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Source: The Condor, 118(1) : 24-32

Published By: American Ornithological Society

URL: <https://doi.org/10.1650/CONDOR-15-51.1>

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COMMENTARY

Population densities of curassows, guans, and chachalacas (Cracidae): Effects of body size, habitat, season, and hunting

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Submitted March 31, 2015; Accepted September 8, 2015; Published November 11, 2015

ABSTRACT

Understanding the factors that determine population densities is critical for conserving viable populations of threatened species. Half of the 50 species in the family Cracidae have experienced population declines. We conducted a literature review to explore the relations of population densities of cracids with body size, habitat, season, and hunting. We compiled 103 density data points for 27 species in 37 localities from Mexico to Argentina. There was no correlation between body mass and density. The larger cracines tended to have lower densities than penelopines, but densities in both subfamilies spanned a similar range of values. Intraspecific and interspecific densities varied among sites over 2 orders of magnitude (1–100 birds km⁻²). Some cracids exhibited plasticity in habitat use, with variable densities among habitats. There is evidence that some species performed local movements related to seasonality in rainfall or resource availability, leading to aggregations around water sources during the dry season or around seasonally abundant food sources. Hunting had a negative effect on population densities, but in some cases low to moderate hunting did not cause a decrease in density in comparison to nonhunted sites. Despite having similar ecologies, densities of cracid species are very variable, and each population seems to respond idiosyncratically to local factors, which requires care if data are extrapolated across populations or species. Future studies that aim to characterize cracid populations for conservation purposes should take into account possible intraspecific density variations related to seasonality, local movements, and habitat heterogeneity.

Keywords: Cracidae, habitat use, hunting, population density, seasonality

Densidades poblacionales de paujiles, pavas y guacharacas: Efectos del tamaño corporal, el hábitat, la estacionalidad y la cacería

RESUMEN

El estudio de los factores que determinan las densidades poblacionales, es crítico para la conservación de especies amenazadas. La mitad de las 50 especies de la familia Cracidae están amenazadas. Hicimos una revisión de literatura para evaluar las relaciones entre las densidades poblacionales de Cracidae y el tamaño corporal, el hábitat, la estacionalidad y la cacería. Obtuvimos 103 datos de densidades para 27 especies en 37 localidades entre México y Argentina. No encontramos correlación entre masa corporal y densidad. Las especies de Cracinae, que son más grandes, tienden a tener densidades más bajas que Penelopinae, pero en ambas subfamilias las densidades abarcan un intervalo similar de valores. Las densidades intra e interespecíficas varían geográficamente en dos órdenes de magnitud (1 a 100 individuos km⁻²). Algunas especies tienen plasticidad en el uso de hábitat y sus densidades varían entre hábitats. Hay evidencia de que algunas especies hacen movimientos locales relacionados con la estacionalidad en la precipitación o disponibilidad de recursos; los individuos se agregan alrededor de fuentes de agua durante la estación seca o alrededor de fuentes abundantes de alimento. La cacería tiene un efecto negativo sobre las densidades poblacionales, pero en algunos casos la cacería baja a moderada no causa una disminución en las densidades, en comparación con sitios sin cacería. A pesar de tener hábitos similares, las densidades de las especies de Cracidae son muy variables y cada población parece responder de manera idiosincrática a los factores locales. Se requiere precaución si se van a extrapolar datos entre poblaciones o especies. Los estudios futuros que busquen caracterizar las poblaciones de Cracidae con propósitos de conservación, deben tener en cuenta las posibles variaciones relacionadas con estacionalidad, movimientos locales y heterogeneidad de hábitat.

Palabras clave: Cracidae, uso de hábitat, la caza, la densidad de población, la estacionalidad

INTRODUCTION

Cracidae is a family of galliform birds endemic to the Neotropics (del Hoyo et al. 1994). The family contains 50 species, with their center of diversity in Colombia and Ecuador. Cracids are classified into 2 subfamilies. The Cracinae (curassows: 14 species) are large, mostly terrestrial birds, whereas the Penelopinae (guans and chachalacas: 36 species) are smaller and arboreal. Cracids are largely frugivorous but have broad diets that include animal matter and other foods (Muñoz and Kattan 2007). This is one of the most threatened families of birds, with 24 species listed in the Threatened, Endangered, or Critically Endangered categories (Brooks 2006). The major causes of population declines in these birds are habitat loss and hunting.

Developing spatially explicit conservation plans and preserving viable populations of cracids requires understanding their patterns of distribution and abundance and the processes that influence those patterns. Density is an important parameter that influences population dynamics through density-dependent vital rates. For example, at low densities, reproductive rates may be reduced as a result of Allee effects (inverse density dependence of per capita growth rate at low densities; Courchamp et al. 1999). Local population densities have been extrapolated to estimate abundance in a larger area or across the geographic range of a species, as a basis to estimate threat status (Renjifo et al. 2014). However, this requires caution because of spatial heterogeneity in density related to habitat structure and other local factors (Hansen et al. 1995). If local densities are highly variable, abundance estimates will be unreliable.

Many factors may influence population density and the spatial dispersion of individuals. Two of the main factors are body size and trophic level. There is a general negative correlation between body size and population density (Gaston and Blackburn 2000). However, most of the variation in bird population density that is explained by body size and trophic level occurs at the family and order taxonomic hierarchies, which suggests that these traits are phylogenetically conserved (McGill 2008).

