P. erythrophthalmus.—From Figure 2 and Table 1 it is seen that territory overlaps between these two species are far less extensive than would be expected on a chance basis, for only 17.6% of *ocai* ground is held in common with *erythrophthalmus* and only 16% of the latter's territory is also occupied by *ocai.* The two species are unlike in appearance, so how is this separation maintained? The answer is apparently by vocalization, because we were unable to assign certain *Pipilo* songs to one species or the other. Eventually we learned that each of the towhee species has a variety of song types. This is limited to two or three similar versions in *erythrophthalmus,* but in *ocai* we could distinguish at least a dozen songs in just two males—songs which were remarkably diverse in length, pattern, and tone. Most importantly, several of these were sufficiently similar to those of *erythrophthalmus* that we were never sure, except by location or sightings, of the specific identity of the performer. On April 1, when S_3 was singing, O_3 replied to each song with an indistinguishable "*erythrophthalmus*-type" song and interspersed "typical *ocai*" songs between them. Further, we had reason to suspect that *ocai* pairs further from *erythrophthalmus* sang mostly song types unlike those of the latter. Regardless of the extent to which song is learned in these species, the effect of the song convergence seems to be spatial separation of the vocalists and can originate or be enhanced by natural selection. Further quantitative observations of the song types and their distribution among males with various types of neighbors are needed.

Overt aggression between these two species was recorded on one occasion (S_3–O_4). Agitation similar to that described above was observed at boundary incidents on three occasions and involved three *erythropthalmus* pairs and four of *ocai.*

A. brunneinucha–P. erythrophthalmus.—The mechanisms of interspecific separation of territories in the first two pairs of species are convergence in appearance and convergence in voice respectively. *A. brunneinucha* has a weak, twittering song, rarely heard, while the typical *erythrophthalmus* song is rendered as "drink-your-tee-ee-ee" by many authors. Thus *brunneinucha* and *erythrophthalmus* not only look but also sound quite different, and we should therefore expect their territories to overlap. This is exactly what we found, for the observed overlaps between the two are, from the Table, 29.2% and 34.4%, which are not significantly dissimilar from the overlaps expected from random disposition of territories, namely 26.5% and 37.9% respectively.

A. pileatus–other species.—*A. pileatus* does not interact with the other species in this assemblage. *A. pileatus* is ecologically quite unlike the two towhees and *brunneinucha,* for at least 90% of its foraging is done above the ground, on the outer branches of bushes and small trees, and it appeared to be insectivorous at this season. It is much smaller than the others in body size, and differs markedly in voice and appearance from them all. *A. pileatus* territories overlapped with those of the three larger finches to an extent predicted by their superposition on a random basis (see Table).

General Considerations

The presumed requirements for interspecific territoriality, with or without character convergence, are pairs of species which are ecologically so similar that more young are raised per pair without the presence in their territory of the other species. One advantage gained by interspecific territoriality is the increased concentration of the food supply over a smaller area, and a reduction in the amount of traveling required for a parent to gather food.

The three species involved here in interspecific territoriality appear to be ecologically identical in this habitat. All apparently breed at the same time, and feed exclusively on the ground by scratching in leaf litter, especially under bushes. No dif-

ferences in feeding behavior between them could be qualitatively or quantitatively recognized, and, as already indicated, no differences in habitat within the scrub belt distinguished the species. Differences in habitat along the strip certainly existed—from forest edge *per se* and dense tall bushes to low open scrub. This is reflected in the range of territory sizes, where the larger territories are strongly associated with more open areas of low vegetation which are presumably "poorer." But all species occurred in all types, and hence are ecologically identical with respect to the use of the strip.

