CHILEAN BIRD DISTRIBUTION[1]

MARTIN L. CODY
Department of Zoology, University of California, Los Angeles 90024

Abstract. The results of bird censuses from 13 Chilean habitats are presented. Any one habitat supports a slightly higher bird species diversity than structurally similar habitats in North America and Australia. The bird species turnover between habitats in the same locale, in contrast to other temperate areas, is very low—an island characteristic. Turnover between geographically distinct habitats within Chile is comparable to that between adjacent habitats in North America. Chilean birds exhibit wide habitat tolerance in narrow geographic areas, which is attributed to a slow development rate of this bird fauna. Character convergence, where similarities in appearance have evolved to facilitate interspecific aggression and aggregation, is a byproduct of this type of distribution.

Chile has a bird fauna of around 230 breeding land and fresh-water species (Johnson 1965, 1967). This number is within a few per cent of that for the state of California (ca. 235 species), an area comparable in size, latitude and the range of habitats it presents (from wet forests to deserts and from high mountains to the sea coast). However, the distribution of these species within Chile differs from that of other known temperate faunas in several respects: i) Many species occur in a much wider variety of habitats; ii) Particular habitats support rather more diverse bird populations than would be expected from interpolation from investigations in other temperate localities; iii) The occurrence of more than one representative of a genus in a particular habitat is a rare event; most genera in Chile include several species which are strictly allopatric or at most stasipatric in their distributions. Furthermore, species within many of the multispecies genera show an unusual lack of divergence in appearance. Such species seem to present further instances of "social mimicry" or "character convergence" (Moynihan 1968, Cody 1969), where divergence in appearance has been prevented by natural selection in order to facilitate either gregariousness between species in the nonbreeding season, aggressiveness in the breeding season, or both.

METHODS, DATA AND ANALYSIS

During the breeding seasons September–December 1965 and 1968, 13 censuses were made in various localities in Chile (Table 1, Appendix A). The areas selected are homogeneous in vegetation composition and between 3 and 5 hectares in size. The grassland areas 7–11 have previously been reported (Cody 1966, 1968), and more extensive community analysis was conducted in areas 1–3, to be published later.

The methods used to census the bird populations and measure foliage characteristics are identical to those of MacArthur and MacArthur (1961) in North America, MacArthur (1964, 1965), MacArthur, Recher, and Cody (1966) for tropical and island censuses and Recher (1969) in Australia, and thus the results are directly comparable. The calculated variables are information-theoretic measures of bird species diversity, foliage height or habitat diversity, and habitat and bird species turnover between different habitats. The Shannon-Wiener formula $H = -\Sigma p_i \log_e p_i$ is employed, where the p_i are the proportions of the total number of individuals in the census which belong to the species i or the proportions of the total foliage density which lie in various horizontal zones; the summation is carried out over the number of species in the census or the number of layers (3 or 4) into which the foliage profile is arbitrarily divided. The difference between two measures of H, calculated for example for two different censuses, is termed the turnover, and is the difference between H calculated for the two censuses combined and the average of H for the separate censuses: $H(\text{turnover}) = H(\text{combined censuses}) - (H_1 + H_2)/2$. The Chilean bird fauna can be compared to other temperate faunas and to those of islands and the tropics in this way.

In addition to the census work, the distribution and ecology of species within the genera *Muscisaxicola* and *Fulica* received special attention. These genera exemplify interspecific character convergence for purposes of aggression. In addition, mixed species flocks of *Muscisaxicola* and mixed species and genera flocks of *Phrygilus*, *Spinus* and *Diuca* were studied, as the species involved show character convergence for reasons of aggregation. The relevant data are discussed below.

RESULTS AND DISCUSSION

The nonmarine birds of Chile fall into three major categories with respect to their breeding distributions:

[1] Received October 8, 1969; accepted December 16, 1969.

TABLE 1. Chilean study areas with bird and foliage characteristics

Location	°S latitude	Altitude (m)	Habitat	Number of species[a]	BSD[b]	Proportions of vegetation in the layers[c] 0-2	2-20	>20	FHD-[d] 3 layers	FHD-4 layers
1 Melipilla	33.40	135	*Acacia-Prosopis* savannah	21	2.701	0.260	0.740	—	0.573	1.005
2 Puchuncaví	32.45	320	*Lithraea-Quillaja* matorral	24	2.784	0.315	0.685	—	0.623	0.892
3 Pichidangui	32.09	20	*Happlopappus-Bahia* low brush	9	1.755	0.870	0.130	—	0.386	0.386
4 Cerro Ñielol, Temuco	38.42	ca.275	*Nothofagus oblicua N. dombeyi* tall forest	17	2.493	0.085	0.355	0.560	0.902	1.229
5 Lago de Yealma	38.46	ca.915	*Nothofagus antacticus* dwarf forest	11	2.238	0.530	0.470	—	0.691	1.007
6 Lagunillas, Rio Negro	33.39	1650	*Kageneckia* brush	18	2.565	0.725	0.275	—	0.588	0.711
7-11 are described in this order in Table 1 of Cody (1966) and further discussed in Cody (1968, eg. Table 1).										
12 Laguna Verde	33.09	60	introduced *Pinus* forest	12	2.271	0.140	0.750	0.110	0.720	0.870
13 Bosque Fray Jorge	30.45	?300	relict *Aextoxicon Mysceugenia*, *Drimys* forest.	12	2.344	0.110	0.750	0.140	0.734	0.938

[a] Number of genera same in each case.
[b] Bird species diversity.
[c] These foliage height categories are in feet, where 2 ft=0.6 m, 20 ft=6.1 m.
[d] Foliage height, or habitat, diversity.