Animal species normally exhibit large variations in abundance of populations across their ranges, with small numbers in most localities and a few abundance hotspots (Brown et al. 1995, Lundberg et al. 2000). One half of the variance in bird abundance (controlling for other factors, such as taxonomic affiliation and trophic level) is due to spatial variation within species (McGill 2008). Part of this variation is related to a spatial cline of abundance from the center to the periphery of the geographic range, which may result from source–sink dynamics (Curnutt et al. 1996). However, the generality of this clinal pattern has been challenged, because densities show much more complex spatial patterns (Sagarin et al. 2006). At local scales,

population densities may vary according to habitat suitability in heterogeneous landscapes, which, in turn, may be related to habitat structure or distribution and abundance of resources (Boyce and McDonald 1999). Density, however, is not a reliable indicator of habitat suitability, because numerous ecological factors may lead birds to settle in poor habitats (Johnson 2007).

Animals may also move in a landscape in response to temporal changes in resource distribution and abundance in different habitats, which may be related to seasonal or aseasonal fluctuations in climate. For example, variations in the availability of food resources are correlated with the local abundance of forest birds (Levey 1988, Poulin et al. 1992), and locally abundant resources may lead to temporary aggregations of individuals (Muñoz et al. 2007). In tropical mountains, birds may perform seasonal elevational movements in response to variations in food availability or climate (Boyle 2010, 2011).

Here, we use a literature review to explore how population density of cracids is related to body size, habitat heterogeneity within a locality, season, and hunting. We expected cracines to exhibit lower population densities than penelopines because of their larger sizes. In particular, chachalacas (*Ortalis* spp.) comprise a group of small penelopines that tolerate disturbed habitats (del Hoyo et al. 1994), so we expected them to be the most abundant. Curassows are considered sensitive to habitat disturbance and hunting (del Hoyo et al. 1994), and we expected these birds to be sedentary and restricted to mature forest. We also expected population densities of cracids to vary in relation to seasonality in rainfall and resource availability. Finally, cracids should be strongly affected by hunting.

METHODS

We searched the scientific literature to build a database on population densities of cracids. We used the keywords “cracid” and “bird population density” to find references in Google Scholar, and looked for citations of these papers as well as papers that they cited. We found 32 studies that reported a total of 103 density data points. Studies encompassed 27 species (10 Cracinae, 17 Penelopinae) and 37 localities distributed from Mexico to Argentina (Table 1).

The 32 studies used 4 main methods to estimate density. Sixteen studies used distance sampling. Birds were detected along transects, and the perpendicular distance to the transect was estimated. Then, using the program Distance (Thomas et al. 2009), data were used to generate detection probability as a function of distance to the transect and then to estimate density. In strip transects (10 studies), a detection distance determined by the observer was used to define the area of the sampled strip (width \times

TABLE 1. Species in the family Cracidae for which population densities have been reported and countries where they were studied.

Species	Country	References
Subfamily Cracinae		
<i>Crax Alberti</i>	Colombia	Rodríguez 2008
<i>C. alector</i>	French Guiana	Thiollay 1989, 1994
<i>C. daubentoni</i>	Venezuela	Silva and Strahl 1997, Strahl et al. 1997, Bertsch and Barreto 2008
<i>C. fasciolata</i>	Brazil	Desbiez and São Bernardo 2011
<i>C. globulosa</i>	Colombia, Brazil, Bolivia, Peru	Alarcón-Nieto and Palacios 2008, Haugaasen and Peres 2008, Hill et al. 2008, Yahuarcani et al. 2009
<i>C. mitu</i>	Peru	Terborgh et al. 1990
<i>C. rubra</i>	Guatemala, Mexico	Martínez-Morales 1999, Eisermann 2004
<i>Mitu tuberosa</i>	Peru, Brazil, Bolivia	Torres 1997, Begazo and Bodmer 1998, Haugaasen and Peres 2008, Hill et al. 2008, Barrio 2011
<i>Nothocrax urumutum</i>	Peru	Parker 2002
<i>Pauxi pauxi</i>	Colombia, Venezuela	Silva and Strahl 1997, Setina et al. 2012
Subfamily Penelopinae		
<i>Aburria aburri</i>	Colombia, Venezuela	Nadachowski 1994, Silva and Strahl 1997, Rios et al. 2005
<i>A. pipile</i>	Trinidad	Hayes et al. 2009
<i>Chamaepetes goudotii</i>	Colombia	Londoño et al. 2007
<i>Oreophasis derbianus</i>	Mexico	Abundis-Santamaría and González-García 2007
<i>Ortalis canicollis</i>	Paraguay, Bolivia	Brooks 1997, Mamani 2001
<i>O. guttata</i>	Peru, Brazil	Torres 1997, Begazo and Bodmer 1998, Haugaasen and Peres 2008
<i>O. ruficauda</i>	Venezuela	Silva and Strahl 1997, Schmitz-Ornés 1999
<i>Penelope argyrotis</i>	Venezuela	Silva and Strahl 1997
<i>P. barbata</i>	Ecuador	Jacobs and Walker 1999
<i>P. jacquacu</i>	Peru, Brazil	Terborgh et al. 1990, Torres 1997, Begazo and Bodmer 1998, Haugaasen and Peres 2008, Barrio 2011
<i>P. marail</i>	French Guiana	Thiollay 1994
<i>P. montagnii</i>	Ecuador, Colombia	Nadachowski 1994, Creswell et al. 1999
<i>P. obscura</i>	Brazil	Guix et al. 1997
<i>P. perspicax</i>	Colombia	Kattan et al. 2006, 2014
<i>P. purpurascens</i>	Venezuela	Silva and Strahl 1997
<i>Pipile cumanensis</i>	Peru	Terborgh et al. 1990, Torres 1997, Begazo and Bodmer 1998, Barrio 2011
<i>P. jacutinga</i>	Brazil	Galetti et al. 1997, Guix et al. 1997

length), and density was calculated as the number of individuals detected divided by that area. Point counts were used in 2 studies. A stationary observer detected birds within a circle and used the maximum detection distance to calculate the area sampled. Finally, 3 studies estimated densities by spot mapping birds within a defined study area.

