Spatial variation in population density of an endemic and endangered bird, the Cauca Guan (Penelope perspicax)

Gustavo H. Kattan¹, Néstor Roncancio²,³, Yurany Banguera⁴, Margarita Kessler-Rios⁵, Gustavo A. Londoño⁶, Oscar Humberto Marín⁷ and Marcia C. Muñoz⁸

¹ Departamento de Ciencias Naturales y Matemáticas, Pontificia Universidad Javeriana Cali, Avenida Cañasgordas No. 118-250, Cali, Colombia (ghkattan@javerianacali.edu.co). ² Wildlife Conservation Society Programa Colombia, Cali, Colombia. ³ Instituto Amazónico de Investigaciones Científicas, Leticia, Colombia (nabel8@yahoo.com). ⁴ Departamento de Biología, Universidad del Quindío, Armenia, Colombia (yuranyb@gmail.com). ⁵ 1962 Hillbrook Cir., Auburn, Alabama 36830, USA (gmargaritarios@gmail.com). ⁶ Florida Museum of Natural History and Department of Biology, University of Florida, Gainesville, FL, 32611, USA (galondo@ufl.edu). ⁷ Grupo de Ornitología (GOUN), Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia (oschumar@gmail.com). ⁸ Biodiversity and Climate Research Centre (BiK-F), Senckenberanaganlage 25, 60325, Frankfurt (Main), Germany (marcarmu@gmail.com).

Corresponding author: G. Kattan (gustavokattan@gmail.com)

Abstract
Endemic species tend to be habitat specialists with low population densities, but densities may vary among sites and may be temporally dynamic. In addition, species may exhibit plasticity in habitat use, with the result that densities vary in different habitats. The Cauca Guan (Penelope perspicax) is an endangered species endemic to the mid-Cauca Valley in Colombia. To assess spatial variation in population densities, we surveyed different habitat types (mature and secondary forest, early regeneration, and vegetation strips along streams) in three sites and compared them to densities reported in previous studies to explore possible changes over a period of several years. At the three sites, densities varied between 10 and 40 birds/km² in different habitats. Variation in population density may be related to forest area and habitat productivity, but guans are known to move among locales and regions in response to temporal fluctuations in resource availability. Cauca Guan densities are comparable to those of other montane Penelope guans with broader geographic distributions. Although the Cauca Guan is not a habitat specialist and may reach high densities under some conditions, globally this guan remains rare and efforts for its conservation should be sustained.

Key words: Cracidae, Colombia, endangered species, endemicity, population density

Resumen
Las especies endémicas tienden ser especialistas de hábitat con bajas densidades poblacionales, pero las densidades pueden variar entre sitios y en el tiempo. Las densidades también pueden variar entre tipos de hábitat. La pava caucana (Penelope perspicax) es una especie amenazada, endémica del valle medio del río Cauca en Colombia. Para evaluar la variación espacial de las densidades poblacionales, hicimos muestreos en diferentes tipos de hábitat (bosques maduros y secundarios, regeneración temprana y bandas de vegetación a lo largo de quebradas) en tres sitios y comparamos las densidades con aquellas reportadas en estudios previos, para determinar si hay cambios temporales. En los tres sitios las densidades variaron entre 10 y 40 individuos/km² en los diferentes hábitats. Las variaciones en la densidad poblacional pueden estar relacionadas con el área de bosque y la productividad del hábitat, pero las pavas también hacen movimientos locales y regionales en respuesta a las fluctuaciones temporales en la disponibilidad de recursos. Las densidades de la pava caucana son similares a las reportadas para otras especies de Penelope guans con distribuciones geográficas más amplias. Aunque la pava caucana no es especialista de hábitat y puede alcanzar altas densidades bajo ciertas condiciones, globalmente es una especie rara y deben mantenerse los esfuerzos para su conservación.

Palabras clave: Cracidae, Colombia, especies amenazadas, endemismo, densidad poblacional
Introduction

Species with small geographic ranges are particularly vulnerable to threats such as habitat transformation, because a large proportion of their range may be affected by human disturbance. Thus, global population size may rapidly decrease. In addition, species with restricted distributions often have low abundances [1], which may be the result of low local population densities or ecological specialization. Endemic bird species in tropical mountains tend to exhibit low population densities [2, 3], but may reach high densities in particular spatially-restricted habitats [4]. Therefore, determining population densities and patterns of habitat use is essential for understanding the vulnerability of endemic species. If local rarity is determined by habitat or resource specialization, the extent and patchiness of that particular habitat or the spatial and temporal patterns of resource availability will limit the species’ distribution and abundance.

