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THE ROLE OF COMPETITION IN THE DISTRIBUTION OF ANDEAN BIRDS¹

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Abstract. The object of our study was to compare the distributions of bird species common to two Andean localities in order to improve our understanding of the factors involved as primary causes in imposing distributional limits. A previous paper (Terborgh 1971) had evaluated the importance of three mechanisms in the avifauna of a control locality: (1) factors that vary continuously and in parallel with the elevational gradient, (2) competitive exclusion, and (3) ecotones. As was discussed in that paper, the method, when applied to a single transect, leads to a systematic underestimation of the incidence of competition-mediated limits and to an overestimation of ecotone effects. By studying appropriately selected test localities, we could overcome many of these deficiencies and obtain results that are several steps closer to expressing reality.

The control locality, the Cordillera Vilcabamba, is a sector of the Cordillera Oriental, or eastern chain of the main body of the Peruvian Andes. It carries what may be regarded as a complete avifauna, as the transect sliced through a continuous belt of forested terrain which, at any elevation, is exposed to invasion by appropriately adapted species from above and below as well as laterally. It differs in this respect from the test locality (Cerros del Sira), which is an isolated massif that rises out of the Amazonian plain some 100 km east of the main Andes. Because of this isolation, the upper portions of the Sira are exposed to invasion principally from below.

An estimated 80%-82% of the species that would have occupied the summit zone of the Sira, had it been a portion of the main body of the Andes, were missing. Such a species deficit provides an ideal test of the efficacy of competition in limiting distributions, because it invites whatever species are available as colonists (in this case, those lower on the mountain) to invade until the community is effectively filled. Of the species that had the opportunity to expand their elevational ranges in the absence of high-elevation congeners that apparently excluded them on the control transect, a minimum of 71% did so, confirming the original assignments of these as competition-limited species in the control locality. In addition, a majority (58%) of the species that had no high-elevation congener on the control transect (assigned to the gradient mechanism), and that had the opportunity to expand into the species-deficit zone of the Sira, were found to do so. This reveals that diffuse competition (as distinguished from the directly observable exclusion of congeners) was really the primary limiting mechanism for most of the species that had been assigned to the gradient mechanism in the control study. Instead of accounting for approximately a third of all distributional limits, as was concluded in the earlier report, it now appears that competition, both direct and diffuse, accounts for something more than two-thirds of the distributional limits of Andean birds whose ranges end somewhere between the lowland plain and tree line.

Key words: *Andes; birds; competition; competitive exclusion; elevational distribution; Peru.*

INTRODUCTION

In a recent article in this journal we described a method for evaluating distributional mechanisms and applied it to the elevational ranges of 261 bird species found on a transect of the eastern slope of the Peruvian Andes (Terborgh 1971). We recognized four types of distributional limits, (1) those that coincided with a natural terminus of the environmental gradient (lowland plain or timberline), (2) those

that appeared to be determined by factors in the physical or biological environment that vary continuously and in parallel with the gradient, (3) those established by competitive exclusion interactions between congeners, and (4) those that coincided with a vegetational ecotone. Little can be said about limits of the first type because these are imposed at arbitrary elevations by local topographic and vegetational conditions. The latter three categories, however, represent plausible biological responses, each of which implies a unique distributional pattern. Many of the features of these patterns relate

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to the statistical behavior of whole communities and thus are discernible only when a collection of species is controlled by the same limiting mechanism. Where several mechanisms are operating simultaneously, as in the Andean avifauna, the statistical approach is of limited value. Alternatively, one may examine the distributions of individual species. This tactic proves more rewarding though it also presents severe difficulties because each species provides only a few clues, which frequently are inadequate to rule out conflicting interpretations. The paucity of available information made it necessary in practice to use very simple criteria in classifying the upper and lower limits of each species.

Congeners having abutting but nonoverlapping distributions were assigned to the competition mechanism. This is a conservative approach, which, for lack of consistently applicable criteria, deliberately neglects competitive exclusion by species placed in different genera and diffuse competition. This was explicitly recognized in the first paper as a methodological weakness. Limits that lay within 20, or sometimes 50 vertical meters of a vegetational discontinuity were assigned to the ecotone mechanism. Here it was acknowledged that some limits would fall near ecotones fortuitously and thus be incorrectly classified. Remaining limits were assigned by default to the gradient category, which, used in this catchall fashion, permitted all distributional limits to be accommodated in the classification.

The inherent frailties of the method, as applied to distributions on a single transect, result in a systematic overestimation of the importance of ecotones and variables associated with the gradient, and a serious underestimation of the importance of competitive interactions. In order to overcome these deficiencies we have investigated several additional localities with two purposes in mind. First, using the original study as a control, we sought to examine the competition mechanism by observing the behavior of some of the same species when exposed to a strong negative diversity gradient to see whether, in response to missing congeners and reduced diffuse competition, they would be induced to expand their ranges. This is primarily the work we shall describe here. Second, to examine the effect of ecotones, we conducted surveys of three Andean localities in which one or more of the vegetational zones was displaced far upwards or downwards in relation to its position on the control transect. Some of the distributional complications that result from displaced ecotones are dealt with in the present report.

GROUND RULES

The ecological literature is charged with controversy over the subject of competition, regarding both

definitions and the proper means of measuring its effects in natural communities. In order to avoid confusion over any of these issues, we shall at the outset define competition by strictly operational criteria in the circumscribed context of the regulation of distributions on environmental gradients. We begin by distinguishing two types of competition: direct and diffuse.

Direct competition is suggested when two closely related species (usually congeners) exhibit sharply abutting ranges, the presumption being that each excludes the other from all or part of its portion of the gradient (Brown 1971, Cody 1974). Competition is demonstrated by testing the presumption and finding the expected result (Diamond 1970, 1973). Specifically, an otherwise similar locality is surveyed in which one of the abutting species is missing. If the species present has conspicuously expanded into the domain of its missing congener we regard the presumption as upheld.

Diffuse competition is demonstrated in an analogous manner, but now the distributional limit is imposed by one to several competitors that usually remain anonymous for lack of any clear distributional or phylogenetic indicators. An adequate test requires more exceptional conditions than are sufficient to reveal direct competition, since the expansion must be observed in a place where a negative diversity gradient is established by the absence of a whole constellation of species. Appropriate range extensions under such circumstances constitute *prima facie* evidence for the operation of diffuse competition as the primary distribution limiting mechanism in the first, or control, locality.

THE LOCALITIES

For our control we used the data gathered in connection with the previous paper (Terborgh 1971). The locality was the Cordillera Vilcabamba, a major section of the eastern Andes in central Peru. Our knowledge of the distribution of birds in this range comes from extensive netting, collecting, and sight and sound records along a continuous transect covering the elevational span of 340–3,540 m. In total, the survey included some 13 party-months of field time spread over six expeditions in 1965–72. Each return to the transect added to our knowledge of the elevational limits of some species, although the last expedition contributed only two previously unrecorded species and a small number of minor range extensions. We feel that this survey has been thorough and accurate and that further work would yield only diminishing returns.

The control locality is distinguished biogeographically, (1) by being a part of a nearly continuous mountain forest that stretches from Venezuela to

TABLE 1. Parameters of bird samples netted in the Cerros del Sira, Peru

Parameter	Vegetation type								
	Lowland rainforest			Montane rainforest		Cloud forest		Elfin forest	
Elevation (m)	260	280	690	900	1,130	1,310	1,570	1,970	2,220
No. nets	24	30	36	36	34	26	23	18	18
No. individuals captured:									
1969		231		301		477	285	165	269
1971	141		264	147	229				
1973	97		219						
No. species captured ^a	57	58	81	70	54	85	62	40	52
Population density (birds/net) ^b	6.6	8.6	13.9	4.6	8.0	11.8	14.2	11.2	14.2
Species diversity (equally common spp.) ^c	27.7	27.3	30.1	28.9	24.2	30.0	26.0	21.2	17.6
Equitability ^d	0.81	0.72	0.79	0.72	0.71	0.77	0.70	0.71	0.61

^a Cumulative species total for all samples taken at a locality.

^b Computed from the first sample taken at a locality as $[N/n]/[1 - (C_F/C_0)]$ where N = the number of different individuals captured, n = the number of nets used, C_F = the final capture rate and C_0 = the initial capture rate (in birds per net-day). C_F and C_0 are taken from the log-linear regression of capture rate vs. accumulated net-days of trapping. Further details on this method in Terborgh and Faaborg (1973).