We analyzed the effect of survey method (distance sampling, strip transect, point counts, and spot mapping) on the natural logarithm of population densities by using a linear mixed model, which included species as a random effect to account for potential taxonomic differences in the methods used. We performed our analyses in R version 3.2 (R Development Core Team 2014). We did not find any significant differences between densities estimated by the various sampling methods (likelihood ratio test [LRT]; $\chi^2 = 1.18$, $df = 3$, $P = 0.75$), although our power to detect an effect of the latter 2 methods was low because of the small number of cases. In subsequent analyses we ignored survey method.

To calculate correlations between body mass and population density, we used only data obtained in the birds' main habitat type (i.e. undisturbed, nonfragmented forest) and in the absence of hunting. This gave us 24 species for analysis. Often, several density values were available for each species in 1 or more localities. Therefore, in conducting a linear regression of $\ln(\text{density})$ against $\ln(\text{mass})$, we included species as a random effect in the model. We also used regression analysis with species as a random effect, to test for differences between cracine and penelopine densities.

Four studies reported density data of 6 species in different habitats within a locality. The study designs, localities, and habitats were very heterogeneous, which precluded a quantitative analysis of how densities varied with habitat. Therefore, we present those results in a descriptive form.

To analyze the effect of hunting on population density, we first used studies in which hunted and nonhunted forests were paired together at the same site. Three

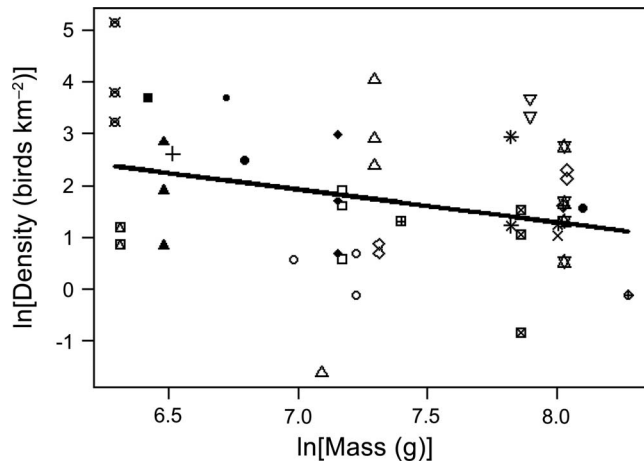


FIGURE 1. Logarithmic relationship between mean density and body mass for 24 species of cracids. Data from undisturbed, nonfragmented sites. Each distinct shape indicates data from a unique species.

studies presented comparative data (Table 2). Begazo and Bodmer (1998) collected data from hunters at 3 sites classified as “protected area,” “moderately hunted,” and “heavily hunted.” Thiollay (1989) classified 3 sites as no “hunting,” “near hunting area,” and “regularly hunted.” Mamani (2001) surveyed sites with subsistence hunting and no hunting. Only Begazo and Bodmer (1998) presented quantitative data on harvested birds, so we used qualitative categories for analysis.

In addition to our paired hunting and no-hunting data, we looked for an effect of hunting across our wider dataset that included unpaired sites. To do this, we modeled the natural logarithm of density as a function of being in a hunted or nonhunted area, with $\ln(\text{body mass})$ included as a covariate. We included habitat type nested within study site as a random effect to control for variance in density across habitats and sites. We tested the likelihood of this model against a model that did not include hunting as a predictor, using the likelihood ratio test.

RESULTS

Body masses of the 27 cracid species included in this sample varied by an order of magnitude, between 400 and 4,000 g. Cracines were larger than penelopines, and with the exception of *Nothocrax urumutum* (Cracinae), whose body mass (1,250 g) was in the upper range of penelopine body masses, there was no overlap between the 2 subfamilies.

In populations that had not experienced habitat disturbance, fragmentation, or hunting, there was no correlation between $\ln(\text{mass})$ and $\ln(\text{density})$ ($t_{21} = -1.6$, $P = 0.12$; Figure 1). We found no significant differences between cracine and penelopine densities ($t_{22} = 0.94$, $P = 0.36$). Mean density (\pm SE) was 8.9 ± 7.4 birds km^{-2} for cracines ($n = 8$ species) and 17.7 ± 9.4 birds km^{-2} for penelopines ($n = 16$ species). However, cracine densities in general were <20 birds km^{-2} , except for *Crax daubentoni*, which reached densities of ≤ 40 birds km^{-2} . The smaller cracine species covered a broad range of densities that included the lowest values observed in this subfamily (Figure 2). Penelopine densities varied between 1 and 42 birds km^{-2} , but *Ortalis canicollis* reached densities of 170 birds km^{-2} . Several penelopines had densities of <10 birds km^{-2} (Figure 2).

Intraspecific and interspecific cracid densities varied geographically over 2 orders of magnitude (1–100 birds km^{-2} ; Figure 2). For species with >1 density estimate in what seemed to be adequate habitat with no hunting, there were large differences in densities among localities. In particular, densities were highly intraspecifically and interspecifically variable among guans in the genus *Penelope*. Densities of *Penelope barbata* in montane habitats (unprotected but undisturbed cloud forest) in Ecuador ranged from 2 to 17 birds km^{-2} (Jacobs and Walker 1999). Other montane species reached comparatively high densities. For example, densities of *P. perspicax* ranged from 10 to 42 birds km^{-2} in several protected sites in the Colombian Andes (Kattan et al. 2014). An Amazonian species, *P. jacquacu*, had a low density in a

TABLE 2. Studies comparing population densities of cracids among sites with different intensities of hunting.