A—The species is the sole representative of its genus in the country, and the genus is very widely distributed throughout at least South America and often both the New and Old World. Such species occupy the widest variety of habitas in Chile, from grasslands or brush to more or less dense forest, and are also widely distributed with respect to latitude and altitude. In fact the wider the geographic distribution of a genus the wider the variety of habitats in which its representatives are found in Chile (Fig. 1). Examples of these genera are *Troglodytes, Turdus, Zonotrichia, Mimus,* and *Elaenia* (all one species except *Turdus,* with two allopatric species).

B—A second group of genera are typically South American, comprising many tyrannids and furnariids, and are each represented by several species in Chile. The common situation is that each species replaces the others geographically within the genus. These species may be monotypic, but are more often split into several races which are of course also allopatric. The representation of these genera by several species notwithstanding, each species still exhibits a wide habitat tolerance and within its geographic range is encountered ubiquitously. The species within a genus replace each other by habitat to a minor extent, but replacement by latitude or altitude is frequent. Thus one finds a single species present in most habitat types within a broadly limited latitudinal range, and a replacing congeneric species equally habitat tolerant in a different latitudinal area. Examples of this type of distribution are the furnariids *Leptasthenura* (two spp., five sspp.), *Upucerthia* (three spp., five sspp.) and *Asthenes* (five spp., seven sspp.), the tyrannids *Anaeretes* (three spp., four sspp.) and *Agriornis* (four spp., seven sspp.) and the fringillids *Sicalis* and *Spinus* (five spp., five sspp. each).

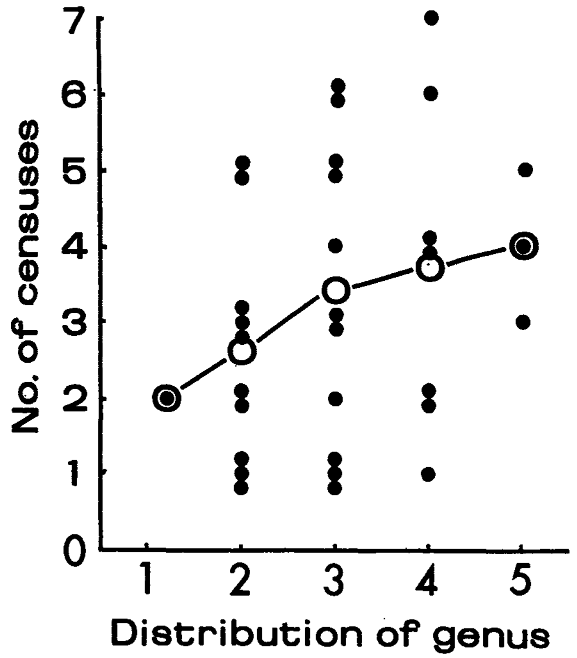

FIG. 1. The geographic distribution of genera is plotted against the number of censuses (out of 13) in which its representatives were recorded in Chile. Distribution classes: 1, Chilean endemic; 2, Chile, Argentina, Bolivia and Peru; 3, South America; 4, North, Central and South America; 5, Old and New World. Correlation coefficient $r = 0.48$; $P(r = 0) < 0.01$.

C—A few genera in Chile are represented by more than one species at the same locality. Among these are the tyrannid *Muscisaxicola* (10 spp., 12 sspp.), the furnariids *Cinclodes* (6 spp., 9 sspp.) and *Geositta* (6 spp., 10 sspp.) and the coot genus *Fulica* (6 spp. and sspp.). Censuses covering a few acres can yield more than one species per genus. The finches *Phrygilus* (9 spp., 11 sspp.) are intermediate between these and *B* above, for only very slight habitat changes separate some of the adjacent forms which marginally overlap. In general habitat changes are more important in determining species turnover within these genera.

Whereas the Australian and North American bird faunas are similar in distributional aspects (Recher 1969), several anomalies appear here: Most species occupy an unusually large range of habitats and most genera are represented by a single species over a wide habitat and geographic range. A quantitative demonstration of this follows.

Within-habitat bird species diversity

Bird species and habitat diversity for 13 Chilean sites are given in Table 1, with complete species listings in Appendix A. MacArthur (1965) shows that these two variables are highly correlated in a wide variety of North American habitats, and recently Recher (1969) has found that southern Australian habitats fall on the same line Bird Species Diversity = 0.75 + 2 × Foliage Height Diversity. However, the Chilean data fall above this line, as is shown in Figure 2.

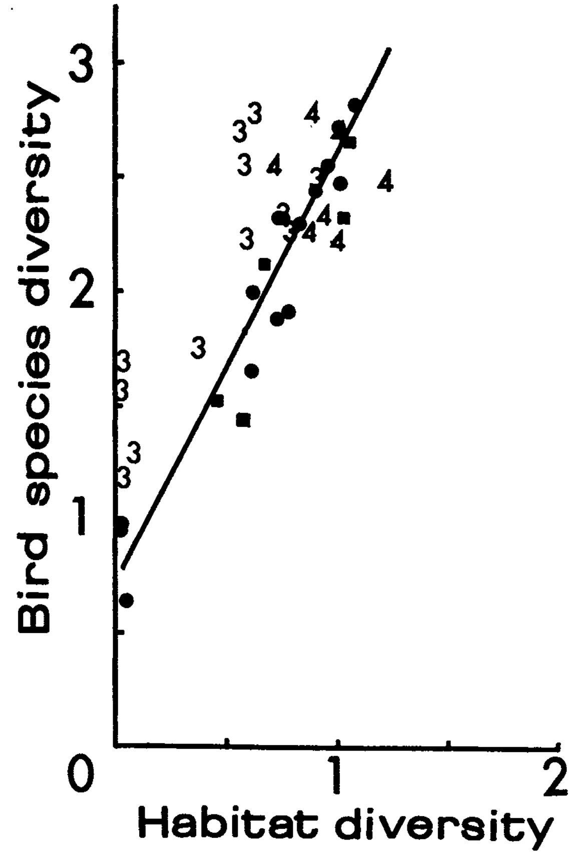

FIG. 2. Bird species diversity versus habitat diversity for 13 Chilean censuses (two of them are superimposed). The regression line and solid circles are taken from the North American data in MacArthur, Recher and Cody (1966), the solid squares are from Recher's (1969) Australian data. The points "3" are plotted from present data using three habitat layers to calculate habitat diversity; the points "4", where these differ from the above, use four habitat layers in the calculation. Thus, there are horizontal pairs "3-4" representing the same data.

