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Rarity in antpittas: territory size and population density of five *Grallaria* spp. in a regenerating habitat mosaic in the Andes of Colombia

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Summary

Between 1995 and 2000, we made a comparative study of ranging patterns of individuals of five sympatric species of antpitta *Grallaria* spp. that differ in body size and extent of geographical range. *Grallaria milleri* is restricted to a small area in the central Andes of Colombia, *G. rufocinerea* is endemic to the Central Cordillera, and *G. ruficapilla, G. nuchalis* and *G. squamigera* are widely distributed in the tropical Andes. Using mist-nets, we captured and banded 76 individuals of the five species during the five year study period. We also radio-tracked six individuals for periods of 30–60 days, to obtain estimates of territory sizes. Recapture patterns revealed that antpittas exhibited high site fidelity, remaining in the same patch for documented periods of up to 34 months. However, some individuals were captured only once, and were probably transient through the area. Territory sizes estimated were 0.5–5.4 ha for *G. milleri* (n = 7), 1.4 and 1.5 ha for *G. rufocinerea* (n = 2), 1.9 ha for *G. ruficapilla* (n = 1), 9.3 ha for *G. nuchalis* (n = 1) and 2 and 4.5 ha for *G. squamigera* (n = 2). We compared these data with territory estimates of other Neotropical Formicariids. Our results indicated that antpittas had relatively small territories, and had population densities higher than assumed previously for these secretive birds of the forest understorey.

Resumen

Entre 1995 y 2000 realizamos un estudio comparativo de los patrones de uso del espacio de cinco especies simpátricas del género *Grallaria* que difieren en tamaño corporal y en la extensión de su distribución geográfica: *G. milleri*, restringida a una pequeña área en la cordillera Central de Colombia, *G. rufocinerea*, endémica de la cordillera Central, y *G. ruficapilla, G. nuchalis* y *G. squamigera*, las cuales tienen amplia distribución en los Andes tropicales. Durante los cinco años de estudio, capturamos en redes y anillamos 76 individuos de las cinco especies. También hicimos seguimiento, por períodos de 30–60 días, de seis individuos dotados de radiotransmisores, para obtener tamaños de los territorios. Los patrones de recapturas revelaron alta fidelidad al sitio en estas especies, con periodos documentados de permanencia de hasta 34 meses. Sin embargo, algunos individuos fueron capturados solo una vez, y podrían haber estado de paso por el área de estudio. Los tamaños de territorio estimados para *G. milleri* fueron de 0.5–5.4 ha (n = 7), para *rufocinerea* 1.4 y 1.5 ha (n = 2), para *ruficapilla* 1.9 ha (n = 1), para *nuchalis* 9.3 ha (n = 1) y para *squamigera* 2 y 4.5 ha (n = 2). Estos datos se comparan con los publicados para otros formicáridos neotropicales. Nuestros resultados indican que las *Grallaria* tienen territorios relativamente pequeños y densidades poblacionales más altas que lo que previamente se ha supuesto para estas tímidas aves del sotobosque.

Introduction

Antpittas *Grallaria* spp. (Formicariidae) are little known, secretive birds of the understorey of Neotropical humid forests. They are usually considered to be ''rare'', for having apparently low densities and high habitat specificity. In addition, several species have very restricted geographical distributions. Indeed, five species are listed as threatened at a global level (Collar *et al*. 1992). In a previous paper (Kattan and Beltrán 1999), we reported on the patterns of habitat use and population density of five species of antpitta that occurred sympatrically at a cloud-forest site in the central range of the Colombian Andes: Brown-banded *G. milleri*, Bicoloured *G. rufocinerea*, Rufous-crowned *G. ruficapilla*, Rufous-naped *G. nuchalis*, and Undulated Antpittas *G. squamigera*. Brown-banded Antpitta is endemic to the central part of the Central Andes, with a total geographical range of less than 1,000 km^2 (Beltrán and Kattan, in press a). Bicoloured Antpitta also has a small geographical range, restricted to the Central Andes of Colombia and extreme northern Ecuador (Nilsson *et al*. 2001, Beltrán and Kattan in press b). The other three species are more widely distributed in the Andes, from Venezuela and Colombia, south to Peru and Bolivia.