^c Diversity is given as the number of equally common species in the sample, computed from the first 100 individuals captured as e^H where $H = -\sum p_i \ln p_i$.

^d Computed as e^H/S_{100} , where S_{100} is the number of species contained in the first 100 individuals captured.

Bolivia; (2) by including the full spectrum of vegetation types from lowland rain forest to alpine grassland; (3) by having a large, tightly packed avifauna (more than 500 species of land birds); and (4) by being accessible to invasion at all elevations. A critical examination of the competition mechanism required, in contrast, a not too distant test locality which was cut off from invasion except from below and which possessed, consequently, a pronounced island effect near the top. After consulting topographic maps of the Andean region, we selected a locality that seemed to have the requisite properties, at least with respect to its geography. It is an anomalous outlier of the Andes called the Cerros del Sira. Both the name and maximum elevation are erroneously recorded on many maps. The center of this singularly isolated Andean satellite lies at approximately 9° 30' S and 74° 40' W between the Pachitea and Ucayali rivers, some 360 km NNW of the control locality and 100 km to the east of the main Andes across a broad expanse of lowlands. The highest points are 20–30 km from the nearest approaches of either river, and because of this remoteness the range was biologically unexplored. The backbone of the Sira is a steep, narrow ridge having roughly a NW–SE orientation. Several collateral ridges radiate outwards in various directions, the longest of which extends towards the northeast. These ridges are deeply and irregularly dissected by numerous steep-walled ravines, a feature that makes a judicious choice of route essential to reaching the principal crest.

The Sira includes three widely separated groups of peaks that rise above 1,500 m: a central cluster of four which comprise the highest elevations, and two others lying in opposite directions, one near Puerto Inca on the Rio Pachitea and the other near Iparia on the Ucayali. Only the central peaks and portions of the ridges connecting them are above 2,000 m. Our highest camp was at 2,220 m on the westernmost of the four central peaks. The other three peaks lie close together several kilometers to the southeast across a long knife edge ridge. Limitations of time and the difficulty of cutting a trail so far through dense elfin forest prevented us from reaching the highest point, whose elevation we estimated to be 2,400–2,500 m. The highest peaks and ridges are so steep sided that the total extension of habitat lying above 2,000 m could not be more than 3–4 km². Below the summit, the amount of living space within successively lower 500-m contours expands rapidly by some power higher than 2. Unfortunately, a lack of even crude contour maps of the area precludes a quantitative estimate of the relation between area and elevation.

In investigating the Sira we used essentially the same methods as on the control transect, except that a shortage of time prevented us from acquiring an equally detailed knowledge of distributional limits. Instead of attempting to locate the extreme limits of occurrence of each species by covering the whole transect as we did in the Vilcabamba, we relied on intensive work in the vicinity of nine camps. Thus we have a series of point censuses to compare with

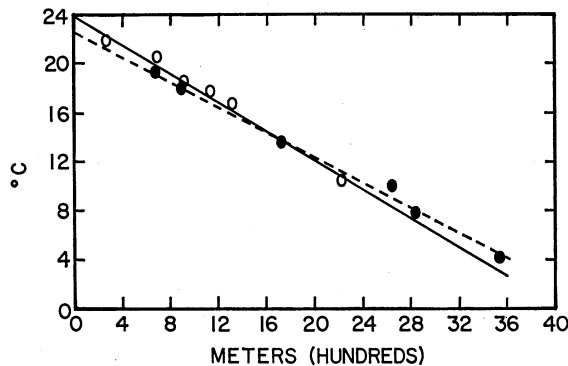


FIG. 1. Regressions of dawn temperature vs. elevation for the control (Cordillera Vilcabamba; dashed line, solid dots) and test (Cerro del Sira; continuous line, open dots) transects. The two lines are not significantly different.

the continuous distributional information available from Vilcabamba, a fact that introduces certain interpretive difficulties to which we shall return later. The faunal surveys at each camp consisted of extensive netting, collecting (especially of montane species and individuals whose identifications were in doubt), and daily observations, these mainly conducted along the net lines. A summary of the netting results is given in Table 1. Altogether we recorded the presence of over 400 species of land birds, of which 146 can be considered montane in that they are absent from the surrounding lowlands. Of these, only 24 (16%) are lacking in the Vilcabamba. Thus, the overall species composition in the two localities is quite similar.

A feature of the Sira which considerably complicates our analysis of competitive interactions is the marked displacement of vegetational zones with respect to the analogous zones in the Vilcabamba. Both the cloud forest and elfin forest ecotones are depressed to lower elevations, 1,050 and 1,800 m, respectively, as contrasted with 1,380 and 2,600 m on the control transect. On the other hand, montane rain forest was first entered at a somewhat higher elevation on our Sira route (750 m as opposed to 600 m on the control transect) because of the more gradually inclined lower slopes. The 300-m depression of the cloud forest boundary preserves a nearly constant difference above the bases from which the two ranges rise (Myers 1969). In contrast, the far greater lowering (by 800 m) of the Sira elfin forest zone seems related to the much increased exposure of the relevant elevations and represents a typical case of Massenerhebung (Grubb 1971, Howard 1968). As a consequence of these uncontrolled differences between the control and the test localities we must be concerned with the re-

ciprocal interactions of competitive release and ecotone displacement.

With respect to climatic variables, the two gradients are satisfactorily similar. There is a moderate seasonal variation in rainfall in both regions, but even during the driest period (June–July), one or two showers a week is the norm for the lowlands. The forests at the foot of the transects are evergreen throughout the year and no more than 1%–2% of the tree crowns in the canopy are ever bare at once. Mean annual rainfall figures are available for Llullapichis (2.5 m) and Pichari (2.9 m), lowland settlements on the Pachitea and Apurimac rivers, respectively. Temperature curves for the two transects are sufficiently alike to be within the range of error in measurement (Fig. 1), an observation which, along with previously published statements, suggests that temperature influences are not involved in the Massenerhebung effect.

A final preliminary point that must be considered is the degree of genetic similarity between conspecific populations in the control and test localities. Because of the Sira's isolation from the main Andes, it could be argued that any observed distributional differences were merely artifacts of a separate evolutionary adjustment of the Sira populations to a novel biogeographical setting. While such an argument cannot be directly refuted, taxonomic evidence indicates that the overwhelming majority of the Sira's montane birds have undergone no discernible morphological divergence from their Andean progenitors. Of the 105 montane species in our collection, only 3 are sufficiently different from nearby Andean races to be regarded as distinct subspecies; and only 1 of these could be considered strongly differentiated (Weske and Terborgh 1971), this being a relict population whose nearest known conspecifics are in Bolivia. These facts imply that the montane bird populations of the Sira have been prevented from evolving strong local characteristics by comparatively recent genetic infusions from Andean stocks, possibly during the Pleistocene (Haffer 1967, 1969, Mayr and Phelps 1967, Vuilleumier 1971). Parenthetically, we mention that the vegetation of the cloud forest and elfin forest zones of the Sira proved to be rich in endemic species (Smith 1971, Wurdack 1972).

METHOD OF ANALYSIS

In our preliminary analysis, the upper and lower elevational limits of all the bird species found on the Vilcabamba control transect were assigned to one of the four categories described in the introduction: (1) gradient terminus, (2) factors varying in parallel with the gradient, (3) competitive exclusion, and (4) ecotones. For convenience, the latter three

mechanisms and the species assigned to them will hereafter be called, respectively, gradient, competition, and ecotone mechanisms (or species), as appropriate. The models corresponding to each mechanism suggest the direction but not the amount of the altered distributions that would result from certain specifiable changes in ecological context. For instance, an ecotone species would be expected to have a higher (lower) limit of occurrence in a locality in which the ecotone in question lay at a higher (lower) elevation. Similarly, a competition-limited species should expand into elevations occupied by its competitor whenever that competitor is absent. However, we have no way of estimating the amount of the expansion, which, clearly, will be limited.