A logical question to ask is: Why has *brunneinucha* converged to *ocai* (or *vice versa*) rather than to *erythrophthalmus*? All three species are distributed as series of isolated populations in mountainous areas. Three northern subspecies of *brunneinucha* contact both towhees to about the same extent geographically. However, within the range of sympatry the altitudinal distribution of *brunneinucha* virtually coincides with that of *ocai,* for both occupy the higher more humid areas and exhibit very limited overlap with the lower *erythrophthalmus*. On Cerro San Felipe these distributions are 8500–10,200, 8000–10,200, and 6300–9000+ feet respectively (Sibley, 1950, for the towhees, adjusted and supplemented by our own observation). Whereas only a small part of the *erythrophthalmus* population actually meets *brunneinucha* (smaller than that which contacts *ocai*), *ocai* and *brunneinucha* are extensively sympatric.

An exact ecological correspondence between two species could not be a stable situation, and differences between *ocai* and *brunneinucha* are brought out by their distributions elsewhere. *A. brunneinucha* is generally called a forest species, and in the forest adjacent to the study area we found seven pairs at widely spaced intervals, chiefly around fallen trees. In that same area one *pileatus* and a possible *erythrophthalmus* but no *ocai* were recorded. Hence there is habitat used by each but not the other (*ocai* occurs at lower elevations and *brunneinucha* alone is found in the forest).

Which species-specific cues in each of *ocai* and *brunneinucha* prevent hybridization between the two? Clearly some such characteristics peculiar to each have this effect; perhaps voice, face markings, or eye color are involved. The descriptions of *ocai* and *brunneinucha* races from areas where the species are in allopatry give us few indications of what these cues might be. In general the sympatric races of the two are most similar to each other; the loss of the pectoral band and yellowish eye-line in some *brunneinucha* races out of contact with *ocai* may be significant, but their retention by other such races diminishes its weight.

P. ocai–P. erythrophthalmus contacts are well described by Sibley (1950). The two species, which hybridize everywhere except on Cerro San Felipe, are ecologically very similar and are excellent candidates (where "good" species) for interspecific territoriality. Their vertical ranges appear to be restricted by each other, for where *ocai* occurs in allopatry it extends farther down the mountainside (*P. o. guerrerensis,* 6400–11,500 feet) and conversely for *erythrophthalmus* (*P. e. chiapensis* and *P. e. repentens,* 6000–13,000 feet). It is suspicious, in view of the above information, that the only area in which hybridization between the towhees does not take place is where *brunneinucha* is also present. We can identify the presence of *brunneinucha* as a strong selective force preventing hybridization and thence loss of the *brunneinucha*-type appearance, for if this occurred the *ocai–brunneinucha* interspecific territoriality would surely break down, to the detriment of both.

There is a possibility that the evolution of interspecific territoriality between the towhees is of rather recent origin. Sibley reported in 1950 that the two occurred in close spatial conjunction, and, while the degree of territory overlap is not specifically given, the impression is gained that it is

considerable. Of great interest, however, is Sibley's remark (p. 154) that: "the songs of the two forms on Cerro San Felipe were quite distinctive, and relatively little variation was noted." Thus in 21 years two changes have apparently occurred: (1) the songs of the two species have become similar through the evolution of an *erythrophthalmus*-type song by *ocai,* among other variations, and (2) the territories of the two have shifted in spatial arrangement so that little overlap occurs between them. The two changes parallel each other according to the present hypothesis.

Summary

On Cerro San Felipe, Oaxaca, Mexico, two pairs of finch species are interspecifically territorial, *Pipilo ocai–Atlapetes brunneinucha* and *P. ocai–P. erythrophthalmus*. *P. ocai* and *brunneinucha* are convergently similar in appearance, while *ocai* and *erythrophthalmus* are alike in their songs. The territories of *brunneinucha* and *erythrophthalmus* differ in both appearance and voice, and are positioned independently of each other. A fourth species, *A. pileatus,* is morphologically, behaviorally and ecologically different from the first three, and its territories overlap with each of them. Interspecific territoriality occurs between the species most similar in their feeding ecology and altitudinal distribution.

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