Species	Region	No hunting	Low-moderate hunting	Heavy-regularly hunted	Reference
<i>Crax alector</i>	French Guiana	8.37	1.38 ^a	0.39	Thiollay 1989
<i>Mitu tuberosa</i>	Peruvian Amazon	1.65	2.08	0.02	Begazo and Bodmer 1998
<i>Ortalis canicollis</i>	Bolivian Chaco ^b	44.6		8.7	Mamani 2001
<i>O. canicollis</i>	Bolivian Chaco ^b	172.1		41.9	Mamani 2001
<i>O. guttata</i>	Peruvian Amazon	3.28	3.6	5.95	Begazo and Bodmer 1998
<i>Penelope jacquacu</i>	Peruvian Amazon	5.46	5.46	0.22	Begazo and Bodmer 1998
<i>Pipile cumanensis</i>	Peruvian Amazon	6.79	9.37	0.44	Begazo and Bodmer 1998

^a Near hunting area (see text).

^b Two different habitats.

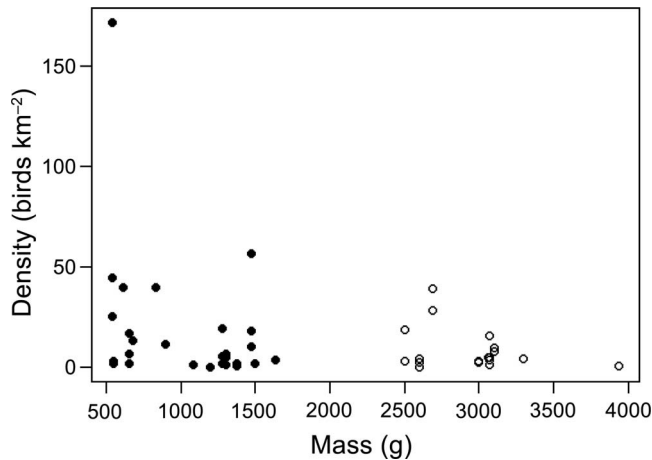


FIGURE 2. Relationship between body mass and density for cracids. This graph includes all data points, so a species may be represented by >1 point ($n = 46$ density data points, $n = 24$ species). Filled circles are penelopines, and open circles are cracines.

protected area (Manu National Park, Peru, 2 birds km^{-2} ; Terborgh et al. 1990), although one study reported densities of ~ 20 birds km^{-2} (Torres 1997). In another Amazonian locality (Rio Purús), densities of this species in different habitats were 0.2–4.4 birds km^{-2} (Haugaasen and Peres 2008).

We found data for 3 species of chachalacas. Two of them (*O. canicollis* and *O. ruficauda*) exhibited the highest densities in the family, but the third one (*O. guttata*) had low densities (3.3 birds km^{-2} in a protected area; Begazo and Bodmer 1998). Densities of chachalacas varied in different habitats. For example, in the Chaco region of Bolivia, densities of *O. canicollis* were 4 \times higher in tall riverine forest than in drier scrub vegetation (Mamani 2001). In Venezuela, densities of *O. ruficauda* were higher in agricultural areas (with fruit plantation fields and deciduous forest in adjacent hills) than in deciduous and

semideciduous forest in a protected area (Schmitz-Ornés 1999).

Density variations and movements among habitat types have also been reported in other forest-dependent species in both cracid subfamilies (Table 3). For example, Bertsch and Barreto (2008) reported that in central Venezuela, *C. daubentoni* inhabited heterogeneous landscapes comprising gallery and dry forest, but also used forest borders, hedges, and open area. Birds reached very high densities during the dry season in seasonally dry forest and gallery forest, which suggests aggregation around water sources. In open savanna, which may be considered a marginal habitat, densities were low in both seasons.

Another cracine, *Mitu salvini*, was studied in the northwestern Colombian Amazon, where Parra et al. (2001) followed a family group for 6 mo. The group had a home range of 72 ha that included riparian, flooded, open, and mature forest. The birds temporally shifted their patterns of habitat use in response to changes in food resources, mainly the availability of fruit in flooded and mature forest.

Patterns of habitat use at the population level have been reported for *P. perspicax* in the Colombian Andes (Kattan et al. 2014). Densities varied, from 10–18 birds km^{-2} in medium-sized (500–700 ha), isolated forest tracts to 42 birds km^{-2} in a continuous forest of several thousand hectares. These guans also used secondary forest, early regeneration, and ribbons of vegetation along streams, where densities were 10–40 birds km^{-2} . At one site, guans congregated at a Chinese ash (*Fraxinus chinensis*) plantation, where they reached densities of 100 birds km^{-2} (Kattan et al. 2006, Rios et al. 2008). Guans aggregated in large numbers at the ash plantation and fed on ash foliage during the period of low fruit availability in the forest (Muñoz et al. 2007).

Two cracines were surveyed on islands. On Cozumel Island, Mexico, densities of *C. rubra* were very low (0.9 birds km^{-2}), and 60% of records were obtained <250 m

TABLE 3. Summary of studies reporting population densities of cracids in different habitat types.