Determining population density is crucial for establishing the status of endangered species. The density of a population depends on its social system and patterns of use of space. In a territorial species, territory size determines how many individuals (or pairs, or groups) can fit in a given area, but measured population density is also affected by the presence of floating individuals. In general, for a given trophic level and habitat type, for energetic reasons body size correlates positively with space requirements (MacNab 1983). Thus, assuming a homogeneous habitat, a larger animal will have a lower population density than a smaller congener.

Population density is also one of three dimensions of rarity, the other two being habitat specificity and size of geographical range (Rabinowitz *et al*. 1986). The degree of correlation between these three dimensions is variable (Gaston 1994). In an analysis of patterns of rarity for the birds of the Cordillera Central of Colombia, Kattan (1992) found that species with wide geographical ranges tended to be abundant habitat generalists, while endemic species tended to have low population densities and high habitat specificity. In general, species with small geographical ranges tend to have low densities, but some rare species may be locally abundant if looked for in the appropriate habitat (Gaston 1994).

In our previous study (Kattan and Beltrán 1999), Brown-banded Antpitta had the highest local density (1.3 individuals/ha), while Undulated Antpitta, which is the largest of the five species, had a low density (0.2 individuals/ha). These densities were estimated by mapping singing birds along transects. The study area of about 100 ha was a small-scale mosaic of habitats that included early (10–15 years old) second growth, 40-year-old secondary forest, and 40-year-old plantations of Andean alder *Alnus acuminata* with an overgrown understorey. Censuses indicated that the five antpitta species extensively overlapped in their patterns of habitat use, using the three habitats in proportion to their areas. Some of the species also showed overlap in body dimensions related to resource use, which suggests that they may be competing for resources. However, the question remained whether the species were territorially segregated.

In this paper we present data on territory size and overlap of the five species, obtained by radio-tracking and by sighting and recapture patterns of banded birds. Censusing with traditional methods such as transect or point counts in short-term studies may underestimate densities, because many individuals may go undetected (Jiménez 2000). On the other hand, small-scale censuses may under- or overestimate densities, depending on the spatial heterogeneity of the area and the distribution of individuals (Gaston 1994). Our intensive sampling over an extended time period allowed us to map the positions of individual birds, and obtain a more precise estimate of territory size and degree of interspecific overlap, as well as permanence of individual birds in their home ranges. Combined with census data, these data allow a more reliable estimation of population densities at our study site.

Study area and methods

The study was conducted at Ucumarí Regional Park, on the western slope of the Central Cordillera of the Andes of Colombia, just east of the city of Pereira. The 4,240 ha park protects the Otún River watershed between elevations of 1,700 and 2,600 m (see Rangel and Garzón 1994, Murcia 1997, and Kattan and Beltrán 1999 for a complete description). Our study area was at the site known as La Pastora, at 2,400–2,600 m elevation. At this site the valley bottom is relatively flat, about 300 m wide but becoming narrower at higher elevations, and framed by abruptly rising, forested slopes. Some portions of the valley bottom are covered with a mosaic of pastures and patches of second growth of different ages, but the southern fringe is covered with a small-scale mosaic of patches of secondary forest and alder plantations. Alder stands were never managed after planting, and were overgrown with native vegetation, although they retain a monodominant canopy (Murcia 1997).

The study was conducted between 1995 and 2000. We established a system of census transects along trails that crossed three habitat types: young second growth (10–15 years-old), alder plantations (40-years-old), and forest (40-years-old) (see Kattan and Beltrán 1999 for description). The study area extended to about 100 ha, but a core area of 17 ha was studied more intensively. In the core area, we opened 8–16 mist-nets from 06h00 to 18h00 for 10–15 days each month, in an effort to capture and colour-band as many birds as possible. Nets were placed in areas of dense understorey vegetation, where we had previously detected the presence of antpittas by their songs. Because antpittas mostly hop on the ground and rarely fly, they typically avoid mist-nets. To increase the chances of capturing them, we let the lower shelf of the net rest on the ground, and camouflaged it with plants. All recaptures and sightings of banded individuals were located on a map of the study area. We measured the distance between recapture points and, for cases in which we had three or more sighting or capture points and a number of song records, we estimated the size of the habitat patch used by the bird, as a rough measure of territory size.