Foliage height diversity in Figure 1 and Table 1 is calculated from the proportions of the total foliage area which fall within the horizontal layers 0–0.6, 0.6–7.6 and > 7.6 m above the ground. Tropical censuses conform to the north temperate (and Australian) relation only if the vegetation profiles are subdivided into four rather than three layers 0–0.6, 0.6–7.6, 7.6–15.3 and > 15.3 m (MacArthur, Recher and Cody 1966). The increased habitat diversity figure thereby obtained predicts tropical bird species diversity from the same temperate relation. This adjustment to the Chilean data achieves an improved fit for the more complex habitats, but the "one-layered" grasslands are unaffected. Thus the Chilean areas support a greater within-habitat species diversity, than other temperate areas, particularly in simpler habitats. It is not that the number of species is appreciably or consistently greater, but rather that individuals are more equitably distributed among species (Lloyd and Ghelardi 1964).

Between-habitat species diversity

Differences between pairs of censuses and the habitats in which they are taken can be measured also in terms of information theory. The two variables, "bird species turnover" and "habitat turnover," are closely related in North America, where a particular habitat change accurately predicts the difference in the bird census between the two areas compared (MacArthur et al. 1966). The only areas which are so compared in the above reference are those which differ in latitude by less than 1°, in altitude by less than 305 m and are similar in vegetation type (both are either coniferous, deciduous, scrub, forest, etc.). This relation for the north temperate is included with the Chilean data in Figure 3.

The Chilean censuses depart further from the North American data with respect to bird species turnover than with respect to the diversity data, and are exceptional in an interesting way. Only one pair of habitats, the point 1 (Fig. 3), can be compared under the above restrictions (grasslands are omitted as it has been shown that the height and density of vegetation under 2 feet determines the presence or absence of grassland bird species: Cody 1968). However, if the altitude restriction is relaxed, three comparisons can be made within the same degree of latitude (the points 2–4). Between these pairs of habitats scarcely any turnover in bird species accompanies considerable change in habitat (abscissa) and altitude (1525 m).

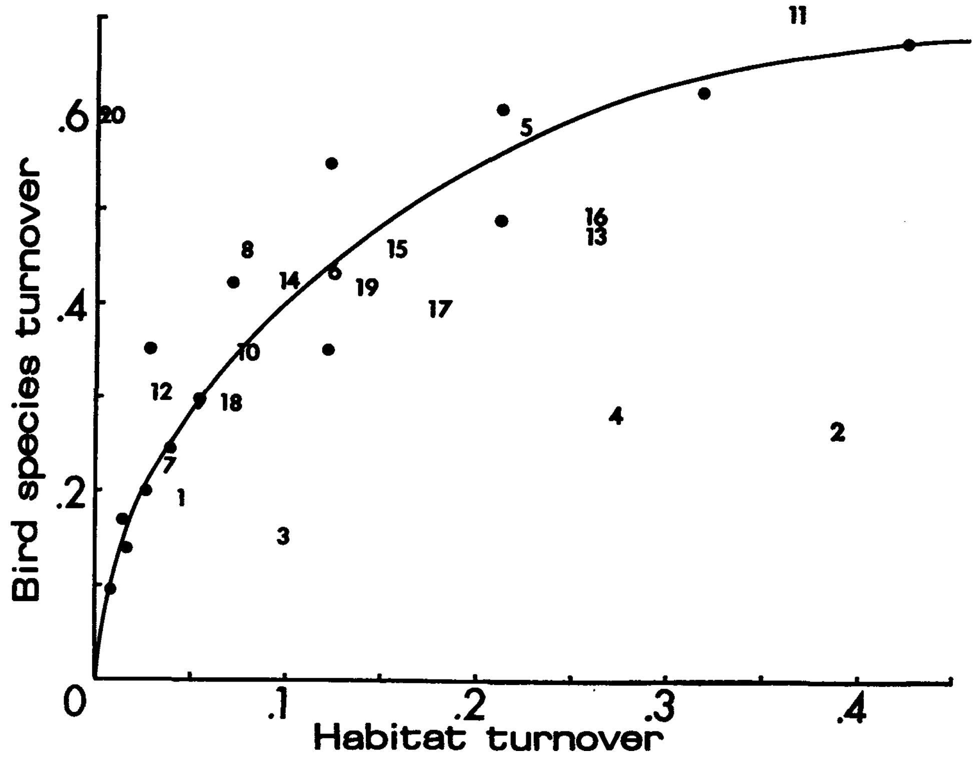

FIG. 3. Bird species turnover is plotted against habitat turnover for various pairs of Chilean censuses. The dots and the regression line are taken from the North American data in MacArthur, Recher and Cody (1966). Each number on the graph represents a pair of censuses numbered in Table 1 as follows: 1 (on graph): 1×2 (in Table); 2: 1×6; 3: 2×6; 4: 4×5; 5: 1×3; 6: 5×13; 7: 1×5; 8: 1×13; 9: 2×5; 10: 2–13; 11: 3×13; 12: 5×6; 13: 6×13; 14: 1×12; 15: 2×12; 16: 3×12; 17: 6×12; 18: 4×12; 19: 5×12; 20: 12×13. Comparisons are grouped as follows: Similar in latitude, altitude and vegetation type, point 1; as above, but different in altitude, points 2–4; dissimilar in latitude but similar in altitude and vegetation type, points 5–6; as the preceding but dissimilar in altitude, points 7–13; dissimilar in vegetation type, points 14–20. See text for discussion.