By bringing comparative data to bear on the problem, we are confronted with numerous instances of altered distributions, many of which make it obvious that the control assignment is no longer valid or applicable. For this reason, we must distinguish two categories of outcome when appraising the findings from a test locality. **First, there is the question of whether or not a given species responded as expected to the test conditions. If it did, then the initial assignment is upheld. If it did not, then the control assignment, for one reason or another, was possibly wrong and may require revision.** Second, given that the values of certain variables are increased or relaxed in the test locality (e.g., ecotones or competitors closer or farther from the center of a given species' range), one must specify a new set of assignments that is consistent with each species' behavior in the test setting. By this procedure we reveal the overlay of limiting factors. **Even though only one primary restraint may function at a particular time and place, several mechanisms may be operative over a species' entire geographical range.** Frequently we find that the immediate limiting cause is only slightly stronger than the next proximal cause, as when a limit expands just 50 or 100 m in the absence of a competitor. Occasionally, however, very striking cases of release are observed in which a species freed of competition doubles the breadth of its distribution.

Given that each species' limit is assigned to one of four categories in both the control and test localities, and that the test result may indicate that revision of the control assignment is in order, it can be appreciated that the total array of possible outcomes is large. To simplify an otherwise unmanageable plethora of possibilities, we apportioned the actual results among a small number of categories representing common distributional patterns, and a residual category that covers a miscellany of rare and aberrant cases. The criteria by which the assignments were made are explained in the Appendix. To

understand them properly, one should keep in mind that each species' performance is judged from the perspective of the center of its distribution. It is perhaps best to illustrate this point with a pair of examples.

Consider a species, one of whose limits coincides with a particular ecotone in the control locality. Now, in a collection of test localities it may happen that the analogous ecotone falls appreciably closer to the distributional midpoint in some and farther in others. If, in some absolute sense, the species' requirements are met by the conditions on the proximal side of the ecotone but not on the distal side, regardless of where the ecotone falls with respect to climatic variables, then the species' limit would contract and expand in strict dependence on the ecotone. The Brown-headed Nuthatch (*Sitta pusilla*) of the southeastern United States exemplifies this sort of behavior in its restriction to pines throughout its range. Its northern limit coincides with the last outposts of certain species of pines (especially *Pinus taeda*) and bears no close relation either to climate or latitude. Such extreme cases are in the minority. More frequently, a species is tied to a recognizable ecotone over only a part of its range, as, for example, the Boat-tailed Grackle (*Cassidix major*), which is confined to coastal salt marshes (*Spartina alterniflora*) in the central Atlantic states, but is quite abundant throughout the inland portions of Florida.

This can be understood in a general way if it is assumed that most aspects of a species' fitness (competitive ability, capacity to resist parasites and disease, tolerance to climatic fluctuations, etc.) are maximal at or near the point of greatest abundance, **which, on a smooth gradient, usually lies close to the middle of the range.** A species that is freely able to use a certain habitat near the center of its range because of its better adaptation in other respects may be unable to do so near the periphery.

Competitive gradients may also be involved in enforcing ecotone-limited boundaries, as in several widespread birds of the Caribbean region that are characteristic of mangroves (e.g., *Coccyzus minor*, *Dendroica petechia*). On large land masses where many species are present (Florida, Greater Antilles) these are most abundant in mangroves and are found in other habitats sparingly, if at all. On small islands (e.g., Lesser Antilles), however, they may be found in a wide range of habitats and can be quite common on islands having no mangroves at all (*pers. observ.* of JT).

Now let us examine a hypothetical comparison with a view to exposing the range of possible outcomes. Imagine a species whose limit falls at an ecotone in the control locality. When tested in places where the equivalent ecotone lies closer or farther

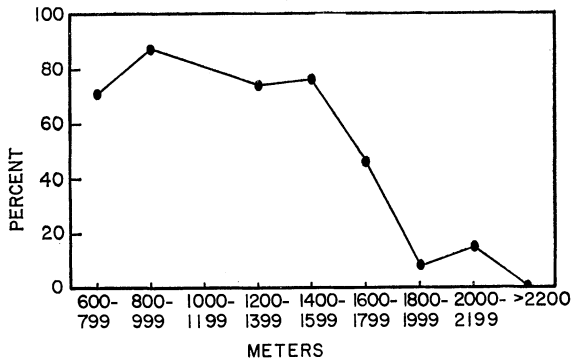


FIG. 2. Insularity in the summit avifauna of the Cerros del Sira, Peru. Of the species whose lower elevational limits on the control (Vilcabamba) transect fell within the intervals indicated on the abscissa, the percentages indicated on the ordinate were found to occur in the Sira.

from its center of distribution, it may behave in the following ways. Where the ecotone is closer to the species' environmental optimum, it may simply retract and continue to be bounded by the ecotone, or it may retract only part way. The first of these possibilities is straightforward; the ecotone is confirmed as the limiting mechanism. In the second instance, partial retraction indicates that the translocation of the ecotone, or the underlying edaphic or climatic factors, produced a discernible displacement. But in the test locality the limiting mechanism must be the gradient, since the species boundary no longer coincides with the ecotone. Taking the counterexample, that of an ecotone displaced away from the center of distribution, again, the species may move with the ecotone or only part way. A partial response implies, for the control locality, that the effect of the ecotone was to truncate the distribution at a point somewhat short of that at which limitation by the gradient would have become effective. Thus, more than one mechanism may serve to contain a species around the periphery of its range. There are other possible outcomes, too, but these are extreme, puzzling and, gratifyingly, rare. For example, in a test locality having a retracted ecotone, the species might be found beyond the limit it achieves in the control locality. Such cases are difficult to interpret. One concludes weakly that the species is responding to an undetermined environmental factor(s) that varies independently of the measured gradient.

At this point it is necessary to impose an important restriction on the classification of results from the Sira. Recall that the relatively short duration of our expeditions prevented us from conducting a continuous survey of the transect. Instead, we only obtained faunal lists for each camp, and judging

from past experience, these are somewhat incomplete. More importantly, the ranges of most species end at undetermined points between camps. Because of these deficiencies in the data, we must draw a sharp distinction between positive and negative results, i.e., those results that rest on records of a species' presence and those that depend on surety of its absence. There is sufficient uncertainty in our knowledge of absolute distributional limits in the Sira that we categorically excluded all negative results from the analysis that follows. To make this distinction clear, let us return for a moment to the hypothetical cases just outlined. In the first of these, a partial response to a retracted ecotone is detectable by finding the species on the distal side of the ecotone—a positive result. But in the second instance, that of an extended ecotone, a partial response can be affirmed only by certain knowledge of the species' absence in the region just proximal to the ecotone. So long as there are no records from the distal side of the ecotone, we shall treat cases of the latter sort as normal, that is, conforming to the expected behavior of the species as judged from the control locality.

RESULTS

Faunal impoverishment

Our choice of the Sira as the most appropriate test locality was predicated on the assumption that many species would be missing from the summit region. This, in fact, proved to be the case beyond our expectations. The faunal impoverishment will be demonstrated in two ways.

First, we subdivide the control fauna into groups of species whose lower limits fall within a series of regular elevational intervals, 600–799 m, 800–999 m, etc. We then note that the fraction of these groups representing species common to the Sira remains nearly constant below 1,600 m at a value of 75%–80% (Fig. 2). The proportion of species in common is less than 100% because (1) there is some species turnover in the intervening 360 km, (2) the faunal survey of the Sira was not so complete, and (3) some island effect is to be expected at all elevations appreciably above the lowest level in the land connections between the Sira and the Andes (ca. 400 m). The fraction present in the Sira of the species entering the control fauna above 1,600 m drops precipitously. Even though the Sira offers elevations up to 2,400 m, we found only five species whose control ranges begin above 1,800 m. Because of the small area of appropriate habitat, such species must have a poor survival potential even when they have succeeded in establishing beachhead colonies. Of the five species, three were represented by single indi-



FIG. 3. Comparison of the vegetation along our net lines on the summit of the Sira (2,220 m) (left) and at 2,840 m in the Cordillera Vilcabamba (right). In addition to the obvious structural similarity, the vegetation of the two locations shares many common genera in roughly equal proportions: a broad-leaved grass and *Chusquea* spp. (Gramineae), *Bomeria* (Liliaceae), *Weinmania* (Cunoniaceae), *Clusia* (Guttiferae), *Schefflera* (Araliaceae), *Miconia* (Melastomataceae), many Ericaceae, Compositae, etc.

viduals in our net samples, and thus seem so rare that they may have been stragglers rather than members of resident populations. The remaining two were notably more abundant than on the control transect, and as well had extended their ranges downward, one by more than 1,000 m.