We affixed 1.5 g radio transmitters with batteries lasting 60 days (Advanced Telemetry Systems) to six antpittas: two *G. rufocinerea*, and one each of the other four species. Transmitters were attached backpack-style with telephone cable. We located the position of the birds by triangulation, taking two or three consecutive

Table 1. Number of captures, interval between first and last capture (months), and distance or area covered (see Methods) for individuals of five species of antpitta, at Ucumarí Regional Park, Colombia, 1995–2000

Individual	No. captures	Interval	Distance/area
G. milleri			
1	5	11	0.5 ha
2	2	1.3	35 m
3	4	30.3	3 ha
4	5	31	4.5 ha
5*	2	1.4	4.1 ha
6	2	1	40 m
7	6	34	2 ha
8	3	25	1 ha
9	3	14.9	5.4 ha
10	2	2	< 50 m
11	2	11	270 m
12	2	2	< 100 m
13	2	2	0 m
G. ruficapilla			
1	2	11	110 m
2	3	15	115 ± 7 m
3*	2	2	1.9 ha
4	2	10.8	150 m
G. rufocinerea			
1	2	0.6	55 m
2*	2	10	1.5 ha
3	2	33.4	330 m
G. nuchalis			
1	2	2.7	55 m
2	2	1.2	120 m
G. squamigera			
1*	2	1.2	4.5 ha
2	4	1.2	2 ha

*Radio-tracked

readings from different positions along a trail. We located the radio-tagged birds at intervals of one hour during early morning and late afternoon (birds were rather inactive around noon). We mapped consecutive positions and found that birds could be at opposite ends of their home range within one hour. Thus, we assumed each data point to be independent. We are confident about the reliability of our readings, because in several cases birds dropped the transmitter, and we were able to locate it and recover it from the forest floor. We estimated territory size by the minimum convex polygon method, measured with a planimeter.

Results

During the five years of the study we captured and banded a total of 76 antpittas: 36 *G. milleri*, 15 *G. ruficapilla*, 11 *G. rufocinerea*, 9 *G. nuchalis* and 5 *G. squamigera*. Of the 76 individuals 24 were recaptured or resighted at least once (Table 1), for an overall recapture rate of 32%. Mean interval between recaptures of individuals

Table 2. Territory size and population density of some formicariids

Species	Locality	Body mass (g)	Territory size (ha)	Density	Source[a]
Grallaria rufocinerea	Andes, Colombia	45	1.4–1.5	0.8 ± 0.2/ha	1, 2
G. milleri	Andes, Colombia	52	0.5–5.4	1.3 ± 0.2/ha	1, 2
G. ruficapilla	Andes, Colombia	83	1.9	0.4 ± 0.1/ha	1, 2
G. nuchalis	Andes, Colombia	101	9.3	0.5 ± 0.2/ha	1, 2
G. squamigera	Andes, Colombia	132	2–4.5	0.2 ± 0.1/ha	1, 2
G. gigantea	Andes, Ecuador	254		1–1.5/ha	3
G. quitensis	Andes, Ecuador			0.3 (0.1–0.9)/ha	4
G. varia	French Guiana			1.5 pairs/100 ha	5
Formicarius colma	French Guiana			2–5 pairs/100 ha	5
F. colma	Amazonia, Peru	49	14	5 pairs/100 ha	6
F. colma	Amazonia, Brazil		5.2–7.7		7
F. analis	French Guiana			7.7–14 pairs/100 ha	5
F. analis	Amazonia, Peru	58	6	13 pairs/100 ha	6
F. analis	Amazonia, Brazil		5.9–21.2		7
Chamaeza nobilis	Amazonia, Peru	123	30	2 pairs/100 ha	6
Hylopezus macularius	French Guiana			6–7 pairs/100 ha	5
Myrmothera campanisoma	French Guiana			5.7–8 pairs/100 ha	5

[a] 1. This study; 2, Kattan and Beltrán 1999; 3, de Soye *et al.* 1997; 4, Creswell *et al.* 1999; 5, Thiollay 1994; 6, Terborgh *et al.* 1990; 7, Stouffer 1997.

that were recaptured once was 5.5 ± S.D. 8.2 months (n = 17). Most of these individuals had recapture intervals of less than 3 months, but four had intervals of 10–11 months. In contrast, the interval between first and last capture for individuals that had 3–6 recaptures or sightings was 23.0 ± S.D. 9.3 months (range 11–34 months, n = 7).