Such comparisons in the north temperate would lie either on the regression line or, more likely, above it, as by widening the altitudinal range of possible comparisons we increase the chances of boosting turnover due to altitudinal replacement by ecological counterparts.

Now when we compare areas which are very different in latitude the points show a good fit to the North American regression line (the points 5–6, similar in altitude, and the points 7–13, dissimilar in altitude). These sorts of comparisons in the north temperate would almost certainly lie well above those for which the latitude remains constant, for reasons of species replacement with latitude parallel to that with altitude. In Chile, however, the enhanced bird species turnover between these broad latitude comparisons produces only figures of a magnitude to be expected from the north temperate data. This illustrates an earlier point: within a limited geographic area, species are extremely widespread and are found in a wide selection of habitats within this range. Such species are replaced geographically by others, either confamilials or congeners, similarly distributed. Of the nine broad latitude comparisons 5–13, two are between areas of similar altitude and the rest not, but no obvious effect on the goodness of fit by altitude can be detected.

One further set of points is included, the points 14–20. In these the restriction that no coniferous-deciduous comparisons be allowed is dropped. No affect is noticeable in the broad latitude comparisons (18–20), but within those comparisons within a single degree of latitude (14–17) the effect has been to shift their positions up (from points 1–4) to the north temperate regression line. This indicates that Chile has failed (not surprisingly) to develop a bird fauna endemic to coniferous forest (the only comparable native gymnosperms are the high-altitude southern *Araucaria* forests). Only one comparison, that between the very different coastal pines and the relict, mountain-top Bosque Fray Jorge labelled 20 in the figure, lies well above the regression line.

A possible cause of these distribution patterns might now be proposed. Chile has physical characteristics which, despite its continental location, restrict access to possible colonists in the same way oceans restrict access to islands in mainland species. This is particularly true for central Chile, the area from which most of the censuses come. For a species to reach the Mediterranean midlatitudes from outside the country it must either cross the barren deserts to the north, the wet and densely-wooded south, or the eastern cordillera from Argentina, over which the lowest passes are above 3,000 m. Thus, while Chile currently has a sizeable species count by any reasonable comparison, this has probably been achieved slowly over a considerable time period. Chile has extremely few species endemic to the country, presumably due to the unrestricted north-south dispersal possibilities within the central section, with inadequate transverse barriers to provide the isolation requisite for speciation. In this case earlier colonists would spread out over a wide range of vegetation types and classify as "habitat generalists" (see MacArthur and Wilson 1967 for discussion and examples). As later species arrived, the pattern of settlement could go in one of two ways. Either the immigrants displace the residents from certain habitat types by competition, with resulting habitat restriction for all species (increased between-habitat diversity and decreased within-habitat diversity), or the later arrivals follow the example of the earlier ones and also occupy many habitat types.

The question becomes: Why has colonization gone the latter way rather than the former? Any displacement of species which has occurred is from geographic areas rather than from habitat types. This could occur as a result of exceeding the within-habitat diversity which can be supported by food resources, and secondarily to the use of the second type of colonization. It may be that the elimination of a species from a habitat by competitive exclusion is a difficult or uncertain process when the defendant is well entrenched in a broad base of habitats (from which it can reinvade) in high densities (because of the initially low within-habitat diversity). Species which live in many habitat types can often be rated as "food specialists," as these characteristics are complementary (e.g. Cody 1968); only when food resources are similar or with graded intermediates are such food specialists expected to be replaced by habitat-restricted species with generalized food requirements. The best attack on this system by potential colonists seems to be to join them, strategically at least. This process would then become canalized at least to the extent permitted by the supportable within-habitat diversity.

The main features of Chilean bird distribution, for reasons most likely associated with the physically isolated nature of the country, can thus be summarized: Species diversity within habitats is high; species turnover between habitats in the same latitudinal zone is extremely low, but, between habitats latitudinally more distinct, is "normal" compared to other temperate areas. Bird species occupy most habitats in limited areas, and are replaced by others only by major shifts in vegetation type or latitude. Some of these patterns more normally characterize island bird faunas.

Functions of color pattern similarities

The strict allopatry among congeners in their breeding range has comparatively few exceptions, and presumably the high bird species diversity within habitats helps to maintain this. The mechanisms which might operate to prevent overlaps in breeding range at a local site seem causally linked with another interesting generalization about Chilean birds. This is that within many of the genera represented by several species a surprising lack of divergence in appearance is noticed, to the extent that genera with numerous species, such as *Cinclodes, Muscisaxicola, Sicalis* and *Geositta,* initially present problems in field identification. (See color plates in Johnson 1965, 1967.) Selection appears to have maintained a similarity in appearance rarely encountered in, for example, congeners in North America. This can be interpreted as social mimicry (Moynihan 1968) or character convergence (Cody 1969), the maintenance or evolution of similarities to facilitate aggregation or aggression between different species. Both of these aspects are elaborated below. The functions are both subserved simultaneously in the genus *Muscisaxicola,* in which species are interspecifically territorial and form mixed-species flocks in the nonbreeding season. Convergence is noted both among *Phrygilus* species and between certain *Phrygilus* species and members of the genera *Spinus* and *Diuca* which flock together.

Early spring mixed-species flocks

Several species of neotropical seed-eating finches, which are remarkably similar in appearance although in different genera, form mixed species flocks in Panama in the nonbreeding season. Moynihan (1960; 1968) builds a convincing case for interpreting these similarities as a result of selection to facilitate flock formation. The formation of larger flocks (by many rather than a single species) is presumed beneficial on ecological grounds. There is also some indication that the same convergent color patterns in the flock species of *Sporophila, Volatinia* and *Oryzoborus* help to separate them on the breeding territories (N. G. Smith, pers. comm.).