Species and site/conditions	Habitat and density (birds km^{-2})			Country	Reference
<i>Crax daubentoni</i>	Gallery forest	Dry forest	Savanna	Venezuela	Bertsch and Barreto 2008
Dry season	161	44	13		
Wet season	40	28	8		
<i>Ortalis ruficauda</i>	Continuous forest	Agricultural-forest	Urban-forest	Venezuela	Schmitz-Ornés 1999
	38	56	20		
<i>Penelope perspicax</i>	Old-growth forest	Second-growth forest	Riparian forest	Colombia	Kattan et al. 2014
Barbas	18		11		
Bremen	11	42	17		
	Terra firme forest	Várzea	Igapó	Brazil	Haugaasen and Peres 2008
<i>P. jacquacu</i>	4	0.2	0.6		
<i>O. guttata</i>		1.5	1		
<i>Mitu tuberosum</i>	1.6	3	1		

from a water source (Martínez-Morales 1999). By contrast, on an island in the Caqueta River, Colombia, densities of *C. globulosa* ranged from 11 birds km⁻² in forest with a dense understory to 19 birds km⁻² in mature forest and 29 birds km⁻² in disturbed forest (Alarcón-Nieto and Palacios 2008). The density reported for this species in riparian varzea in Bolivia was 3.4 birds km⁻² (Hill et al. 2008).

Movements on a larger scale have been documented in *P. purpurascens* and *Chamaepetes unicolor* in the Tilarán mountains of Costa Rica (Chaves-Campos 2003), by quantifying changes in abundance at different elevations. Both species breed in lower montane rainforest at 1,400 m and apparently move downslope to elevations of 800 m (premontane rainforest), with *P. purpurascens* going as low as 400 m at the transition of tropical wet forest to premontane forest. These movements coincided with a general pattern of altitudinal migration for bird species at this site.

In our analysis of studies with paired data on hunting (Table 2), we found a significant effect of hunting on population density (LRT; $\chi^2 = 11.13$, $df = 2$, $P = 0.004$). Tukey's HSD revealed that although there was no difference between areas with no hunting and areas with low hunting ($z = 0.41$, $P = 0.91$), areas with heavy hunting had significantly lower population densities than areas with no hunting ($z = 4.24$, $P < 0.001$). Indeed, populations in areas with low hunting pressure also had higher densities than those in areas with heavy hunting pressure ($z = 3.33$, $P < 0.002$). In our analysis of the entire dataset that included both paired and unpaired sites, we found that hunting continued to have a significant negative effect on $\ln(\text{population density})$ ($\chi^2 = 6.01$, $P = 0.014$). Hunting of some species may favor other species. In the study of Begazo and Bodmer (1998), *O. guttata* was more abundant in hunted areas, because it is little hunted compared with the other 3 (larger) species.

DISCUSSION

We found no clear relationship between body size and population density in Cracidae. Some of the small species exhibited low densities, and a few of the large species had relatively high densities. In addition, the smaller penelopines were not necessarily more abundant than cracines. In analyses that included a broad range of body sizes (≥ 7 orders of magnitude) and density data obtained from multiple localities, mean density of a species scaled to the $-3/4$ power of body mass (White et al. 2007). Our dataset includes a body-mass range of only 1 order of magnitude, which represents a small part of the global range. Thus, in this context, the lack of correlation in our analysis is due to regression scale. Cracids are highly frugivorous, but their diets are very broad and plastic (Muñoz and Kattan 2007). Therefore, diet is unlikely to explain the observed variability in population density.

Cracid population densities varied over 2 orders of magnitude. In some cases, densities were relatively high, even compared to small passerines. At several Neotropical forests sites where bird densities have been estimated, densities of nonpasserine species varied between 1 and 100 birds km⁻² (Terborgh et al. 1990, Robinson et al. 2000, Haugaasen and Peres 2008). Insectivorous passerine densities also varied within the same range, although many species had densities of < 20 birds km⁻² (Stouffer 2007, Kikuchi 2009). In Manaus, Amazonian Brazil, median density of 228 bird species was 5 birds km⁻², and 55 species had ≤ 2 birds km⁻² (Johnson et al. 2011). Thus, cracid densities in general are not particularly low.

Intraspecific densities of cracids are geographically variable, although few species have been evaluated at more than 1 locality. Geographic variability in abundance is a general phenomenon observed in birds and other animals, as population densities respond to combinations of factors that include variation in environmental conditions and species interactions (Lundberg et al. 2000, Sagarin et al. 2006). The factors that drive geographic variability in cracid populations have not been investigated, but one possible factor is productivity related to latitude, elevation, temperature, and precipitation patterns.

Habitat specialization is a dimension of rarity and an important factor of vulnerability (Arita et al. 1990, Brooks 1998). Therefore, documenting spatial and temporal patterns of habitat use is critical for conserving cracid populations. Many cracids seem to be plastic and use different habitats in heterogeneous landscapes. Variability among habitats in the numbers of birds may reflect 1 of 3 situations: (1) Different individuals show consistent preferences for a particular type of habitat, where they remain most of the time; (2) individuals move among habitats over short-term periods; or (3) populations move seasonally among habitats (e.g., Parra et al. 2001, Rios et al. 2006). Habitat shifts and local to regional movements in response to food availability have been documented in some avian species (Law and Dickman 1998, Renton 2001, Holbrook et al. 2002, Haugaasen and Peres 2007). Plasticity in habitat use promotes population stability because it provides a range of resources and microclimates at the landscape scale (Oliver et al. 2010). Thus, habitat mosaics are important, and the protection of a single habitat may be insufficient for the conservation of populations (Law and Dickman 1998). The seasonal patterns of habitat use in cracids require better documentation.