The Cauca Guan (Penelope perspicax, Cracidae; Fig. 1) is endemic to the middle Cauca Valley in southwestern Colombia. Its original geographic distribution of 11,000 km² encompassed dry to humid montane forest between elevations of 1,000 and 1,800 m in the departments of Cauca, Valle del Cauca, Quindío and Risaralda. Currently this range is reduced by forest fragmentation to an area of occupancy of 560 km² [5]. Less than ten populations are currently known, restricted to isolated forest patches on the western slope of the Central Cordillera and the eastern slope of the Western Cordillera [6].

Guans (Penelopinae, Cracidae; for taxonomy we follow del Hoyo [7]) are thought to be restricted to primary forest and vulnerable to habitat transformation [8], but previous work has shown that Cauca Guans use different habitat types and find food resources both in second growth forest of different ages and in monospecific tree plantations overgrown with native vegetation [9, 10]. Animal populations may exhibit spatial and temporal variations in density related to habitat quality and seasonal availability of resources. Population density is in general, but not always, correlated with habitat quality [11, 12]. Thus, documenting density variation in different habitat types within and among sites is an important step for assessing the vulnerability of the remaining Cauca Guan populations.

Two previous studies reported population densities of the Cauca Guan at two sites, Yotoco and Otún Quimbaya (Fig. 1), on the western and central ranges of the Andes, respectively [6, 10]. In this paper we present new data for Yotoco and for two new sites (Barbas and Bremen), and compare the densities obtained in this study with those obtained in previous studies, to explore possible changes over a period of several years. In addition, we asked whether the densities of the Cauca Guan are comparable to those of other montane species of Penelopinae with similar ecologies that have broader geographical distributions.
Methods
We estimated population densities of Cauca Guan at three sites on the Cauca Valley slopes: Yotoco, Barbas and Bremen (Fig. 2). Yotoco is an isolated, 559 ha reserve on the eastern slope of the Western Cordillera of the Andes. It is divided by a road in two patches of 459 and 100 ha. It encompasses elevations between 1,200 and 1,700 m and has a mean annual precipitation of 1500 mm. Yotoco is a mature forest in the transition between dry and humid premontane life zones. It is isolated in a pasture-dominated landscape where remnant forest fragments are <10 ha in size. We surveyed this site between February and April 2004 and sampled each transect 21 times during this period (Table 1). Observations at this site were made between 8:00-12:00 and 14:00-17:00.

The other two sites are humid, highly diverse forests on the western slope of the Central Cordillera and are relatively close to each other (Fig. 2). Barbas is an elongated forest tract along the Barbas River between elevations of 1,500 and 2,000 m. This stretch of the river forms a deep canyon with abrupt topography. Mean annual precipitation is 3,277 mm. Here we surveyed old-growth forest that extends...
over 782 ha, and riparian vegetation along streams with a total area of 203 ha. The landscape around Barbas is dominated by pastures and forestry plantations (exotic pines and eucalypts). Field work in Barbas was conducted between November 2008 and April 2009 and each transect was sampled four times each month. Transects were sampled at different times of day (5:30-7:30, 7:45-9:45, 14:00-16:00 and 16:00-18:00), alternating between forest and stream transects (Table 1).

Bremen is a nature reserve between elevations of 1,500 and 2,100 m located 1 km south of Barbas but currently isolated. It encompasses 336 ha of native old-growth and second-growth forest (>35 years old) and 411 ha of early regeneration <10 years old. Mean annual precipitation is 2,674 mm. At Bremen we sampled old-growth forest, secondary forest, early regeneration and riparian vegetation. Each transect in Bremen was sampled 12 or 13 times (Table 1) between September and December 2009, alternating repetitions at different times (6:00, 9:00, 15:30).