The second approach to the measurement of impoverishment is more direct, and consists of estimating the outstanding species deficit. The environment of the Sira summit ridge can be equated with conditions on the control transect in two distinct ways: with respect to elevation or vegetation. At the same elevation (2,220 m) the Vilcabamba cloud forest harbors 91 species, of which 50 are lacking in the Sira. The Sira summit vegetation compares very closely, both in structure and generic composition, with the vegetation at our 2,800-m camp in the Vilcabamba, some 600 m higher (Fig. 3). The avifauna there consists of 81 species, of which 67 were not found in the Sira. In spite of these deficiencies in the fauna, we recorded 63 species on

the Sira summit over 8 days of netting and observation. Judged from past experience, additional time and effort would have increased the total asymptotically to a final value around 70, which we will take as representative of an effort equal to that expended at the camps on the control transect. Accordingly, the Sira summit fauna is left with a net deficit of 10 to 20 species, depending on whether vegetation or elevation is taken as the standard of comparison. This is the deficiency that remains uncompensated by niche shifts in the available fauna. Later, we shall estimate the gross species deficit and consider why it is only partially offset by the ecological responses of the species on hand.

Distributional shifts

The recorded lower and upper elevational limits of the 246 species in common to the two transects are given in the Appendix, along with an evaluation of the mechanisms controlling their distributional limits in the Cordillera Vilcabamba and Cerros del

TABLE 2. Distributional performance of 246 bird species in the Cerros del Sira, Peru, as judged in comparison with their behavior on a control transect in the Cordillera Vilcabamba. Row and column headings explained in Appendix. N = number of species

Control classification	N	A. Lower distributional limits								
		Status in Sira								
		Con	$G \times E$	GR	CR	CRS	$C \times E$	ΔE	$E \times G$	Misc
T	127	127								
G	42	24	13	2						3
C	28	11			2	6	8			1
E	39	14						23		2
M	5	5								
U	5	5								
Total	246	186	13	2	2	6	8	23		6

B. Upper distributional limits										
T	8	8								
G	132	94	2	25	2					9
C	64	39			15	3	4			3
E	33	7						4	16	6
M	5				1					4
U	4	1								3
Total	246	149	2	25	18	3	4	4	16	25

Sira. A summary of these results is presented in Table 2 under abbreviated row and column headings that represent defined categories of performance in, respectively, the control and test localities. It will be assumed that the reader has now acquainted himself with the abbreviations corresponding to the categories and with the criteria that distinguish them.

Most (76%) of the lowest records of occurrence in the Sira fell within the control elevations, the greater proportion of these being species having wide lowland distributions. Of the species recorded below their control limits, a large majority (73%) appear to have shifted in parallel with the downward displaced cloud forest and elfin forest ecotones (categories $G \times E$, $C \times E$, ΔE). Most (10) of the remaining 17 species possess montane distributions and exhibited some form of competitive release (CR, CRS, GR).

Quite a different picture emerges from the classification of upper limits because of the asymmetries inherent in the geographical situation: a rich lowland fauna merging into an impoverished montane fauna and two out of three ecotones displaced downward. Range extensions resulting from competitive release consequently prevail over ecotone effects. Uppermost recorded occurrences were beyond the control limits more frequently than was the case for lowest occurrences (39% vs. 24%). The largest component of these consists of species displaying some form of competitive release (47%: CR, CRS, GR), followed distantly by ecotone species breaching the limits of cloud forest or elfin forest at reduced elevations (16%: $E \times G$) and by species reacting to the displaced montane forest ecotone (10%:

$G \times E$, $C \times E$, ΔE). An appreciable number of species (25) fell into the miscellaneous category.

A more revealing version of these results is obtained by restricting the compilation to the 97 control species that were found above 1,500 m in the Sira. Here, a considerably higher fraction of the species showed perturbed distributions (48% lower, 51% upper; Table 3). A breakdown of the lowest occurrences gives very much the same result as previously, with ecotone effects predominating (74%: $G \times E$, $C \times E$, ΔE). On the uphill side, however, there is a major increase in the proportion of altered distributions fitting the criteria for competitive release (84%: CR, CRS, GR).

A summary overview of distributional phenomena

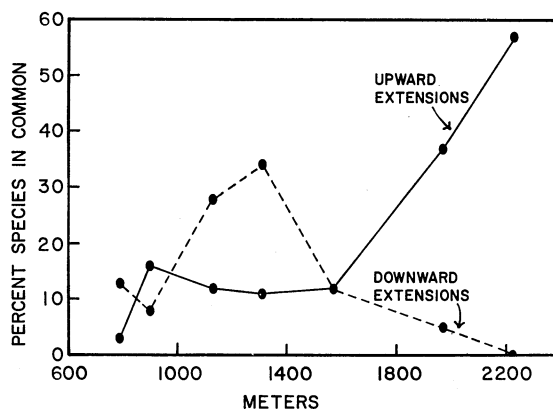


FIG. 4. Incidence of upward and downward range extensions in the avifauna of the Cerros del Sira, Peru. At each camp, all species in common with the control transect were considered in relation to their control distributions.

TABLE 3. Distributional performance of 97 bird species found at elevations above 1,500 m in the Cerros del Sira, Peru, as judged by comparison with their behavior on a control transect in the Cordillera Vilcabamba. Row and column headings explained in Appendix. *N* = number of species

A. Lower distributional limits										
Control classification	<i>N</i>	Status in Sira								
		Con	G×E	GR	CR	CRS	C×E	ΔE	E×G	Misc
T	12	12								
G	33	17	12	2						2
C	18	6			2	5	5			
E	29	10						18		1
M	3	3								
U	2	2								
Total	97	50	12	2	2	5	5	18		3
B. Upper distributional limits										
T	8	8								
G	52	29		21	2					
C	28	11			14	3				
E	5								4	1
M	3				1					2
U	1									1
Total	97	48		21	17	3			4	4

in the Sira is obtained by presenting the data graphically. Figure 4 shows, for each Sira camp, the proportion of species in common with the Vilcabamba that were above and below their control limits. An excess of downward extensions between 1,000 and 1,500 m reflects the depression of the cloud forest ecotone, while the much larger excess of upward extensions towards the summit demonstrates the faunal response to a species deficit that becomes increasingly pronounced above 1,600 m.

Revelations from the summit

Some additional conclusions follow from a closer scrutiny of the Sira summit fauna. Of 53 species shared with the control transect, 10 (19%) were living out of their normal habitat (tall cloud forest) and 30 (57%) were both out of habitat and beyond their control elevational limits, leaving only a minority of 13 species (25%) within both the control habitat and elevation. Thus, in the absence of any compensatory niche shifts, the Sira summit would be occupied by these 13 species plus about 3 out of the 10 species not found in the Vilcabamba assuming that these respond in the same way as species that are shared (13 of 52 is about equal to 3 of 10). Given that 81 species were found in equivalent vegetation and 91 at the same elevation on the control transect, the gross species deficit is estimated to be, respectively, 65 or 75 species. As we noted earlier, colonizing species from the lower slopes of the mountain have filled most of this void, but not all of it. There are at least two reasons for this. One is that the invading species are probably less well adapted to the summit environment than are

the missing forms they replace. The second reason is that the colonizing fauna is an assemblage of opportunists which has probably not had much time to evolve toward an optimal species packing; hence a high marginal resistance to invasion is encountered at a lower species density than in the better co-adapted control fauna (Wilson and Taylor 1967). A hint of this is apparent in the reduced equitability of species abundances in the net samples taken at the highest camps (Table 1).

We will now exploit the summit results further to obtain minimum quantitative estimates of the expansion induced by release from direct and diffuse competition. Of the 30 species that were above their control limits, 16 had taken the places of missing elevationally exclusive uphill congeners and 14 had apparently responded more generally to the species deficit (GR status) (see Table 4 in Appendix). The two groups of species, respectively, had undergone mean expansions of 429 and 237 m. The difference between the means is significant ($P < 0.05$, Wilcoxon test), and in amount (192 m) is remarkably close to the 220-m compression shown by the lower members of elevationally exclusive pairs of congeners in the Vilcabamba (Terborgh 1971, Table 3).