Distances between recaptures for individuals with two captures varied between 0 (one *G. milleri* recaptured at exactly the same place with an interval of two months) and 330 m, but in most cases (14 of 16) the distance was < 200 m (Table 1). For six *G. milleri* for which we had 3–6 recaptures (time intervals of 11 to 34 months), we estimated territory sizes of 0.5–5.4 ha. For one *G. squamigera* with four recaptures, territory size was estimated at 2 ha in a period of 1.2 months.

We obtained continuous periods of 30–60 days of data for the six radio-tagged birds. Territory sizes obtained by this method were 1.4 and 1.5 ha for *G. rufocinerea*, 4.1 ha for *G. milleri*, 9.3 ha for *G. nuchalis*, 1.9 ha for *G. ruficapilla*, and 4.5 ha for *G. squamigera*. Antpittas did not use territories homogeneously. Some areas were used intensely, while other areas were used only occasionally (Figure 1). We could not discern any particular habitat feature of the intensely used areas that made them more attractive to the birds.

There was a high degree of interspecific overlap in space use in the five species. For example, in a patch of 4 ha that was intensely studied, at least four *G. milleri*, one *G. rufocinerea*, one *G. nuchalis*, and one *G. squamigera* (all banded) coincided over a period of two years, and were captured in the same nets. The territory of a radio-tracked *G. rufocinerea* was 90% contained within the territory of the radio-tracked *G. squamigera*, and the territory of the radio-tracked *G. milleri* was