To estimate Cauca Guan population densities, we used distance sampling along linear transects. This method involves counting the animals (single individuals or groups) detected by an observer and measuring or estimating the perpendicular distance between the animal (or the center of the group) and the transect [13]. The distribution of detection distances is then used to build a detection function that determines detection probabilities as a function of distance from the transect, assuming that there is a 100% probability of detecting an animal on the transect and the probability decreases with perpendicular distance. The detection function allows an estimation of densities within a band extending on both sides of the transect, based on encounter rates and correcting for undetected individuals [13]. With this method, transects can be resampled to increase the sample size for calculating encounter rates, and no individual recognition is necessary. A coefficient of variation is calculated from the variances in encounter rates, detection probabilities and group sizes. The CV is then used to calculate a confidence interval.

Table 1. Number of transects and sampling effort to estimate Cauca guan densities at three sites on the Cauca Valley slopes, Colombia. a All transects had the same length

| Locality/Habitat | Number of transects | Transect length (m) | Number of repetitions | Total sampling effort (km) |
|------------------|---------------------|---------------------|-----------------------|---------------------------|
|                  |                     | Mean (SD)           |                       |                           |
| Yotoco Forest    | 32                  | 359 (8)             | 21                    | 241                       |
| Yotoco Stream    | 4                   | 750 a               | 47                    | 140                       |
| Bremen Old-growth forest | 4               | 450 (123)           | 12                    | 22                        |
| Bremen Secondary forest    | 3                  | 700 a               | 13                    | 27                        |
| Bremen Early regeneration | 3              | 700 a               | 12                    | 26                        |
| Bremen Stream    | 3                   | 700 a               | 12                    | 24                        |

The number and length of transects varied depending on the extension and shape of the study area and its topography (Table 1). Transects were distributed throughout the study areas to obtain a representative density estimate. Maps showing the location of transects are available from the authors. We analysed data with the program Distance 6.0 [14]. Analyses were performed separately for each locality. We
graphed histograms of detection distances and for Yotoco and Bremen we truncated the distribution at 30 m, to eliminate outliers, i.e. distant detections that are beyond the main clump of detection data points [13]. For the Barbas data no truncation was necessary. Encounter rates were calculated assuming a Poisson distribution.

Detection functions were selected according to the fit between the frequency distribution of detection distances and theoretical models (main and adjustment functions) provided by the software Distance. The models we tested were: half-normal (cosine, hermite polynomial), uniform (cosine, simple polynomial) and hazard rate (cosine, simple polynomial). We chose the model providing the best fit according to the Akaike Information Criterion [13]. The variance of population densities was empirically calculated as the sum of the sampling variances of encounter rate, the estimate of detection probability, and group size [13].

Table 2. Group sizes and population densities of Cauca Guan in different habitats at three sites on the Cauca Valley slopes, Colombia.

| Locality/habitat       | Group size (individuals) | Density (ind./km²) |
|------------------------|--------------------------|--------------------|
|                        | Mean | 95% CI  | Mean | 95% CI | CV%   |
| **Yotoco**             |      |        |      |        |       |
| Total                  | 1.6  | 1.4-1.9 | 10.8 | 7.4-16  | 19.3  |
| Barbas                 |      |        |      |        |       |
| Total                  | 1.1  | 1.0-1.2 | 14   | 8.2-23.9 | 23.6  |
| Forest                 | 1.1  | 1.0-1.2 | 18.4 | 7.8-43.8 | 25.1  |
| Stream                 | 1.1  | 1.0-1.2 | 10.6 | 5.5-20.4 | 32    |
| **Bremen**             |      |        |      |        |       |
| Total                  | 1.2  | 1.1-1.3 | 21.3 | 13.6-33.5 | 21.3  |
| Old-growth forest      | 1.4  | 1.1-1.8 | 10.8 | 3.6-31.6 | 38.4  |
| Secondary forest       | 1.5  | 1.2-1.7 | 42.2 | 31.7-56.2 | 12.2  |
| Early regeneration     | 1.2  | 1.0-1.5 | 14.8 | 4.3-50.6 | 42.6  |
| Stream                 | 1.5  | 1.0-2.3 | 16.5 | 5.0-55.0 | 47.8  |

In the three sites we found an inverse relationship between detection probability and group size. This is a statistical artifact resulting from the small group sizes, and in this case, using the mean group size to calculate population density yields an underestimated value [13]. Therefore, we used the expected group size estimated from the regression between group size and detection probability. We used confidence intervals to compare population density estimates among localities. An overlap of >25% between the confidence intervals of two localities was interpreted as no significant differences in population densities [15].