Reassessment

In conclusion, we return to the two questions that provided the incentive for this work: how much the importance of the competition mechanism was underestimated in the Vilcabamba analysis, and whether the competition assignments made at that time hold up to test. Beginning with the first question, we note that 52 gradient species were found in the Sira

above 1,500 m (Table 3). Of these, 23 exhibited upward expansions, 12 occur in the Vilcabamba at elevations higher than the Sira summit and so had no opportunity to expand, and the remaining 17 had the opportunity to expand but were not found to do so. This latter subgroup consisted of 1 vulture, 13 species of the cloud forest mid-story or canopy, and 3 understory species whose control ranges fall below 1,800 m. It is likely that many of these are ill adapted for life in the extremely dense elfin forest vegetation. **Nevertheless, to make the most conservative judgment, we conclude that 23 (58%) of the 40 gradient species that had the opportunity to expand in the species-deficit zone were actually found to do so.** From this it follows that at least 58% of the species that received gradient assignments in the Vilcabamba evaluation were actually limited by diffuse competition.

There were five ecotone species in the upper zone of the Sira, all of which broadly crossed the presumptively confining vegetational boundaries. **Such uniformity of response suggests that ecotone species are also subject to the pull of a species deficit, as was anticipated in the earlier discussion of Caribbean mangrove birds.**

Last, the deficit-zone fauna contained 28 competition-limited species, of which 17 were found to expand. Three of the remaining 11 species were within the control ranges at the top of the Sira, and a 4th, whose uphill competitor was present, behaved normally. **Consequently, 24 species had the opportunity to expand and at least 17 (71%) did so. The remaining seven are birds of heavy cloud forest that simply may not have been able to make the necessary transition into elfin forest.**

Several considerations imply that these estimates of the incidence of diffuse and direct competition in the control fauna are on the low side. (1) A number of extensions could have escaped detection in the unsurveyed 400-m interval between our 1,570- and 1,970-m camps in the Sira. (2) Additional species probably would have been induced to expand had cloud forest continued to the top of the mountain, or (3) had the net species deficit been even greater. (4) Our netting effort at the two highest camps was intensive but certainly not exhaustive. The pattern established by the species that were captured suggests that more than 80% of any additional species turned up by a prolonged sampling period would have been birds that were present at lower elevations on the mountain. (5) Had we been able to work on the Sira's highest peak (2,400–2,500 m), it is probable that expansion would have been recorded for several more species whose control limits lie within the interval of 2,230 to 2,400 m. On the other hand, overestimation of competition effects would result from

observational errors in the recorded limits of occurrence on the control transect. As explained previously, we have attempted to minimize this type of error by assigning to the Misc category all species whose limits in the Vilcabamba are imprecisely known. Thus, in sum, the weight of the errors of measurement is decidedly on the side of underestimating the incidence and intensity of competition.

These remaining errors of estimate notwithstanding, it will be instructive to make a new assessment of the importance of competition in limiting the elevational ranges of Andean birds. On the control transect we found that roughly a third of all the distributional limits that fell within the termini of the gradient were attributable to the direct competitive exclusion of congeners. That 71% of such species responded as expected by expanding their ranges in the Sira in the absence of their congeners, provides a resounding confirmation of their control status, given the numerous handicaps, as itemized above, in the measurement. In addition, we found that at least 58% of the species that had gradient status in the control locality expanded upwards in the Sira when exposed to a low-diversity zone on the summit. Since 56% of all upper limits in the control study were assigned to the gradient mechanism, our result implies that 58% of these, or another third (32%) of the control limits were imposed by diffuse competition and erroneously assigned to the gradient mechanism for lack of sufficient information. Finally, the fact that all five presumptive ecotone species present in the upper part of the Sira invaded the elfin forest on the summit indicates that these too are responsive to a partial competitive vacuum. **Taking these results together, we conclude conservatively that a minimum of two-thirds of all distributional limits in Andean birds are attributable to direct or diffuse competitive exclusion.**

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We dedicate this paper to the memory of Dr. Maria Koepcke, esteemed colleague, friend, and member of the first two Sira expeditions. Her boundless energy and contagious enthusiasm for Peruvian ornithology inspired all who were privileged to know her during a productive but tragically abbreviated life. We are grateful to her husband, Dr. Hans-Wilhelm Koepcke, for frequent scientific counsel and hospitality at their Panguana Biological Station, and for many other invaluable forms of assistance in a corner of the world so remote that one must travel a full week to obtain even the most trivial supplies. Especially warm thanks are due Vittorio Modena and his family for providing instant hospitality on numerous occasions and for donating storage facilities that immensely simplified the logistics of our expeditions. **The first-named author's life was saved in a grueling ordeal of emergency by the extraordinary exertions of several unnamed Campa Indians and four Peruvian assistants: Klaus Wehr, Manuel Sanchez, Erasmo Guerra, and Moro Vasquez.**

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APPENDIX

Here we present the data upon which this paper is based. The following table contains a list of the 246 bird species found in common on our transects of the Cordillera Vilcabamba and Cerros del Sira. The information given in several of the columns is coded according to designations that require explanation.

In the columns that specify elevational ranges, L indicates that the species in question was found at one or more stations in the lowlands at the base of the transect.

Column 4 gives, for the lower and upper limits of occurrence on the control transect, the assignments each species received in the preliminary analysis (Terborgh 1971). In the present paper these are referred to as "control assignments." The notation corresponds to the row headings used in Tables 2 and 3. T, G, C, and E, respectively, designate species whose limits on the control transect coincided with a natural terminus of the elevational gradient (the valley floor or timberline) or were assigned to the gradient, competition, or ecotone mechanisms. M refers to nonforest species inhabiting matorral (riparian vegetation; Terborgh and Weske 1969) in the control region, a few of which curiously occur in the Sira forests. U (unknown) separates a small number of species whose control ranges are imperfectly known because they are rare or particularly difficult to observe or identify.

The last two columns give the status of the lower and upper limits of each species in the light of its performance in the Sira. The results have been classified into a number of categories, each of which is indicated in the tables (column headings of Tables 2 and 3) by an appropriate abbreviation as explained below.

- | | |
|-------|---|
| Con | Conforming distributions: extreme occurrence in the Sira within the elevational range circumscribed by the control limits, or control limits undefined as in T, and many M and U species. Such distributions are given no designation (left blank) in Table 4. |
| G × E | Gradient–ecotone interaction: gradient species found in the Sira beyond their control limits within the displacement zone of an extended ecotone. |
| GR | Gradient species that expanded their ranges upwards (or downwards, 2 cases) within the species deficit zone of the Sira (above 1,500 m). The presumptive interpretation is that these are species responding to release from diffuse competition. Their control status should be revised accordingly. |
| CR | Competitive release: (mostly) competition-limited species whose ranges in the Sira have expanded upwards (or downwards, 2 cases) in the absence of an elevationally exclusive congener. |
| CRS | Competitive release into sympatry: upward or downward expansion of competition-limited species accomplished by entry into sympatry with a congener that was excluded on the control transect. |
| C × E | Competition–ecotone interaction: transposition of the boundary between two excluding congeners within the zone of displacement of an ecotone. Only the one member of each pair whose distribution extended beyond its control limit was so designated. |
| ΔE | Response of ecotone species to a displaced ecotone: cases in which the extreme occurrence in the Sira was distal to the control elevational |

limit but within the zone of displacement of an extended ecotone.

E × G Ecotone species found transgressing (distal to) a retracted ecotone but within control elevational limits.

Misc Miscellaneous. Species were placed in this category when their behavior did not conform with one of the above categories. Five types of cases are recognizable among the 31 upper and lower limits given this status: (1) Possible observational errors involving species that were scarce or difficult to observe in the control locality (G and U species, 4 upper limits). (2) Gradient species that occurred beyond their control limits in the Sira but at elevations below the species deficit zone (3 lower, 8 upper limits). Most of these extensions were small (less than 200 m). Possible reasons: greater productivity of food resources in the Sira, more abundant microhabitat (nesting, roosting sites, etc.), non-measurable reduction in diffuse competition,

etc. Three instances of major displacements (≥ 600 m) are more puzzling. (3) Displacements of competitive boundaries between elevationally exclusive congeners (1 lower, 3 upper). Only one of these represents a major shift, but in this case the boundary in the Sira is 550 m above its position in the Vilcabamba and above the control upper limit of the upper member of the pair. (4) Ecotone species found in the Sira both beyond their control elevational limits and distal to the corresponding ecotones (2 lower, 6 upper limits). (5) Matorral species (five) that unexpectedly were present in the forests of the Sira. One of these replaced a missing montane congener and was given CR status.