Hunting is a major threat for cracids, which may constitute the main hunted item in some ethnic communities (Begazo and Bodmer 1998). The risk is increased if the hunted animals are rare (Brooks 1999). Even if populations are not extirpated, heavy hunting reduces population densities to the point where they may be

demographically inviable because of Allee effects. The impact of hunting will depend on harvest rates and the extent of the area affected (Brooks 1999). For an area of 276 km² in Amazonian Peru, Begazo and Bodmer (1998) estimated that harvest rates of *M. tuberosa* and *P. cumanensis* were unsustainable, but harvest of *P. jacquacu* was within sustainable levels. The persistence of hunted populations also depends on the presence of nonhunted, adjacent areas that may function as refuges or populations sources, although the hunted area may be a population sink (Powell et al. 1996).

Cracids are usually among the largest species in Neotropical bird assemblages, but they are not necessarily scarce—the rarest species are not necessarily the largest ones. Despite differences in body size and terrestrial versus arboreal habits, cracid species exhibit many ecological similarities, such as highly frugivorous but opportunistic and broad diets. Cracid densities are geographically variable and exhibit temporal fluctuations as they move among habitats tracking resources. Results from our small, but geographically and taxonomically broad, sample suggest that cracid populations respond idiosyncratically to local factors. Therefore, researchers and managers should be cautious when extrapolating data across species or even among populations of the same species. Future studies that aim to characterize cracid populations should take into account possible intraspecific density variations related to seasonality, local movements, and habitat heterogeneity.

ACKNOWLEDGMENTS

We thank Dan Brooks and an anonymous reviewer for helpful comments on the manuscript.

Author contributions: G.H.K. and M.C.M. conceived the idea. G.H.K. and M.C.M. collected data and conducted the research. D.W.K. and G.H.K. analyzed the data. And G.H.K. and D.W.K. wrote the paper.

LITERATURE CITED

- Abundis-Santamaría, A., and F. González-García (2007). Propuesta de protocolo para el monitoreo de la población de pavón (*Oreophaps derbianus*) en la Reserva de la Biosfera El Triunfo, Chiapas. In *Memorias del III Simposium Internacional sobre Oreophaps derbianus* (J. Cornejo and E. Secaira, Editors). Comité Internacional para la Conservación de *Oreophaps derbianus* y su Hábitat, Veracruz, Mexico. pp. 28–34.
- Alarcón-Nieto, G., and E. Palacios (2008). Estado de la población del pavón moquirrojo (*Crax globulosa*) en el bajo río Caquetá, Amazonía colombiana. *Ornitología Neotropical* 19:371–376.
- Arita, H. T., J. G. Robinson, and K. H. Redford (1990). Rarity in Neotropical forest mammals and its ecological correlates. *Conservation Biology* 4:181–192.
- Barrio, J. (2011). Hunting pressure on cracids (Cracidae: Aves) in forest concessions in Peru. *Revista Peruana de Biología* 18: 225–230.
- Begazo, A. J., and R. E. Bodmer (1998). Use and conservation of Cracidae (Aves: Galliformes) in the Peruvian Amazon. *Oryx* 32: 301–309.
- Bertsch, C., and G. R. Barreto (2008). Abundancia y área de acción del paují de copete (*Crax daubentoni*) en los llanos centrales de Venezuela. *Ornitología Neotropical* 19 (Supplement):287–293.
- Boyce, M. S., and L. L. McDonald (1999). Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution* 14:268–272.
- Boyle, W. A. (2010). Does food abundance explain altitudinal migration in a tropical frugivorous bird? *Canadian Journal of Zoology* 88:204–213.
- Boyle, W. A. (2011). Short-distance partial migration of Neotropical birds: A community-level test of the foraging limitation hypothesis. *Oikos* 120:1803–1816.
- Brooks, D. M. (1997). Population and ecological parameters of the Chaco chachalaca (*Ortalis canicollis*). In *The Cracidae: Their Biology and Conservation* (S. D. Strahl, S. Beaujon, D. M. Brooks, A. J. Begazo, G. Sedaghatkish, and F. Olmos, Editors). Hancock House, Blaine, WA, USA. pp. 412–417.
- Brooks, D. M. (1998). Habitat variability as a predictor of rarity in large Chacoan mammals. *Vida Silvestre Neotropical* 7:115–120.
- Brooks, D. M. (1999). *Pipile* as a protein source to rural hunters and Amerindians. In *Biology and Conservation of the Piping Guans (Pipile)* (D. M. Brooks, A. J. Begazo, and F. Olmos, Editors). Special Monograph Series of the Cracid Specialist Group 1. pp. 42–50.
- Brooks, D. M. (Editor) (2006). *Conserving cracids: The most threatened family of birds in the Americas*. Miscellaneous Publications of the Houston Museum of Natural Science 6.
- Brown, J. H., D. W. Mehlman, and G. C. Stevens (1995). Spatial variation in abundance. *Ecology* 76:2028–2043.
- Chaves-Campos, J. (2003). Changes in abundance of Crested Guan (*Penelope purpurascens*) and Black Guan (*Chamaepetes unicolor*) along an altitudinal gradient in Costa Rica. *Ornitología Neotropical* 14:195–200.
- Courchamp, F., T. Clutton-Brock, and B. Grenfell (1999). Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution* 14:405–410.
- Creswell, W., M. Hughes, R. Mellanby, S. Bright, P. Catry, J. Chaves, J. Freile, A. Gabela, H. Martineau, R. McLeod, F. McPhie, et al. (1999). Densities and habitat preferences of Andean cloud-forest birds in pristine and degraded habitats in north-eastern Ecuador. *Bird Conservation International* 9: 129–145.
- Curnutt, J. L., S. L. Pimm, and B. A. Maurer (1996). Population variability of sparrows in space and time. *Oikos* 76:131–144.
- del Hoyo, J., A. Elliott, and J. Sargatal (Editors) (1994). *Handbook of the Birds of the World*, vol. 2: New World Vultures to Guinea-fowl. Lynx Edicions, Barcelona, Spain.
- Desbiez, A. L. J., and C. São Bernardo (2011). Density estimates of the Bare-faced Curassow (*Crax fasciolata*) in the Brazilian Pantanal. *Revista Brasileira de Ornitologia* 19:385–390.
- Eisermann, K. (2004). *Estatus de Crax rubra en Punta de Manabique, Guatemala: hábitat, tamaño de población e*