I have observed mixed-species finch flocks in the central valley and in the cordillera in central Chile, but chiefly in the Andean foothills. The situation in three finch genera in particular is worth describing. Four species of *Phrygilus* are involved, with *Diuca diuca* and several *Spinus* species.

The monospecific *Diuca,* perhaps the commonest species over central Chile, breeds in open scrub and savannah areas. Of the four *Phrygilus* species at the latitude of Santiago, *alaudinus* is common in grasslands and breeds up to 1830 m. *P. fruticeti* is common in the lower foothill scrub association, *P. unicolor* breeds high in the Andes on rocky hillsides and *P. gayi* maintains populations on the coast in plantations and in the mountains between medium altitudes. *Diuca* and the first three *Phrygilus* species share common color characteristics in that all are grey or grey-black and white, with specific differences in the amounts and distribution of the colors. In October flocks involving up to three of these four species were commonly observed in the Rio Maipo system, in which any of the four were well represented. These aggregations were not attractive to *gayi,* for only 7 of nearly 600 individuals in the flocks were of this species. In fact *P. gayi,* which is very different in coloration, being bright yellow over its posterior half with a slate grey anterior hood, frequently formed single species flocks in close proximation to *Diuca* and the other flocking *Phrygilus* species. The only mixed-species flocks in which *P. gayi* was commonly found were those also involving *Spinus barbatus* and *S. uropygialis.* These siskins, the former a lowland and the latter a montaine species, have, in striking agreement with *gayi,* a generally yellow body color contrasting with a dark head or hood (black rather than grey in the siskins). Other *Phrygilus* species were never found in the *Spinus-P. gayi* flocks. Thus the color patterns of *Phrygilus* divide the genus into those species which look like and flock with *Diuca* (all grey, black and white), and a single species which is similar to, and flocks with, *Spinus* species (all yellow, and grey or black). Besides being associated by color pattern, the species within each group are linked by similar habitat requirements. The next question is, obviously, what are the advantages of multi-species flocks such that (by hypothesis) even coloration is influenced? This question will be treated in a later paper.

Six species of *Muscisaxicola* occur in the Andes in the vicinity of Santiago. These form an altitudinally replacing series as discussed below. There are size differences among the species (the largest is 36% larger than the smallest), but all are alike in having uniformly colored bodies of greyish-buff. With practice, body coloration can be seen to differ between some species, but only slightly; some species are decidedly greyer, others more brownish. Most species differ in head, or more strictly, cap coloration (see color plate in Johnson 1967), the only useful field mark, but the group as a whole exhibits an unusual lack of divergence in appearance. All are virtually identical in ecology and behavior, being close to the north temperate *Oenanthe* species in these respects. At this latitude all species (*alpina, frontalis, rufivertex, flavinucha, albilora* and *maculirostris*) migrate north to a greater or lesser extent for the southern winter, but in the prebreeding weeks form mixed-species flocks in the foothills. I have observed in the latter half of October, flocks comprised of up to four species (excluding the first two species in the list above, which have the highest breeding ranges: Fig. 4) and up to several score individuals. Later, when species were distributed on their breeding grounds, a late snowstorm forced individuals above 1,830 m back down the mountains, and the individuals of four species (the second and the last three in the list) segregated in a field in the Rio Negro valley at 1,325 m by defending small mobile feeding territories about 3 m across (cf. Stresemann 1950 for *Oenanthe*). These were defended against all other individuals, regardless of species.

Breeding distribution in Muscisaxicola

Muscisaxicola is the most prominent example of the few genera of Chilean birds in which more than one congeneric species can be found breeding in the same few acres. The six species which breed at midlatitudes have limited altitudinal distribution as shown in Figure 4. The figure incorporates information I gathered in the field with that from Johnson (1967 and pers. comm.). My own observations were made at Farallones and on the Rio Maipo and its tributaries (Rios Negro, Colorado, Yeso and El Volcan).

The breeding system of this genus is one of vigorously-defended nonoverlapping territories. All species, with the partial exception of *maculirostris,* which enters open scrub habitat at the lower end of its altitudinal range, are open-country birds which hawk for flies and pounce on moving insects which are spotted from elevated perches on rocks several inches off the ground. This habitat changes little if at all with altitude. The most extensive observations I made on feeding and

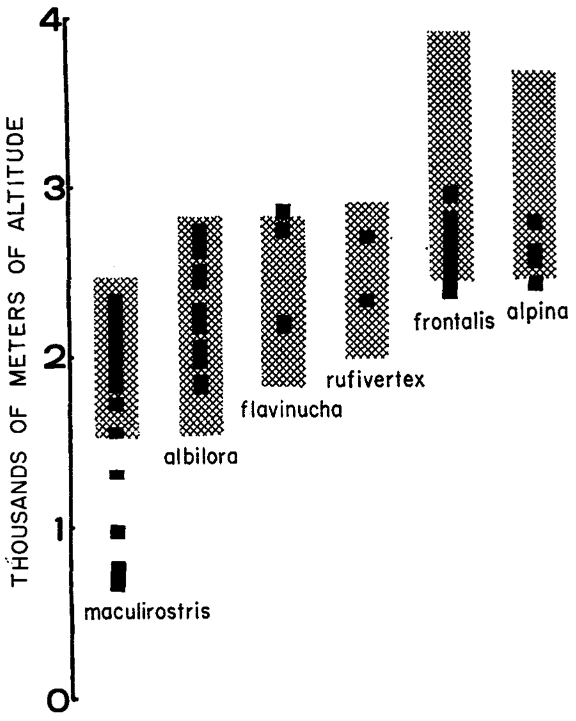

FIG. 4. The altitudinal distribution of the genus *Muscisaxicola,* with six species at the latitude of Santiago. Solid bars, my own records; shaded bars, records from Johnson 1967 and pers. comm. Records for the breeding season only.

territorial behavior were in the Cajon del Yeso at 2,575 m and 2,750 m during breeding in the first half of December and immediately prior to breeding at the end of October in the Rio Negro valley at 1,325 m.