E Indicates (in Table 4 only) occurrences in the Sira beyond an ecotone that was distal to the species' limit on the control transect. In many instances (G, C species) no revision of status is required. The designation is included to indicate the high frequency with which ecotones are crossed by species of all categories.

TABLE 4. Limiting mechanisms in the elevational distributions of 246 bird species found in common on transects of the Cordillera Vilcabamba and Cerros del Sira of Peru

Families and species	Elevational range in Cordillera Vilcabamba (m)		Lower and upper control assignments		Extreme recorded occurrence in Cerros del Sira (m)		Classification of distributional limits in Cerros del Sira	
	Lowest	Highest			Lowest	Highest	Lower	Upper
Tinamidae								
<i>Tinamus tao</i>	685	1,050	C	G	-	900		
<i>Tinamus major</i>	L	600	T	C	L	690		C × E
<i>Crypturellus soui</i>	L	1,000	T	G	L	900		
Cathartidae								
<i>Sarcorampus papa</i>	L	2,130	T	G	L	1,570		
<i>Coragyps atratus</i>	L	600	T	E	L	-		
<i>Cathartes melambrotos</i>	L	900	T	G	L	900		
Accipitridae								
<i>Elanoides forficatus</i>	L	2,600	T	G	L	2,225		E
<i>Ictinia plumbea</i>	L	600	T	E	L	690		ΔE
<i>Accipiter striatus</i>	1,320	3,540	G	T	1,310	2,225		
<i>Leucopternis albicollis</i>	L	600	T	E	L	690		ΔE
<i>Spizastur melanoleucus</i>	-	2,800	U	G	L	2,225		
<i>Spizaetus tyrannus</i>	L	1,760	T	G	L	690		
Falconidae								
<i>Micrastur ruficollis</i>	685	1,710	U	G	690	-		
<i>Daptius americanus</i>	L	685	T	G	L	900		Misc
<i>Falco rufigularis</i>	L	850	T	G	L	900		
Cracidae								
<i>Penelope jacquacu</i>	L	1,415	T	C	L	1,130		E
<i>Mitu mitu</i>	L	1,340	T	E	L	700		
Phasianidae								
<i>Odontophorus stellatus</i>	L	470	T	C	L	-		
<i>Odontophorus speciosus</i>	1,500	1,750	C	C	1,130	1,970	C × E	CR, E
Columbidae								
<i>Columba speciosa</i>	L	560		M	L	1,400		Misc, E
<i>Columba plumbea</i>	L	2,170	T	C	L	1,570		
<i>Geotrygon montana</i>	L	1,070	T	C	L	900		
<i>Geotrygon frenata</i>	1,360	1,980	C	G	1,150	2,225	C × E	GR, E
Psittacidae								
<i>Ara macao</i>	L	685	T	G	L	690		
<i>Pyrrhura picta</i>	L	1,620	T	G	-	900		
<i>Pionus menstruus</i>	L	1,480	T	G	L	900		
<i>Amazona ochrocephala</i>	L	1,400	T	C	L	690		
<i>Amazona farinosa</i>	L	600	T	G	L	1,150		Misc, E
Cuculidae								
<i>Piaya cayana</i>	L	2,515	T	G	L	2,225		E
Strigidae								
<i>Otus watsonii</i>	L	600	T	C	L	300		
<i>Otus ingens</i>	1,370	1,520	C	C	-	2,225		CR, E
<i>Pulsatrix perspicillata</i>	L	1,500	T	G	L	1,130		
<i>Glaucidium brazilianum</i>	L	600	T	E	L	690		ΔE
<i>Glaucidium minutissimum</i>	L	1,660	T	C	L	1,570		
<i>Ciccaba virgata</i>	L	900	T	C	L	300		

TABLE 4. Continued

Families and species	Elevational range in Cordillera Vilcabamba (m)		Lower and upper control assignments		Extreme recorded occurrence in Cerros del Sira (m)		Classification of distributional limits in Cerros del Sira	
	Lowest	Highest			Lowest	Highest	Lower	Upper
Apodidae								
<i>Streptoprocne zonaris</i>	L	3,540	T	T	L	2,225		
<i>Cypseloides rutilus</i>	L	3,540	T	T	1,310	2,225		
Trochilidae								
<i>Doryfera ludoviciae</i>	1,280	2,830	G	G	900	2,225	G × E	
<i>Threnetes leucurus</i>	L	685	T	G	L	690		
<i>Phaethornis guy</i>	685	1,690	G	G	1,100	1,350		
<i>Phaethornis superciliosus</i>	L	930	T	G	L	900		
<i>Eutoxeres condensmini</i>	L	2,640	T	G	900	1,570		
<i>Florisuga mellivora</i>	L	930	T	G	L	900		
<i>Lophornis delattrei</i>	L	—			—	900		
<i>Thalurania furcata</i>	L	1,435	T	M	L	1,130		Misc, E
<i>Adelomyia melanogenys</i>	1,500	2,160	G	E	L	1,130	G × E	E × G, E
<i>Heliodoxa leadbeateri</i>	930	1,735	G	G	1,300	2,225		GR, E
<i>Heliodoxa branickii</i>	910	1,290	G	C	1,300	2,225		CR, E
<i>Coeligena coeligena</i>	1,290	2,220	G	C	900	1,570		GR, E
<i>Ocreatus underwoodii</i>	1,480	1,950	G	G	1,130	2,225	G × E	E
<i>Agliocercus kingi</i>	1,830	2,210	E	G	1,310	—	ΔE	
<i>Schistes geoffroyi</i>	1,390	1,660	G	G	—	2,225		GR, E
<i>Heliothrix aurita</i>	685	900	U	U	1,130	2,225		Misc, E
			E	G	—	900		
Trogonidae								
<i>Trogon viridis</i>	L	600	T	E	L	900		Misc, E
<i>Trogon collaris</i>	700	1,520	E	C	L	2,225	Misc, E	CRS, E
<i>Trogon personatus</i>	1,630	2,600	C	E	1,570	2,225	CRS	E × G, E
<i>Trogon curucui</i>	L	1,600	T	G	L	1,310		
<i>Trogon melanurus</i>	L	470	T	G	L	—		
<i>Pharomachrus auriceps</i>	1,630	2,160	G	C	1,030	1,130	G × E	
Momotidae								
<i>Baryphthengus ruficapillus</i>	685	1,430	C	E	690	—		
<i>Momotus momota</i>	L	600	T	C	L	—		
Bucconidae								
<i>Malacoptila fusca</i>	L	930	T	C	L	900		
<i>Nonnula ruficapilla</i>	L	1,520	T	G	L	—		
<i>Monasa nigrifrons</i>	L	860	T	G	L	360		
<i>Monasa morpheus</i>	L	685	T	G	L	690		
Capitonidae								
<i>Capito niger</i>	L	1,110	T	G	L	1,310		GR, E
<i>Eubucco richardsoni</i>	L	940	T	C	L	—		
Ramphastidae								
<i>Aulacorhynchus derbianus</i>	1,520	1,735	E	C	1,130	1,570	ΔE	
<i>Aulacorhynchus prasinus</i>	L	1,700	T	C	690	—		
<i>Pteroglossus mariae</i>	L	1,370	T	E	L	—		
<i>Pteroglossus beauharnaesii</i>	L	700	T	G	L	690		
<i>Selenidera reinwardtii</i>	L	1,550	T	G	L	1,130		
<i>Ramphastos cuvieri</i>	L	700	T	G	L	960		Misc
Picidae								
<i>Piculus rubiginosus</i>	1,285	1,940	C	C	1,260	1,970	C × E	CR, E
<i>Dryocopus lineatus</i>	L	600	T	E	L	—		
<i>Melanerpes cruentatus</i>	L	700	T	G	L	690		
<i>Veniliornis affinis</i>	L	950	T	C	L	900		
<i>Phloeocastees melanoleucos</i>	L	680	T	G	L	690		
<i>Phloeocastees rubricollis</i>	L	900	T	C	L	500		
Dendrocolaptidae								
<i>Dendrocincla tyrannina</i>	1,800	2,150	G	G	1,310	2,225	GR	GR, E
<i>Dendrocincla fuliginosa</i>	L	930	T	G	L	900		
<i>Dechonychura longicauda</i>	685	—	E	G	690	1,570	E	GR, E
<i>Sittasomus griseicapillus</i>	L	1,390	T	E	L	1,130		E × G, E
<i>Glyphorhynchus spirurus</i>	L	1,425	T	E	L	1,310		E × G, E
<i>Dendrocolaptes certhia</i>	L	370	T	C	L	900		Misc, E
<i>Dendrocolaptes picumnus</i>	340	600	C	E	910	1,310	Misc, E	Misc, E
<i>Xiphorhynchus ocellatus</i>	685	1,520	C	C	900	1,570		CRS
<i>Xiphorhynchus guttatus</i>	L	600	T	C	L	690		C × E
<i>Xiphorhynchus triangularis</i>	1,520	2,160	C	G	1,310	1,970	CRS	E
<i>Lepidocolaptes albolineatus</i>	L	685	T	G	900	2,225		CR, E
Furnariidae								
<i>Margarornis squamiger</i>	2,100	3,540	G	T	—	2,225		
<i>Premnornis guttuligera</i>	1,290	1,830	E	G	1,310	1,970		GR, E
<i>Premnoplex brunescens</i>	1,290	2,230	G	E	1,130	2,225	G × E	E × G, E
<i>Pseudocolaptes boissonneautii</i>	1,700	3,400	G	T	1,570	2,225	G × E	
<i>Hylocistetes subulatus</i>	L	685	T	G	L	1,310		GR, E
<i>Syndactyla rufosuperciliata</i>	1,300	1,830	E	G	1,310	2,225		GR, E
<i>Syndactyla subalaris</i>	1,360	1,830	E	G	1,310	1,970	ΔE	GR, E
<i>Philydor erythrocerus</i>	1,150	1,520	C	C	1,130	1,570		GR
<i>Philydor ruficaudatus</i>	L	1,050	T	C	—	900		
<i>Automolus ochrolaemus</i>	L	1,360	T	E	690	1,570		Misc, E
<i>Thripadectes melanorhynchus</i>	1,290	1,520	G	C	1,310	—		
<i>Xenops rutilans</i>	1,480	1,780	C	G	1,130	1,310	C × E	
<i>Xenops minutus</i>	L	1,400	T	C	L	900		
<i>Sclerurus mexicanus</i>	1,290	1,830	G	G	690	1,130	Misc, E	
<i>Sclerurus caudacutus</i>	L	370	T	G	L	690		Misc
<i>Lochmias nematura</i>	685	—	E	U	—	1,310		Misc, E