**Results**

Cauca Guans were mostly observed singly or in pairs. Mean group size varied from 1.1 to 1.6 individuals at the three sites (Table 2). Larger groups were family units composed of a pair and one or two fledglings, or occurred as aggregations of up to five individuals at fruiting trees.
Overall population densities were similar in Yotoco, Barbas and Bremen, with 10.8 to 21.3 individuals per km² (Table 2). In Bremen and Barbas, guans used mature forest, second-growth forest of different ages, and riparian vegetation strips. Densities observed in different habitats in the latter two sites were similar and varied between 10 and 18 birds/km², except for the secondary forest at Bremen where we found significantly higher densities than in the other forest types (less than 25% overlap in confidence intervals; Table 2).

**Discussion**

Cauca Guan densities in old-growth forest in the three sites surveyed in this study varied between 10.8 ind/km² (Yotoco and Bremen) and 18.4 ind/km² (Barbas). A previous study at Yotoco in 2000-2001 [6] found a mean density of 8.6 ind/km², but this study used the variable-strip transect method, which may underestimate densities compared to distance sampling. Studies at Otún Quimbaya, a 411 ha flora and fauna sanctuary at elevations of 1,900-2,100 m, embedded in a landscape of continuous forest in the Otún River watershed (see Fig. 1 and a complete description in [9, 10]), have reported guan densities of 31 to 42 ind/km² in old-growth forest [6, 10, 16]. These densities are within the range of values reported for other montane species of Penelopine guans (Table 3). Thus, the endemic condition of the Cauca Guan does not imply low densities.

Table 3. Comparison of population densities estimated for montane species of Penelopine guans at different sites and times. Compare to data reported in this study for *P. perspicax* in Table 2.

| Species/site | Density (ind/km²) | Reference |
|--------------|-------------------|-----------|
| **Cauca Guan (*Penelope perspicax*)** | | |
| Otún Quimbaya total (1991) | 31 | [16] |
| Otún Quimbaya forest (1999-2001) | 42 | [6] |
| Otún Quimbaya ash (1999-2001) | 70-100 | [6] |
| Otún Quimbaya forest (2002-2003) | 31 | [10] |
| Otún Quimbaya ash (2002-2003) | 88 | [10] |
| Yotoco (2001) | 8.6 | [6] |
| **Andean Guan (*Penelope montagnii*)** | | |
| Ucumari, Colombia | 2 | [16] |
| NE Ecuador | 20-40 | [23] |
| **Bearded Guan (*Penelope barbata*)** | | |
| Selva Alegre, Ecuador | 17.1 | [17] |
| Chila, S. Ecuador | 2.3 | [17] |
| **Sickle-winged Guan (*Chamaepetes goudotii*)** | | |
| Otún Quimbaya | 13.7 | [20] |
| **Wattled Guan (*Aburria aburri*)** | | |
| Otún Quimbaya | 0.9 | [16] |
| Otún Quimbaya | 0.9 | [24] |
Density estimates of montane Penelopines exhibit great intraspecific variation (Table 3). For example, densities of Bearded Guan (P. barbata) in Ecuador vary between 2 and 17 ind/km² [17]. This variation is probably related to spatial variation in habitat productivity and other characteristics (e.g., composition of plant species that provide different fruit resources), as well as the extent of habitat available and the composition of the habitat mosaic. At Otún Quimbaya there are over 2,000 ha of forest within the altitudinal range of the Cauca Guan, so high densities may be related to the extent of available habitat (but may also be related to the availability of an abundant food resource; see below). Our data do not allow identification of the factors that determine differences in densities among sites, because the four sites that have been studied are each unique in the extent and composition of habitat types, so we have no replicates. This limitation is inherent to working with an endangered species that is found in few sites, which does not allow a design with adequate replication at the landscape scale.

Density variations may also be related to local movements by guans following resource availability. Many studies on cracids have short durations and have no information on temporal variabiliy [18], but it is known that some montane populations of guans conduct altitudinal migrations, tracking fruit and other resources [19]. At Otún Quimbaya, Cauca Guans feed on the young leaves of Chinese ash (Fraxinus chinensis), which were planted in monospecific stands during a revegetation program in the 1960s [6, 9, 10]. Previous studies at Otún Quimbaya [6, 9, 10] reveal a constant presence of guans in the forest, but densities increase in the ash plantation during November and December, with a parallel decrease in the forest, suggesting that guans are congregating in the ash plantation. Muñoz et al. [9] showed that the availability of fruit resources decreases in the forest during this period. Guans congregating at the plantation may be coming from an undetermined area in the vicinity of the plantation. Interestingly, the sympatric and ecologically similar Sickle-winged Guan (Chamaepetes goudotii), which also exploits ash at the same site, remains much rarer [20].