At 2,575 m in the Yeso, five pairs of *albilora,* two of *frontalis* and one of *alpina* occupied about 14 hectares of flat valley floor. During many hours over several days the territory of each pair was plotted and found to be limited in each to a precise area a few acres in extent. These territories were entirely mutually exclusive both within and between species, for at no time was an individual of a pair found feeding where individuals of other pairs fed. No aggressive reinforcement of these apparent boundaries was observed here. At 2,750 m further up the same valley five pairs of *Muscisaxicola* used the same 24 hectares of valley floor: two pairs of *flavinucha,* one of *frontalis,* one of *albilora* and one of *alpina.* The parts of their territories within this area were plotted, and again found to be mutually exclusive. Aggressive encounters were observed between *frontalis-albilora, flavinucha-alpina* and *albilora-alpina,* with the smaller bird giving way in each case at territory boundaries. All pairs were feeding young in the nest. In parts of the Rio Negro valley between 1,525 m and 2,135 m the *maculirostris* and *albilora* populations defended contiguous territories, and aggressive encounters between neighbors in both species were frequently observed; the presence of a neighboring individual of whatever species at a territory boundary would provoke a territory owner to attack. From these observations it seems that interspecific territoriality is the rule among *Muscisaxicola* species. Thus the second interpretation of the lack of divergence in appearance, that similarities have been maintained to promote interspecific aggression in the breeding season (Cody 1969) is justified. That the same color patterns function to promote mixed-species flocking out of the breeding season illustrates Moynihan's (1968) interpretation of such similarities.

As no mixed species pairs were observed and no hybrids have been reported, interbreeding must be prevented by the cap or head markings, which show all the signs of species-specific recognition cues. (All species lack songs or distinct call notes.) The species *maculirostris* and *alpina* do not show cap or head markings, and are the only two species whose altitudinal ranges were found not to overlap; *frontalis* has a black and white head pattern, *flavinucha* a lemon yellow cap and both *rufivertex* and *albilora* have reddish-brown caps. The only species with a distinct white eyestripe, however, is *albiflora.*

No differences in habitat selection could be observed between species in the zones of overlap. Territory sizes seem to be proportional to body size (although this cannot be documented with the available data), and the larger birds dominate interspecific encounters. All *Muscisaxicola* species have a generally similar feeding behavior, flycatching, as already described. This behavior can be measured quantitatively (after Cody 1968), and is to some extent size-dependent. Table 2 shows that the average speed of the bird whilst feeding and the per cent of movements that are flights (rather than walks) increase, as the size of the bird decreases. The similarities between species are far greater than those found in coexisting grassland birds (Cody 1968). Thus the species are, a priori, excellent candidates for interspecific territoriality.

Two other series of altitudinally replacing bird species were observed, but less extensively. *Sicalis luteola* of the central valley and lower foothills is replaced at medium and high altitudes by *S. auriventris.* The ranges of the two were not found to overlap along the Rio Maipo, but no interactions between them were recorded. They are the same size and are very similar in appearance. *Geositta* is represented by three species in the Maipo valley; all are a uniform brown color

TABLE 2. Size and feeding behavior of the six *Muscisaxicola* species resident in the Rio Maipo valley, central Chile

Species	Total length (cm)	Bill length (cm)	Bill depth / Bill length	Avg. speed (cm/sec)	Per cent flights
frontalis	20.5	1.90	0.26	17	0%
flavinucha	20	1.89	0.27	10	0%
albilora	18	1.67	0.26	22	14%
rufivertex	17	1.65	0.26	20	35%
alpina	17	1.45	0.35	26	50%
maculirostris	15	1.33	0.29	65	34%

TABLE 3. Pond zonation and feeding methods of *Fulica* species

Species	Total length (cm)	Number and percentages of feeding individuals in				Per cent of individuals feeding		
		vegetation and banks	weed beds + 2m	2m-30m	30m-lake center	on surface	by ducking	by diving (average duration)
Rufifrons	48	30(32%)	59(63%)	5(5%)	0(0%)	78%	11%	11%(1.5 sec)
Leucoptera	45	9(20%)	18(41%)	7(16%)	10(23%)	33%	34%	33%(1.5 sec)
Armillata	55	3(1%)	34(10%)	133(38%)	180(51%)	13%	50%	37%(5.2 sec)

more or less barred with rufous on the wings. The lowest species, *cunicularia,* was found up to 1,220 m, and presumably did not overlap with the medium altitude *rufipennis,* which was recorded down to 1,675 m. However *rufipennis* and the higher *isabellina* co-occur extensively in the Cajon del Yeso, where their territories overlap. No interactions were observed between them and they fed almost side by side. The size difference between the two is slight (1:1.07) and less than that between most coexisting congeners of similar behavior. To which ecological factors their coexistence is owing is not known.

The distribution of Fulica

The similarities in coloration among South American coots, genus *Fulica* (Rallidae), was suggested as an example of social mimicry by Moynihan (1968). Three coot species occur in central Chile, *Fulica armillata, F. rufifrons* and *F. leucoptera.* The three species are very similar in appearance; while there are size differences (Table 3), these are of no use in the field identification of lone individuals. All species are uniformly black bodied, and differ only in the color of their bills and frontal shields, which are yellow-and-red, red, and yellow respectively (color plate in Johnson 1965).