TABLE 4. Continued

Families and species	Elevational range in Cordillera Vilcabamba (m)		Lower and upper control assignments		Extreme recorded occurrence in Cerros del Sira (m)		Classification of distributional limits in Cerros del Sira	
	Lowest	Highest			Lowest	Highest	Lower	Upper
Formicariidae								
<i>Cymbilaimus lineatus</i>	L	1,000	T	G	L	–		
<i>Thamnophilus schistaceus</i>	L	685	T	G	L	690		
<i>Thamnophilus murinus</i>	L	600	T	E	L	900		
<i>Thamnophilus caerulescens</i>	1,420	1,900	E	G	1,310	2,225	ΔE	Misc, E
<i>Thamnophilus aethiops</i>	L	370	T	E	L	690		GR, E
<i>Thamnistes anabatinus</i>	980	1,420	G	E	–	1,310		Misc
<i>Dysithamnus mentalis</i>	900	1,480	C	G	900	1,310		E × G, E
<i>Thamnomanes ardesiacus</i>	L	685	T	C	L	900		C × E, E
<i>Thamnomanes schistogynus</i>	L	470	T	G	L	690		Misc
<i>Myrmotherula brachyura</i>	L	685	T	G	L	900		G × E
<i>Myrmotherula haematonota</i>	600	950	C	C	900	1,150		Misc, E
<i>Myrmotherula ornata</i>	470	600	T	C	–	690		C × E
<i>Myrmotherula axillaris</i>	L	930	T	G	L	690		
<i>Myrmotherula schisticolor</i>	1,290	1,735	C	G	1,160	1,570	C × E	
<i>Myrmotherula menetriesii</i>	L	685	T	G	L	900		G × E
<i>Herpsilochmus pileatus</i>	1,480	1,720	C	G	1,310	–	C × E	
<i>Herpsilochmus rufimarginatus</i>	L	1,000	T	C	690	900		
<i>Drymophila caudata</i>	1,295	2,230	E	E	1,400	2,225		E × G, E
<i>Cercomacra cinerascens</i>	L	1,150	T	G	L	690		
<i>Cercomacra nigrescens</i>	685	1,740	G	G	1,310	1,570		
<i>Myrmoborus myotherinus</i>	L	600	T	E	L	900		Misc, E
<i>Hypocnemis cantator</i>	L	600	T	E	L	–		
<i>Myrmeciza hemimelaena</i>	L	1,290	T	G	L	690		
<i>Pithys albifrons</i>	L	930	T	G	L	690		
<i>Rhegmatorhina melanosticta</i>	L	600	T	E	–	900		Misc, E
<i>Hylophylax naevia</i>	L	930	T	G	L	1,130		Misc, E
<i>Hylophylax poeilonota</i>	L	930	T	G	L	1,130		Misc, E
<i>Formicarius analis</i>	L	1,170	T	C	L	690		
<i>Myrmothera campanisona</i>	L	600	T	C	L	690		CR
<i>Grallaricula flavirostris</i>	1,455	2,190	E	C	1,310	1,570	ΔE	
Conopophagidae								
<i>Conopophaga castaneiceps</i>	1,170	1,800	G	G	1,130	1,570	G × E	
<i>Corythopsis torquata</i>	L	1,350	T	E	L	–		
Rhinocryptidae								
<i>Scytalopus femoralis</i>	1,290	1,735	G	C	1,130	2,225	G × E	CR, E
Cotingidae								
<i>Laniisoma elegans</i>	370	–	U	U	1,130	1,310		Misc, E
<i>Pipreola frontalis</i>	1,520	1,630	E	G	1,130	1,570	ΔE	
<i>Rhytipterna simplex</i>	L	1,520	T	G	L	1,310		
<i>Lipaugus vociferans</i>	L	600	T	G	L	900		Misc, E
<i>Pachyrhamphus versicolor</i>	–	2,640	C	G	1,570	1,970	CRS	
<i>Pachyrhamphus albogriseus</i>	1,520	1,780	C	C	1,310	1,570	C × E	
<i>Querula purpurata</i>	L	685	T	G	L	350		
<i>Attila spadiceus</i>	L	600	T	E	L	690		ΔE
Rupicolidae								
<i>Rupicola peruviana</i>	680	1,950	E	G	900	1,570		
Pipridae								
<i>Pipra chloromeros</i>	685	1,360	C	C	L	1,310		E
<i>Pipra pipra</i>	930	1,730	C	G	L	1,570	CRS, E	
<i>Pipra caeruleocephala</i>	930	1,730	G	G	900	1,570		
<i>Pipra fasciicauda</i>	L	685	T	C	L	690		
<i>Chloropipo unicolor</i>	930	1,830	C	G	1,130	2,225		GR, E
<i>Chloropipo holochlora</i>	685	930	G	C	690	1,130		Misc, E
<i>Piprites chloris</i>	470	1,520	G	G	690	1,310		
<i>Schiffornis turdinus</i>	685	1,520	G	G	900	1,310		
Tyrannidae								
<i>Ochthoeca pulchella</i>	2,100	2,670	G	C	1,970	2,225	GR	E
<i>Myiodynastes maculatus</i>	L	930	T	C	L	900		
<i>Myiarchus cephalotes</i>	1,480	1,700	E	C	1,310	2,225	ΔE	CRS, E
<i>Myiarchus tuberculifer</i>	1,520	2,170	C	G	1,310	–	CRS	
<i>Contopus fumigatus</i>	1,520	2,130	E	G	1,130	1,970	ΔE	E
<i>Empidonax euleri</i>	L	1,350	T	E	690	1,130		E × G, E
<i>Terenotriccus erythrurus</i>	L	930	T	G	L	690		
<i>Myiobius villosus</i>	930	1,400	G	E	1,130	1,330		E × G, E
<i>Myiotriccus ornatus</i>	910	1,730	G	G	1,100	1,570		
<i>Pyrrhomyias cinnamomea</i>	1,480	2,830	E	G	1,310	1,970	ΔE	
<i>Myiophobus flavicans</i>	1,730	1,830	C	G	1,570	–	CR	
<i>Myiophobus fasciatus</i>	L	–	M		–	1,970		Misc, E
<i>Myiophobus roraimae</i>	1,320	1,520	E	C	1,310	1,520		
<i>Platyrinchus platyrhynchos</i>	L	930	T	C	L	690		
<i>Platyrinchus mystaceus</i>	930	1,830	C	G	1,130	1,570		
<i>Tolmomyias assimilis</i>	470	930	T	G	L	900		
<i>Rhynchocyclus olivaceus</i>	685	930	E	C	690	–	E	
<i>Todirostrum chrysocrotaphum</i>	L	1,150	T	G	L	690		
<i>Lophotriccus pileatus</i>	870	1,830	G	C	1,310	1,570		
<i>Myiornis ecaudatus</i>	L	980	T	G	L	900		
<i>Pseudotriccus pelzelni</i>	1,520	1,880	G	C	1,570	2,225		CR, E
<i>Phylloscartes ventralis</i>	1,480	1,760	E	G	1,160	2,225	ΔE	GR, E
<i>Tyranniscus bolivianus</i>	1,390	2,830	E	G	1,310	–	ΔE	
<i>Leptopogon supercilialis</i>	685	1,620	E	C	900	1,570		
<i>Leptopogon amaurocephalus</i>	340	930	T	G	L	–		
<i>Mionectes striaticollis</i>	600	3,500	G	T	900	2,225		
<i>Mionectes olivaceus</i>	L	1,430	T	E	L	1,310		E × G, E