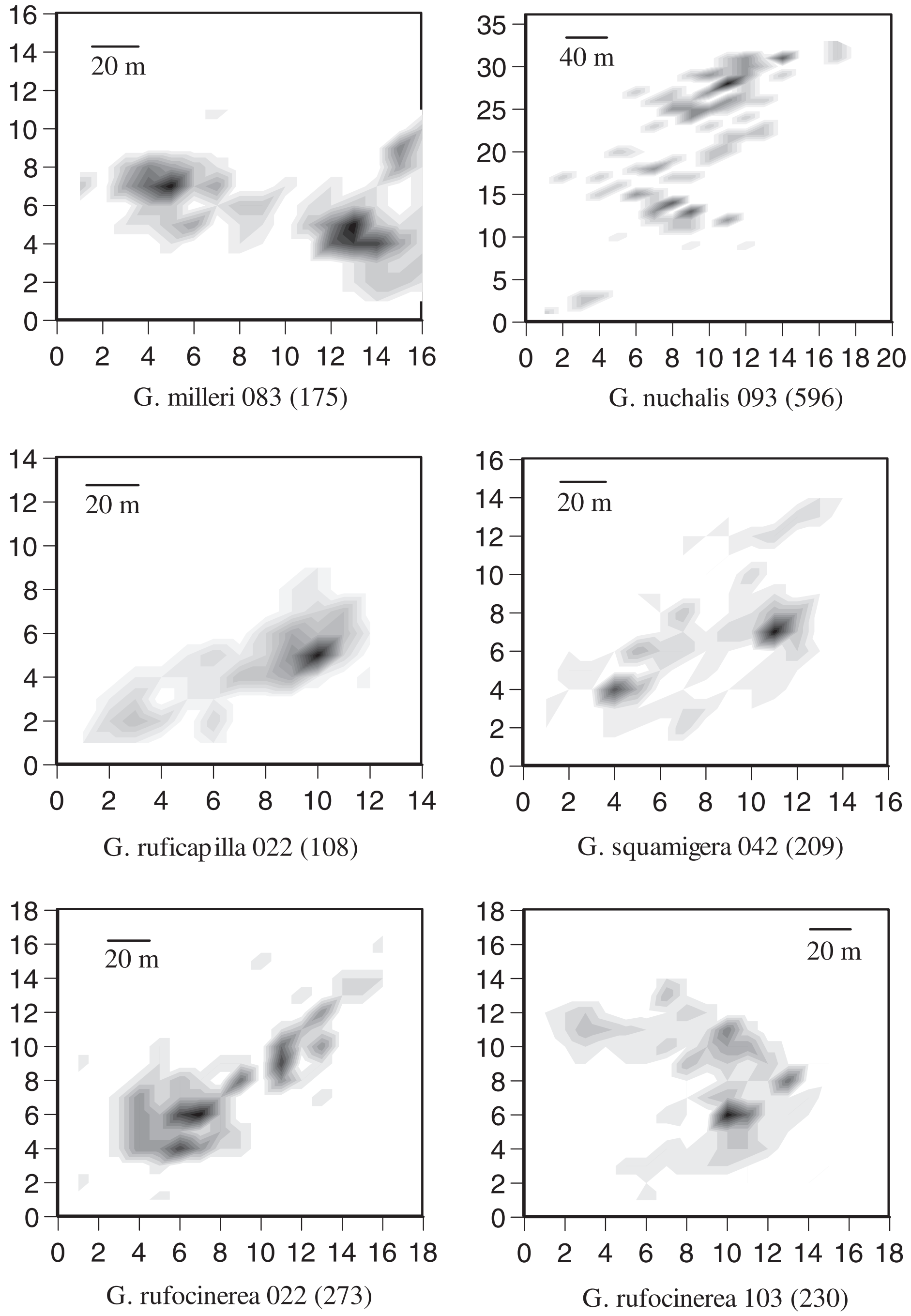

Figure 1. Representation of the territories of six antpittas of five species obtained by radio-tracking individuals for periods of 30–60 days at Ucumarí Regional Park, Colombia, 1995–2000. Intensity of shading indicates density of records and intensity of use of space. Numbers in parenthesis indicate number of records on which the figure is based. Axis scales are relative measures of distance. The scale for *G. nuchalis* is distorted on the Y axis.

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50% within the same *G. squamigera* territory (but the *G. milleri* and *G. rufocinerea* territories did not overlap).

Discussion

In our previous study (Kattan and Beltrán 1999), we censused antpittas by mapping singing birds along transects, and inferred a high degree of site fidelity. Data reported in this study, based on individually identified birds, indeed indicated that antpittas remained in the same area for variable periods of time. Some individuals were apparently transient and may have formed a floating population, probably composed of juveniles and other non-territorial individuals. In the case of *G. milleri*, which had the largest sample size in this study, 23 of 36 individuals were banded and never captured or seen again. The remaining 13 individuals were recaptured at least once, and seven of them had recapture intervals of 11 to 34 months. Territory sizes estimated for these birds varied between 0.5 and 5.4 ha (including a radio-tracked individual with a territory of 4.1 ha; Table 1).

We had previously estimated a density of *G. milleri* of 1.3 ± S.E. 0.2 individuals/ha, and 106 individuals in about 100 ha (Kattan and Beltrán 1999). The measurements of territory size reported in this paper were, in general, concordant with those density estimates. Assuming antpittas were paired year-round, at the smaller extreme of territory size (0.5 ha), there would be four individuals/ha (two pairs). At the other extreme, there would be about 0.4 individuals/ha. Because our study area was a mosaic of three forest habitat types interspersed with patches of pasture, some spatial variation in habitat quality may have been expected (although our previous data showed no significant differences in density among habitats). On the other hand, data on radio-tracked birds indicated that antpittas did not use their territories homogeneously. Thus, taking into account the presence of floaters (which may sing in response to playbacks) and heterogeneity of the area, our estimate of territory size was within a range that agreed with our previous data (the 10-fold range of territory size may be the result of small scale differences in habitat productivity).

These results indicate that mid-term transect censusing is an appropriate technique, at least for the more vocal species of antpitta (density of less vocal species may be underestimated). A combination of methods gives more confidence in the results, but requires a very intense sampling effort throughout an extended period of time. However, when estimating population densities and population sizes of endangered species, a high degree of confidence in the results is desirable, and decisions should not be made based on rapid, superficial studies. For hard-to-study species such as antpittas, even an intensive study like ours, may produce very few data points.