Twenty-six fresh water bodies were surveyed for coots in central Chile, including all of those around Santiago. Small weedy ponds supported only *Ortygonax* and *Porphyriops* (both Rallidae). *F. rufifrons* alone occurred on the rivers visited and on the lakes with little open water and thick reed beds. The open lakes (chiefly reservoirs) of the lowlands support only *armillata,* while on those of higher altitudes, according to Johnson (1965), only *leucoptera* are found. These habitat differences are fairly clear-cut; however, most of the permanent natural lakes of this part of Chile are the coastal dune-locked lagoons, which vary in size from small ponds to lakes of several dozen acres (2.5 acres ≃ 1 ha), and are bordered with reed beds. These lagoons support a rich avifauna, including swans, many ducks, four grebe species and all three *Fulica* species.

I focused considerable attention on these lagoons. The numbers of coots on them reach extraordinary levels—as many as 2,000 individuals on a 4-hectare lake near Cartagena. The distribution of each species on such waters is far from random. Table 3 shows that *rufifrons* is commonest around the edge and absent from the center away from the weed beds, while *armillata* is commonest in the center of the lake in the deeper open water (parallel to their habitat preferences where they occur alone). *Leucoptera* is intermediate in this respect. All species, however, eat the same water plants, and correspondingly the outer species can obtain these from the surface whereas the inner species must duck and dive for the same items (Table 3).

These coots are semisocial, and will tolerate the presence of other feeding individuals within a radius of about 1 meter. When individuals find themselves closer than this, brief but spectacular scuffles take place and a tolerable spacing is regained. Several of these interactions would be taking place at any one time on the Cartagena lake. Such scuffles were observed not only within species but also between species in every combination, and thus the coots behave as a single species with regard to the spacing of individuals. As there are no apparent food differences between them, the maintenance of the spacing is obviously as important among as within species, and could explain the retention of the similarities in appearance. The specific differences in the frontal shield coloration would presumably function in mating behavior to prevent hybridization.

SUMMARY

Thirteen censuses of bird populations and their habitats were made in Chile during the 1965 and 1968 breeding seasons. Within-habitat bird species diversity is rather greater than that in the other temperate areas which have been studied, North America and Australia. However, the turnover of bird species between habitats in a limited geographic area is much lower. When habitats of greater latitudinal separation within Chile are compared, the turnover is that expected from other temperate data. Thus most Chilean bird species occupy limited geographic ranges within which they utilize a greater variety of habitat types than their north temperate counterparts. It is hypothesized that these distributional patterns are due to the physical characteristics of the country, which have limited access to potential colonists from other parts of South America, and allowed a slow development of the current bird fauna. An initial low within-habitat diversity permitted habitat expansion in the early residents, which, together with later colonists, could not be displaced by competition by succeeding immigrants.

Of the few genera of birds which are not monotypic in their representation in Chile, the species show a striking lack of divergence in appearance. This phenomenon has recently been described as "social mimicry" or "character convergence," in which similarities in appearance are maintained by natural selection to facilitate interspecific aggression or aggregation. The genera *Phrygilus, Diuca* and *Spinus* take part in mixed-species flocks, as do the species of *Muscisaxicola.* The species in the genera *Muscisaxicola,* which are territorial, and *Fulica,* which are not, maintain spacing patterns in the breeding season in which individuals or pairs interact both intraspecifically and interspecifically without regard to species identity, and in a sense the whole genus behaves ecologically as a single species. Species-specific recognition clues are retained in the color patterns and presumably function to prevent hybridization.

ACKNOWLEDGMENTS

This work was financially supported by the National Science Foundation (GB-6150) and the University of California–University of Chile Exchange Program (Ford Foundation). F. DiCastri of the University of Chile helped in many ways, and Marianno Pisarro and Braulio Araya provided invaluable assistance on the field trips. I express my gratitude to these people and sources.

LITERATURE CITED

Cody, M. L. 1966. The consistency of intra- and intercontinental grassland bird species counts. Amer. Naturalist **100**: 371–76.

———. 1968. On the methods of resource division in grassland bird communities. Amer. Naturalist **102**: 107–147.

———. 1969. Convergent characteristics in sympatric populations: A possible relation to interspecific territoriality. Condor **71**: 222–239.

Johnson, A. W. 1965. The birds of Chile. vol. I. Buenos Aires: Platt Establecimientos Gráficos S.A.

———. 1967. The birds of Chile. vol. II. Buenos Aires: Platt Establecimientos Gráficos S.A.

Lloyd, M., and R. J. Ghelardi. 1964. A table for calculating the equitability component of species diversity. J. Animal Ecol. **33**: 217–226.

MacArthur, R. H. 1964. Environmental factors affecting bird species diversity. Amer. Naturalist **98**: 387–397.

———. 1965. Patterns of species diversity. Biol. Rev. **40**: 510–533.

MacArthur, R. H., and J. MacArthur. 1961. On bird species diversity. Ecology **42**: 594–598.

MacArthur, R. H., H. Recher, and M. L. Cody. 1966. On the relation between habitat selection and bird species diversity. Amer. Naturalist **100**: 319–332.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Monogr. Pop. Biol. No. 1, Princeton University Press, New Jersey.

Moynihan, M. 1960. Some adaptations which help to promote gregariousness. Proc. 12th Int. Ornith. Congr., Helsinki 1958: 523–541.

———. 1968. Social mimicry; Character convergence versus character displacement. Evolution **22**: 315–331.

Recher, H. 1969. Bird species diversity and habitat diversity in Australia and North America. Amer. Naturalist **103**: 75–79.

Stresemann, E. 1950. Interspecific competition in chats. Ibis **92**: 148.

APPENDIX

List of bird species found in 13 census areas in central and southern Chile. Areas are numbered as in Table 1. Nomenclature follows Johnson (1965, 1967). Entries are the number of pairs observed, ++ = low density.