TABLE 4. Continued

Families and species	Elevational range in Cordillera Vilcabamba (m)		Lower and upper control assignments		Extreme recorded occurrence in Cerros del Sira (m)		Classification of distributional limits in Cerros del Sira	
	Lowest	Highest			Lowest	Highest	Lower	Upper
Hirundinidae								
<i>Notiochelidon cyanoleuca</i>	L	—		M	L	2,225		CR, E
Corvidae								
<i>Cyanocorax violaceus</i>	L	350	T	G	L	350		
<i>Cyanocorax yncas</i>	1,270	2,500	E	G	1,570	2,225		E
Troglodytidae								
<i>Troglodytes solstitialis</i>	1,710	3,300	G	G	—	2,225		
<i>Henicorhina leucophrys</i>	1,360	3,100	E	G	1,310	2,225	ΔE	
<i>Microcerculus marginatus</i>	L	1,150	T	G	L	1,130		E
Turdidae								
<i>Entomodestes leucotis</i>	2,100	2,830	G	G	900	2,225	Misc, E	
<i>Platycichla leucops</i>	1,400	1,550	E	C	900	1,310	Misc, E	
<i>Turdus serranus</i>	1,750	3,520	C	T	900	2,225	CRS, E	
<i>Turdus nigriceps</i>	685	930	U	U	—	900		
Vireonidae								
<i>Cyclarhis gujanensis</i>	L	600		M	1,130	1,570		Misc, E
<i>Smaragdolanus leucotis</i>	600	1,150	T	G	690	1,310		GR, E
<i>Vireo olivaceus</i>	L	1,300	T	G	L	900		
<i>Vireo gilvus</i>	1,480	1,760	E	G	—	2,225		GR, E
<i>Hylophilus hypoxanthus</i>	L	1,100	T	G	L	900		
<i>Hylophilus ochraceiceps</i>	L	930	T	G	L	900		
Icteridae								
<i>Cacicus cela</i>	L	1,000	T	C	L	400		
<i>Psarocolius decumanus</i>	L	1,100	T	C	L	—		
Parulidae								
<i>Parula pitiayumi</i>	940	1,620	G	G	900	1,570	G × E	
<i>Myioborus miniatus</i>	930	1,780	G	C	900	2,175	G × E	
<i>Basileuterus chrysogaster</i>	685	940	E	C	—	900		CR
<i>Basileuterus tristriatus</i>	1,290	1,830	C	G	1,310	1,570		
<i>Basileuterus coronatus</i>	1,390	2,150	E	C	1,310	2,225	ΔE	CR, E
Coerebidae								
<i>Conirostrum albigrons</i>	1,950	2,200	G	C	—	2,225		CR, E
<i>Diglossa caerulea</i>	1,735	2,100	G	C	1,310	2,225	Misc	CR, E
<i>Diglossa glauca</i>	1,520	2,200	E	G	1,130	2,225	ΔE	GR, E
<i>Cyanerpes caeruleus</i>	L	1,600	T	G	L	1,970		GR, E
<i>Chlorophanes spiza</i>	L	1,360	T	E	L	900		
<i>Dacnis cayana</i>	L	1,360	T	E	L	1,130		E × G, E
<i>Dacnis lineata</i>	L	1,180	T	G	L	900		
Thraupidae								
<i>Chlorophonia cyanea</i>	600	1,630	T	G	900	1,130		
<i>Tanagra xanthogaster</i>	L	2,130	T	G	900	2,225		GR, E
<i>Tanagra rufiventris</i>	L	980	T	G	L	900		
<i>Tanagra mesochrysa</i>	1,100	1,760	C	G	900	1,130	C × E	
<i>Tanagra chrysopasta</i>	L	930	T	C	—	900		
<i>Chlorochrysa calliparaea</i>	1,480	1,875	E	G	1,310	—	ΔE	
<i>Tangara chilensis</i>	L	1,250	T	E	L	1,130		E × G, E
<i>Tangara schrankii</i>	L	1,300	T	E	L	1,130		E × G, E
<i>Tangara arthus</i>	1,480	1,700	E	G	1,310	—	ΔE	
<i>Tangara xanthocephala</i>	1,480	2,600	E	E	1,310	—	ΔE	
<i>Tangara parzudakii</i>	1,480	2,130	E	G	—	2,225		GR, E
<i>Tangara cyanotis</i>	1,480	1,620	E	G	1,310	1,570	ΔE	
<i>Tangara nigrocincta</i>	600	1,120	T	G	900	1,130		E
<i>Tangara gyrola</i>	L	1,480	T	G	L	1,130		
<i>Tangara nigroviridis</i>	1,650	2,130	G	G	1,130	2,225	G × E	GR, E
<i>Tangara vassorii</i>	1,770	2,600	G	E	1,970	2,225		E × G, E
<i>Iridosornis analis</i>	1,320	2,100	E	C	1,130	2,225	ΔE	CR, E
<i>Anisognathus flavinucha</i>	1,370	1,950	E	G	1,310	2,225	ΔE	CR, E
<i>Calochaetes coccineus</i>	1,480	1,950	E	G	1,130	1,570	ΔE	
<i>Piranga leucoptera</i>	1,480	1,540	E	G	1,310	1,570	ΔE	GR
<i>Habia rubica</i>	L	950	T	G	L	900		
<i>Lanio versicolor</i>	L	1,150	T	G	690	900		
<i>Tachyphonus rufiventer</i>	L	1,300	T	G	L	1,130		E
<i>Trichothraupis melanops</i>	1,150	1,520	G	G	1,130	1,570	G × E	GR
<i>Chlorospingus ophthalmicus</i>	1,700	2,640	C	G	1,570	2,225	CR	E
<i>Chlorospingus flavigularis</i>	880	1,520	G	C	900	1,570		CR
<i>Hemispingus frontalis</i>	1,460	1,790	E	C	1,310	2,225	ΔE	CR, E
Fringillidae								
<i>Saltator maximus</i>	L	930	T	G	900	1,310		GR, E
<i>Ptylus grossus</i>	L	930	T	G	L	690		
<i>Cyanococcyz cyanoides</i>	L	1,290	T	G	L	900		
<i>Haplospiza rustica</i>	1,740	3,520	G	T	1,970	2,225		
<i>Atlapetes tricolor</i>	1,660	2,100	G	C	—	2,225		CR, E
<i>Atlapetes brunneinucha</i>	1,320	2,250	G	C	950	1,570	G × E	