Estimates of population densities and territory sizes of Neotropical birds are scarce, especially for secretive, understorey species such as antpittas and other Formicariids (Table 2). With the exception of species that have notorious songs, such as *G. ruficapilla*, antpittas are usually reported as having low population densities. For example, Creswell *et al.* (1999) sighted only one individual of *G. squamigera*, one of *G. quitensis* and two of *G. rufula* in 7.6 km of transects. Our data suggest that such low densities may be artefacts of census techniques, inadequate for the secretive behaviour of these birds in forest habitats. In open, páramo habitat, where birds are more visible, Creswell *et al*. (1999) obtained a density of *G. quitensis* of 0.3 individuals/ha. Our combination of intensive censusing and mist-netting over an extended time period in dense forest, revealed that antpittas were more common than expected, with population densities similar or higher than those of other passerines in a variety of habitats (e. g. Greenberg and Gradwohl 1986, Thiollay 1994, Robinson *et al*. 2000).

There is the possibility of geographical variation in population densities, as is the case for *Formicarius colma* and *F. analis* in Amazonia (Stouffer 1997). One reason densities may vary between sites is heterogeneity of the study area. If a species uses only some habitat patches within a heterogeneous area, densities calculated for the whole area underestimate the density in the appropriate habitat. Our study area is a regenerating mosaic of different types of forest, but the five species used the three habitats with equal intensity (Kattan and Beltrán 1999). Thus, densities are representative of the total study area. It is possible that densities in regenerating habitats are higher than in mature forest, because the denser understorey may be more productive and provide a better refugium. Compared with the little data available for lowland forests, antpitta densities in montane forest are high (Table 2). For example, Thiollay (1994) reports 1.5 pairs of *G. varia* in 100 ha in French Guiana. Whether this is a generalized phenomenon remains to be determined.

There was no clear relationship between body size and territory size in the five antpitta species. The smaller species (*G. rufocinerea* and *G. milleri*) had small territories and high densities, but territory sizes for two of the large species, *G. ruficapilla* and *G. squamigera*, were small (Table 2). In particular, the small territory of *G. squamigera* is noteworthy, as it would be expected to require much more space, by virtue of its large size (132 g). On the other hand, at an Ecuadorian locality, density of *G. gigantea*, the largest species in the genus, has been estimated as 1–1.5 individuals/ha (de Soye *et al*. 1997). Our density estimate for *G. squamigera* may be low, as this species sings infrequently and does not readily respond to playbacks (Kattan and Beltrán 1999).

The results of our work have important implications for how ''rare'' these antpittas are considered. The high local population density of *G. milleri* is noteworthy, as it is a species with a very restricted geographical range. Presently, this species is known from four localities along a strip less than 200 km long on the Central Cordillera, between elevations of 2,300 and 3,100 m (Beltrán and Kattan, in press a). Within this range, however, the species is relatively abundant, at least in some localities. Likewise, the population of *G. rufocinerea* may be larger than previously supposed. In addition, the geographical range of *G. rufocinerea* has been recently documented to extend into Ecuador (Nilsson *et al*. 2001). Another antpitta, *G. alleni*, previously known from only two localities in Colombia, has also been found to occur in Ecuador (Krabbe and Coopmans 2000). Thus, the ''rarity'' of antpittas may be more a reflection of their secretive behaviour than true scarcity. Our work also suggests that some antpittas are more plastic in terms of habitat use than previously thought. Although still requiring attention, both *G. milleri* and *G. rufocinerea* occur within protected areas in Colombia (Beltrán and Kattan, in press a, b) that probably have enough habitat for their persistence, as long as the integrity of these areas is guaranteed.

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References

Beltrán, J. W. and Kattan, G. H. (in press, a) *Grallaria milleri*. In L. M. Renjifo, A. M. Franco, B. López-Lanús, G. H. Kattan, J. D. Amaya and M. F. Gómez, eds. *Libro Rojo de especies de aves amenazadas de Colombia*. Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Beltrán, J. W. and Kattan, G. H. (in press, b) *Grallaria rufocinerea*. In L. M. Renjifo, A. M. Franco, B. López-Lanús, G. H. Kattan, J. D. Amaya and M. F. Gómez, eds. *Libro Rojo de especies de aves amenazadas de Colombia*. Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Collar, N. J., Gonzaga, L. P., Krabbe, N., Madroño Nieto, A., Naranjo, L. G., Parker III, T. A. and Wege, D. C. (1992) *Threatened birds of the Americas. The ICBP/IUCN Red Data Book*. Third edition, part 2. Washington, DC: Smithsonian Institution Press.