- impacto humano. Boletín de IUCN/Birdlife/WPA Grupo de Especialistas en Crácidos 18:4–8.
- Galetti, M., P. Martuscelli, F. Olmos, and A. Aleixo (1997). Ecology and conservation of the jacutinga *Pipile jacutinga* in the Atlantic forest of Brazil. *Biological Conservation* 82:31–39.
- Gaston, K. J., and T. M. Blackburn (2000). *Pattern and Process in Macroecology*. Blackwell Science, Oxford, UK.
- Guix, J. C., S. Mañosa, V. Pedrocchi, M.-J. Vargas, and F. L. Souza (1997). Census of three frugivorous birds in an Atlantic rainforest area of southeastern Brazil. *Ardeola* 44:229–233.
- Hansen, A. J., W. C. McComb, R. Vega, M. G. Raphael, and M. Hunter (1995). Bird habitat relationships in natural and managed forests in the west Cascades of Oregon. *Ecological Applications* 5:555–569.
- Haugaasen, T., and C. A. Peres (2007). Vertebrate responses to fruit production in Amazonian flooded and unflooded forests. *Biodiversity and Conservation* 16:4165–4190.
- Haugaasen, T., and C. A. Peres (2008). Population abundance and biomass of large-bodied birds in Amazonian flooded and unflooded forests. *Bird Conservation International* 18: 87–101.
- Hayes, F. E., B. Sanasie, and I. Samad (2009). Status and conservation of the critically endangered Trinidad Piping-guan *Aburria pipile*. *Endangered Species Research* 7:77–84.
- Hill, D. L., H. Arañibar-Rojas, and R. MacLeod (2008). Wattled Curassows in Bolivia: Abundance, habitat use and conservation status. *Journal of Field Ornithology* 79:345–351.
- Holbrook, K. M., T. B. Smith, and B. D. Hardesty (2002). Implications of long-distance movements of frugivorous rain forest hornbills. *Ecography* 25:745–749.
- Jacobs, M. D., and J. S. Walker (1999). Density estimates of birds inhabiting fragments of cloud forest in southern Ecuador. *Bird Conservation International* 9:73–79.
- Johnson, E. I., P. C. Stouffer, and C. F. Vargas (2011). Diversity, biomass, and trophic structure of a central Amazonian rainforest bird community. *Revista Brasileira de Ornithologia* 19:1–16.
- Johnson, M. D. (2007). Measuring habitat quality: A review. *The Condor* 109:489–504.
- Kattan, G. H., A. León, G. Corredor, W. Beltrán, and M. Parada (2006). Distribution and population density of the endangered Cauca Guan *Penelope perspicax*. *Bird Conservation International* 16:299–307.
- Kattan, G. H., N. Roncancio, Y. Banguera, M. Kessler-Rios, G. A. Londoño, O. H. Marín, and M. C. Muñoz (2014). Spatial variation in population density of an endemic and endangered bird, the Cauca Guan (*Penelope perspicax*). *Tropical Conservation Science* 7:161–170.
- 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.
- Law, B. S., and C. R. Dickman (1998). The use of habitat mosaics by terrestrial vertebrate fauna: Implications for conservation and management. *Biodiversity and Conservation* 7:323–333.
- Levey, D. J. (1988). Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* 58:251–269.
- Londoño, G. A., M. C. Muñoz, and M. M. Rios (2007). Density and natural history of the Sickie-winged Guan (*Chamaepetes goudotii*) in the Central Andes, Colombia. *The Wilson Journal of Ornithology* 119:228–238.
- Lundberg, P., E. Ranta, J. Ripa, and V. Kaitala (2000). Population variability in space and time. *Trends in Ecology & Evolution* 15:460–464.
- Mamani, A. M. (2001). Aspectos biológicos y evaluación de la densidad poblacional de la charata *Ortalis canicollis* en Izozog, Prov. Cordillera del Dpto. Santa Cruz, Bolivia. In *Cracid Ecology and Conservation in the New Millenium* (D. M. Brooks and F. González-García, Editors). *Miscellaneous Publications of the Houston Museum of Natural Science* 2. pp. 87–100.
- Martínez-Morales, M. A. (1999). Conservation status and habitat preferences of the Cozumel Curassow. *The Condor* 101:14–20.
- McGill, B. J. (2008). Exploring predictions of abundance from body mass using hierarchical comparative approaches. *The American Naturalist* 172:88–101.
- Muñoz, M. C., and G. H. Kattan (2007). Diets of cracids: How much do we know? *Ornithologia Neotropical* 18:21–36.
- Muñoz, M. C., G. A. Londoño, M. M. Rios, and G. H. Kattan (2007). Diet of the Cauca Guan: Exploitation of a novel food source in times of scarcity. *The Condor* 109:841–851.
- 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* (J. O. Rangel, Editor). *Corporación Autónoma Regional de Risaralda, Pereira, Colombia*. pp. 329–339.
- Oliver, T., D. B. Roy, J. K. Hill, T. Brereton, and C. D. Thomas (2010). Heterogeneous landscapes promote population stability. *Ecology Letters* 13:473–484.
- Parker, T. A., III (2002). Behavior, habitat, and status of the Nocturnal Curassow (*Nothocrex urumutum*) in northern Peru. *Ornithologia Neotropical* 13:153–158.
- Parra, J. L., M. Agudelo, Y. Molina, and G. A. Londoño (2001). Use of space by a pair of Salvin's Curassows (*Mitu salvini*) in northwestern Colombian Amazon. *Ornithologia Neotropical* 12:189–204.
- Poulin, B., G. Lefebvre, and R. McNeill (1992). Tropical avian phenology in relation to abundance and exploitation of food resources. *Ecology* 73:2295–2309.
- Powell, R. A., J. W. Zimmerman, D. E. Seaman, and J. F. Gilliam (1996). Demographic analyses of a hunted black bear population with access to a refuge. *Conservation Biology* 10:224–234.
- R Development Core Team (2014). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Renjifo, L. M., M. F. Gómez, J. Velásquez-Tibatá, A. M. Amaya-Villareal, G. H. Kattan, J. D. Amaya-Espinel, and J. Burbano-Girón (2014). *Libro Rojo de aves de Colombia volumen I. Bosques húmedos de los Andes y la costa pacífica*. Editorial Pontificia Universidad Javeriana, Bogotá, Colombia.
- Renton, K. (2001). Lilac-crowned Parrot diet and food resource availability: Resource tracking by a parrot seed predator. *The Condor* 103:62–69.
- Rios, M. M., G. A. Londoño, and M. C. Muñoz (2005). Densidad poblacional e historia natural de la pava negra (*Aburria aburri*) en los Andes centrales de Colombia. *Ornithologia Neotropical* 16:205–217.
- Rios, M. M., G. A. Londoño, M. C. Muñoz, and G. Kattan (2008). Abundancia y endemismo en la pava caucana (*Penelope*