Population densities of cracids may also be affected by hunting. A study in the Peruvian Amazon [21] found that moderate hunting did not significantly reduce population densities of three species of cracids, compared to non-hunted areas, but heavy hunting reduced densities by one order of magnitude. The four sites we studied are protected areas and hunting is negligible, so we are not including this factor in our analysis.

**Implications for conservation**

In this paper we documented population density variations of an endangered species throughout the geographic range and within sites. Although these variations are theoretically expected, there is very little documentation of actual densities for tropical birds in general and endangered species in particular. In absolute terms our data show that an endemic, large-bodied species can attain high densities, similar to those of many small passerines (e.g., [22]). In relative terms we show that endemic cracids can attain higher densities than similar species with larger geographic distributions.

Although persistence of the Cauca Guan in fragmented landscapes requires the presence of relatively large forest fragments (>120 ha; J. Mendoza et al. unpublished data), the species is not restricted to mature forest and does not avoid edges. Secondary forest offers abundant fruit resources that are commonly eaten by guans (e.g., Araliaceae, Melastomataceae; [9, 18]), which may explain the high density observed in this habitat type in Bremen. Cauca Guans also use vegetation strips along streams. This opens the possibility of using corridors to connect populations currently isolated in forest patches, but to implement this strategy other factors such as increased vulnerability to hunting have to be taken into account.
Remnant forest fragments in the altitudinal range of the Cauca Guan in the Cauca Valley are small and isolated, and most are currently unoccupied by the guan [6]. The four sites we studied are protected areas, and have not changed significantly in the years since the study was made. Populations in the smaller fragments are small and vulnerable. For example, extrapolating the population density in Yotoco to the entire forest patch gives a population of 60 individuals (95% CI: 41-89). Therefore, under current conditions the Cauca Guan is a globally rare species and sustained efforts for its conservation are required. Conservation plans should recognize that the species exhibits spatial and temporal variations in population density (which may reflect local movements) in order to conserve the full range of conditions required by each population. In general, we suggest that studies seeking to quantify population densities of threatened species should have sufficient duration and spatial coverage to include natural variations in density.

Acknowledgments
We thank the National Parks Unit and the staff at the Santuario de Fauna y Flora Otún Quimbaya for logistical support. Work at Otún Quimbaya was funded by the Wildlife Conservation Society, Fundación EcoAndina and the John D. and Catherine T. MacArthur Foundation. Work at Yotoco was possible through permits and financial support from the Corporación Autónoma Regional del Valle del Cauca, the John D. and Catherine T. MacArthur Foundation, the Wildlife Conservation Society and Fundación EcoAndina. Work at Barbas-Bremen was funded by Corporación Autónoma Regional de Risaralda.

References
[1] Gaston, K. J. and Blackburn, T. M. 2000. *Pattern and process in macroecology*. Blackwell Science Ltd., Oxford, UK.
[2] Kattan, G. H. 1992. Rarity and vulnerability: the birds of the Cordillera Central of Colombia. *Conservation Biology* 6:64–70.
[3] Jankowski, J. E. and Rabenold, K. N. 2007. Endemism and local rarity in birds of neotropical montane rainforest. *Biological Conservation* 138:453–463.
[4] Kattan, G. H. and Beltrán, J. W. 1999. Altitudinal distribution, habitat use, and abundance of *Grallaria* antpittas in the Central Andes of Colombia. *Bird Conservation International* 9:271–281.
[5] Renjifo, L. M. 2002. *Penelope perspicax*. In: *Libro Rojo de aves de Colombia*. Renjifo, L. M., Franco-Mayra, A. M., Amaya-Espinell, J. D., Kattan, G. H. and López-Lanús, B. (Eds), pp. 124-130. Instituto de Investigación de Recursos Biológicos A. von Humboldt and Ministerio del Ambiente, Bogotá.
[6] Kattan, G. H., León, A., Corredor, G., Beltrán, W. and Parada, M. 2006. Distribution and population density of the Endangered Cauca guan *Penelope perspicax*. *Bird Conservation International* 16:299–307.
[7] del Hoyo. 1994. Family Cracidae (chachalacas, guans and curassows). In: *Handbook of the birds of the world, vol. 2. New World vultures to guineafowl*. del Hoyo, J., Elliott, A., Sargatal, J. (Eds), pp. 310-363. Lynx Edicions, Barcelona.
[8] Brooks, D. M. and Fuller, R. A. 2006. Biology and conservation of Cracids. In: Conserving Cracids: the most threatened family of birds in the Americas. Brooks, D. M. (Ed.), pp. 9-21. Miscellaneous Publications, Houston Museum of Natural Sciences No. 6, Houston.