	Census areas												
Species	1	2	3	4	5	6	7	8	9	10	11	12	13
Pterocnemia pennata	—	—	—	—	—	—	—	++	—	—	++	—	—
Nothoprocta perdicaria	—	0.2	—	—	—	0.25	—	—	—	—	—	—	—
Theristicus caudatus	—	—	—	—	—	—	—	—	—	—	++	—	—
Vultur gryphus	—	—	—	—	—	—	++	—	—	—	++	—	—
Cathartes aura	++	++	++	—	—	—	—	—	—	—	—	—	—
Coragyps atratus	—	—	—	1.5	—	—	—	—	—	—	—	—	—
Buteo fuscescens	—	—	—	—	—	++	++	—	—	—	—	—	++
Buteo polysoma	—	—	—	—	—	—	—	—	—	++	—	—	—
Parabuteo unicinctus	—	++	—	—	—	—	—	—	++	—	—	—	—
Elanus leucurus	—	—	—	—	—	—	—	—	++	++	—	—	—
Milvago chimango	0.5	++	0.5	1	—	0.5	—	—	++	++	—	—	—
Caracara plancus	—	—	—	—	—	—	—	++	—	—	++	—	—
Falco peregrinus	—	—	++	—	—	—	—	—	—	—	++	—	—
Lophortyx californica	2	1	—	—	—	1	—	—	—	—	—	3	2
Belanopterus chilensis	—	—	—	—	—	—	1	—	0.5	1.5	1	—	—
Oreopholus ruficollis	—	—	—	—	—	—	—	0.5	—	—	—	—	—
Zonibyx modestus	—	—	—	—	—	—	—	1.5	—	—	—	—	—
Gallinago magellanicus	—	—	—	—	—	—	1	—	—	—	—	—	—
Attagis gayi	—	—	—	—	—	—	1	—	—	—	—	—	—
Thinocorus dorbignyanus	—	—	—	—	—	—	—	1	—	—	0.3	—	—
Columba araucana	—	—	—	1	—	—	—	—	—	—	—	—	—
Zenaidura auriculata	3.5	1.5	—	—	—	—	—	—	—	—	—	—	—
Metriopelia melanoptera	—	—	—	—	—	1.5	—	—	—	—	—	—	—
Microsittace ferruginea	—	—	—	1	—	—	—	—	—	—	—	—	—
Bubo virginianus	—	—	—	++	—	—	—	—	—	—	—	++	—
Caprimulgus longirostris	—	0.3	—	—	—	—	—	—	—	—	—	—	—
Sephanoides sephanoides	—	—	—	2	1	—	—	—	—	—	—	1	—
Patagona gigas	—	2	—	—	—	—	—	—	—	—	—	—	2
Dendrocopus lignarius	1.5	—	—	—	1	—	—	—	—	—	—	—	3
Colaptes pitius	0.5	—	—	0.5	—	1	—	—	—	—	—	1	—
Geositta cunicularia	—	—	—	—	—	—	—	—	3	—	—	—	—
Geositta rufipennis	—	—	—	—	—	—	4	—	—	—	—	—	—
Chilia melanura	—	—	—	—	—	1	3	—	—	—	—	—	—
Sylviornithorhynchus desmurii	—	—	—	2	—	—	—	—	—	—	—	6	—
Aphrastura spinicauda	—	—	—	7.5	—	—	—	—	—	—	—	3	5
Leptasthenura aegithaloides	3	1	—	—	—	—	—	—	—	—	—	—	1
Asthenes humicola	2.5	1.5	—	—	—	3	—	—	—	—	—	—	—
Pygarrhichas albogularis	—	—	—	1	—	—	—	—	—	—	—	—	—
Pteroptochos megapodius	—	1	—	—	—	0.75	—	—	—	—	—	—	—
Pteroptochos tarnii	—	—	—	2	—	—	—	—	—	—	—	—	—
Scelorchilus albicollis	—	—	—	—	—	—	—	—	—	—	—	—	1
Scytalopus magellanicus	2	—	—	2	1	—	—	—	—	—	—	3	—
Agriornis livida	0.75	0.5	1	—	—	—	—	—	—	—	—	—	—
Neoxolmis rufiventris	—	—	—	—	—	—	—	8	—	—	—	—	—
Muscisaxicola alblora	—	—	—	—	—	—	4	—	—	—	—	—	—
Lessonia rufa	—	—	—	—	—	—	—	6	—	—	4.5	—	—
Pyrope pyrope	0.75	1.25	—	—	2	2	—	—	—	—	—	1	—
Elaenia albiceps	1	1.5	—	9.5	4	1	—	—	—	—	—	—	6
Anaeretes parulus	4	5	—	3	—	3	—	—	—	—	—	1	1
Phytotoma rara	—	1.5	—	—	—	—	—	—	—	—	—	—	—
Tachycineta leucopyga	—	2	—	—	—	—	—	—	—	—	—	—	3
Notiochelidon cyanoleuca	—	—	1	—	—	—	—	—	—	—	—	—	—
Troglodytes aedon	1	3	—	3	3	6	—	—	—	—	—	—	—
Mimus tenca	2	2	2	—	—	2	—	—	—	—	—	—	—
Turdus falklandii	—	1.5	—	2	2	—	—	—	—	—	—	—	2
Anthus correndera	—	—	—	—	—	—	—	8	—	5	8	—	—
Curaeus curaeus	4	1	—	5	2	2	—	—	—	—	—	—	—
Pezites militaris	3	—	3	—	—	—	—	—	2	2.5	2.5	—	—
Spinus barbatus	—	0.5	—	4.5	2	—	—	—	—	—	—	1	—
Sicalis luteola	0.5	—	—	—	—	—	—	—	—	13	—	—	—
Diuca diuca	5	1.5	4	—	1	2	—	—	—	—	—	—	—
Phrygilus gayi	—	—	—	—	—	4	—	—	—	—	—	4	3
Phrygilus alaudinus	0.5	—	5	—	—	—	—	—	4	—	—	—	—
Zonotrichia capensis	7.5	3.75	—	—	5	3	—	3	1	—	—	2	—
Totals	45.5	33.5	16.5	48.5	24	34	14	28	10.5	22	16.3	26	29