Cresswell, W., Hughes, M., Mellanby, R., Bright, S., Catry, P., Chaves, J., Freile, J., Gabela, A., Martineau, H., McLeod, R., McPhie, F., Anderson, N., Holt, S., Barabas, S., Chapel, C. and Sanchez, T. (1999) Densities and habitat preferences of Andean cloud-forest birds in pristine and degraded habitats in north-eastern Ecuador. *Bird Conserv. Internatl*. 9: 129–145.

de Soye, Y., Shuchmann, K. L. and Matheus, J. C. (1997) Field notes on Giant Antpitta *Grallaria gigantea. Cotinga* 7: 35–36.

Gaston, K. J. (1994) *Rarity*. London: Chapman and Hall.

Greenberg, R. and Gradwohl, J. (1986) Constant density and stable territoriality in some tropical insectivorous birds. *Oecologia* 69: 618–625.

Jiménez, J. E. (2000) Effect of sample size, plot size, and counting time on estimates of avian diversity and abundance in a Chilean rainforest. *J. Field Orn*. 71: 66–87.

Kattan, G. H. (1992) Rarity and vulnerability: the birds of the Cordillera Central of Colombia. *Conserv. Biol*. 6: 64–70.

Kattan, G. H. and Beltrán, J. W. (1999) Altitudinal distribution, habitat use, and abundance of *Grallaria* antpittas in the Central Andes of Colombia. *Bird Conserv. Internatl*. 9: 271–281.

Krabbe, N. and Coopmans, P. (2000) Rediscovery of *Grallaria alleni* (Formicariidae) with notes on its range, song and identification. *Ibis* 142: 183–187.

McNab, B. K. (1983) Ecological and behavioral consequences of adaptation to various food sources. Pp. 664–697 In J. F. Eisenberg and D. G. Kleiman, eds. *Advances in the study of mammalian behavior*. Special Publication 7, American Society of Mammalogists.

Murcia, C. (1997) Evaluation of Andean alder as a catalyst for the recovery of tropical cloud forests in Colombia. *Forest Ecol. Mgmt*. 99: 163–170.

Nilsson, J., Jönsson, R. and Krabbe, N. (2001) First record of Bicoloured Antpitta *Grallaria rufocinerea* from Ecuador, with notes on the species' vocalisations. *Cotinga* 16: 105–106.

Rabinowitz, D., Cairns, S. and Dillon, T. (1986) Seven forms of rarity and their frequency

in the flora of the British Isles. Pp. 182–204 in M. E. Soulé, ed. *Conservation biology: the science of scarcity and diversity*. Sunderland, MA: Sinauer Associates.
Rangel, J. O. and Garzón, A. (1994) Aspectos de la estructura, de la diversidad y de la dinámica de la vegetación del Parque Regional Natural Ucumarí. Pp. 85–108 in J. O. Rangel, ed. *Ucumarí: un caso típico de la diversidad biótica andina*. Pereira, Colombia: Corporación Autónoma Regional de Risaralda.
Robinson, W. D., Brawn, J. D. and Robinson, S. K. (2000) Forest bird community structure in central Panama: influence of spatial scale and biogeography. *Ecol. Monogr*. 70: 209–236.
Stouffer, P. C. (1997) Interspecific aggression in *Formicarius* antthrushes? The view from central Amazonian Brazil. *Auk* 114: 780–785.
Terborgh, J., Robinson, S. K., Parker, T. A., Munn, C. A. and Pierpont, N. (1990) Structure and organization of an Amazonian forest bird community. *Ecol. Monogr*. 60: 213–238.
Thiollay, J. M. (1994) Structure, density and rarity in an Amazonian rainforest bird community. *J. Trop. Ecol*. 10: 449–481.

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