[9] Muñoz, M. C., Londoño, G. A., Rios, M. M. and Kattan, G. H.. 2007. Diet of the Cauca guan: exploitation of a novel food source in times of scarcity. Condor 109:841–851.

[10] Rios, M. M., Londoño, G. A., Muñoz, M. C. and Kattan, G. H. 2008. Abundancia y endemismo en la pava caucana (Penelope perspicax): ¿Ecología o historia? Ornitológía Neotropical 19(suppl):295–303.

[11] Bock, C. E. and Jones, Z. F. 2004. Avian habitat evaluation: should counting birds count? Frontiers in Ecology and the Environment 2:403-410.

[12] Buler, J. J., Moore, F. R. and Woltmann, S. 2007. A multi-scale examination of stopover habitat use by birds. Ecology 88:1789-1802.

[13] Buckland, S., Anderson, D., Burnham, K., Laake, J., Borchers, D. and Thomas, L. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford, UK.

[14] Thomas, L., Laake, J., Rexstad, E., Strindberg, S., Marques, F. F. C., Buckland, S. T., Borchers, D. L., Anderson, D. R., Burnham, K. P., Burt, M. L., Hedley, S. L., Pollard, J. H., Bishop, J. R. B. and Marques, T. A. 2009. Distance 6.0. Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK.

[15] Cumming, G., Fidler, F. and Vaux, D. 2007. Error bars in experimental biology. Journal of Cell Biology 177:7-11.

[16] Nadachowski, E. 1994. Observaciones sobre la ecología de cuatro especies de paujiles (Cracidae) en el Parque Regional Natural Ucumari. In: Ucumari: un caso típico de la diversidad biótica andina. Rangel, J. O. (Ed), pp. 329-339. Corporación Autónoma Regional de Risaralda, Pereira, Colombia.

[17] Jacobs, M. D. and Walker, J. S. 1999. Density estimates of birds inhabiting fragments of cloud forest in southern Ecuador. Bird Conservation International 9:73–80.

[18] Muñoz, M. C. and Kattan, G. H. 2007. Diets of Cracids: how much do we know? Ornitológía Neotropical 18:21–36.

[19] Chaves-Campos, J. 2003. Changes in abundance of crested guan (Penelope purpurascens) and black guan (Chamaepetes unicolor) along an altitudinal gradient in Costa Rica. Ornitológía Neotropical 14:195–200.

[20] Londoño, G. A., Muñoz, M. C. and Rios, M. M. 2007. Density and natural history of the Sickle-winged Guan (Chamaepetes goudotii) in the Central Andes, Colombia. Wilson Journal of Ornithology 119:228–238.

[21] Begazo, A. J. and Bodmer, R. E. 1998. Use and conservation of Cracidae (Aves: Galliformes) in the Peruvian Amazon. Oryx 32:301-309.

[22] Kikuchi, D. W. 2009. Terrestrial and understorey insectivorous birds of a Peruvian cloud forest: species richness, abundance, density, territory size and biomass. Journal of Tropical Ecology 25:523-529.
[23] Creswell, 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 Sánchez, T. 1999. Densities and habitat preferences of Andean cloud-forest birds in pristine and degraded habitats in north-eastern Ecuador. *Bird Conservation International* 9:129–146.

[24] Rios, M. M., Londoño, G. A. and Muñoz, M. C. 2005. Densidad poblacional e historia natural de la pava negra (*Aburria aburri*) en los Andes centrales de Colombia. *Ornitologia Neotropical* 16:205–217.