- perspicax*): ¿ecología o historia? Ornitología Neotropical 19 (Supplement):295–303.
- Rios, M. M., M. C. Muñoz, and G. A. Londoño (2006). Historia natural de la Pava Caucana (*Penelope perspicax*). Ornitología Colombiana 4:16–27.
- Robinson, W. D., J. D. Brawn, and S. K. Robinson (2000). Forest bird community structure in central Panama: Influence of spatial scale and biogeography. Ecological Monographs 70: 209–235.
- Rodríguez, E. L. (2008). Densidad y estructura poblacional del Paujil Piquiazul (*Crax alberti*) en la Reserva Natural de las Aves El Paujil, serranía de Las Quinchas, Colombia. Conservación Colombiana 4:46–59.
- Sagarin, R. D., S. D. Gaines, and B. Gaylord (2006). Moving beyond assumptions to understand abundance distributions across the ranges of species. Trends in Ecology & Evolution 21:524–530.
- Schmitz-Ornés, A. (1999). Vulnerability of Rufous-vented Chachalacas (*Ortalis ruficauda*, Cracidae) to man-induced habitat alterations in northern Venezuela. Ornitología Neotropical 10: 27–34.
- Setina, V., D. J. Lizcano, D. M. Brooks, and L. F. Silveira (2012). Population density of the Helmeted Curassow (*Pauxi pauxi*) in Tamá National Park, Colombia. The Wilson Journal of Ornithology 124:316–320.
- Silva, J. L., and S. Strahl (1997). Presión de caza sobre poblaciones de Crácidos en los parques nacionales al norte de Venezuela. In The Cracidae: Their Biology and Conservation (S. D. Strahl, S. Beaujon, D. M. Brooks, A. J. Begazo, G. Sedaghatkish, and F. Olmos, Editors). Hancock House, Blaine, WA, USA. pp. 437–448.
- Stouffer, P. C. (2007). Density, territory size, and long-term spatial dynamics of a guild of terrestrial insectivorous birds near Manaus, Brazil. The Auk 124:291–306.
- Strahl, S., J. L. Silva, and R. Buchholz (1997). Variación estacional en el uso del hábitat, comportamiento de grupo y un sistema aparentemente polígamo en el pauji copete de plumas, *Crax doubentoni*. In The Cracidae: Their Biology and Conservation (S. D. Strahl, S. Beaujon, D. M. Brooks, A. J. Begazo, G. Sedaghatkish, and F. Olmos, Editors). Hancock House, Blaine, WA, USA. p. 79.
- Terborgh, J., S. K. Robinson, T. A. Parker III, C. A. Munn, and N. Pierpont (1990). Structure and organization of an Amazonian forest bird community. Ecological Monographs 60:213–238.
- Thiollay, J. M. (1989). Area requirements for the conservation of rain forest raptors and game birds in French Guiana. Conservation Biology 3:128–137.
- Thiollay, J. M. (1994). Structure, density and rarity in an Amazonian rainforest bird community. Journal of Tropical Ecology 10:449–481.
- Thomas, L., J. Laake, E. Rexstad, S. Strindberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, M. L. Burt, S. L. Hedley, et al. (2009). Distance 6.0 release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK.
- Torres, B. (1997). Densidades poblacionales de la comunidad de crácidos en el Parque Nacional Manú (Peru). In The Cracidae: Their Biology and Conservation (S. D. Strahl, S. Beaujon, D. M. Brooks, A. J. Begazo, G. Sedaghatkish, and F. Olmos, Editors). Hancock House, Blaine, WA, USA. pp. 376–379.
- White, E. P., S. K. M. Ernest, A. J. Kerkhoff, and B. J. Enquist (2007). Relationships between body size and abundance in ecology. Trends in Ecology & Evolution 22:323–330.
- Yahuarcani, A., K. Morote, A. Calle, and M. Chujandama (2009). Estado de conservación de *Crax globulosa* en la Reserva Nacional Pacaya Samiria, Loreto, Perú. Revista Peruana de Biología 15:41–49.