Research Article

A Cross-Site Analysis of Neotropical Bird Hunting Profiles

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Abstract

Subsistence hunting of neotropical birds is common and widespread in the tropical forests of Latin America. Although its sustainability under different scenarios is subject to debate, hunting has already contributed to the decline and local extirpation of several taxa and is considered to be a significant threat to a range of large-bodied species. Gaining a better understanding of the variability of hunting patterns, as well as the factors that can potentially be used to predict them, is important if we are to develop conservation strategies that target the species most likely to be experiencing declines. In this article, we examine the avian hunting profiles of 65 communities in the neotropics. We describe their variability and look at the relationship between a hunting profile and (a) its geographical location, (b) the community's age, (c) the community's population size, and (d) the year in which the survey was carried out. We find that there is a significant but weak relationship between a community's geographic location and the composition of its bird hunting profile, and that prey profiles can be considerably different even among close neighbors. We found no relationship between a community's age or size and the mean biomass of bird prey hunted. Our results challenge the assumption that older and larger settlements have a predictable impact upon avian prey communities and suggest that cultural preferences or the starting availability of prey species can change rapidly over short distances.

Keywords

hunting, bushmeat, birds, neotropics, Cracidae, preferences

Introduction

Subsistence hunting of birds, mammals, and reptiles for their meat and other body parts is common and widespread among both indigenous and settler communities in the tropical forests of Latin America. Some species have historically provided an important source of protein (Begazo & Bodmer, 1998; Lenselink, 1972; Smith, 1976; Vickers, 1980) and fats (Sirén & Machoa, 2008), whereas others are sources of tools, traditional medicine, and adornments that play a prominent role in the culture of many indigenous groups (Bezerra, de Araujo, Alves, & Alves, 2013; Fernandes-Ferreira, Mendonça, Albano, Ferreira, & Alves, 2012; Mena, Stallings, Regalado, & Cueva, 2000; Santos-Fita, Naranjo, & Rangel-Salazar, 2012). Hunting for the above purposes, however, is considered to be one of the major drivers of global biodiversity loss and has led to population declines in several species whose life history traits or perceived value makes them vulnerable to overexploitation (Brooks & Strahl, 2000; Cullen, Bodmer, & Valladares Pádua, 2000; Nuñez-Iturri & Howe, 2007; Peres, 1990, 2000; Rosin & Swamy, 2013). A recent synthesis of 176 studies found that bird and mammal abundances are an average of 58% and 83% lower in hunted sites than nonhunted sites respectively (Benítez-López et al., 2017), with higher declines associated with areas that are close to access points (such as roads) and have greater access to urban markets (Benítez-López et al., 2017). Rapid increases in the rate of infrastructure construction in Latin America (Fraser, 2014), as well as the potential development of

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commercial wild meat markets similar to those monitored in Africa (see Suárez et al., 2009), are raising important questions about the sustainability of future wild meat harvests, as well as the implications that species declines will have for the ecology of tropical forests.

Much of the hunting literature in the neotropics has focused on mammals, and the susceptibility of species such as tapirs, peccaries, and large ateline primates to declines. Birds, however, have received less attention, though hunting is recognized to be a major threat to several neotropical species (BirdLife International, 2017a; Galetti, Martuscelli, Olmos, & Aleixo, 1997), and some communities prefer their meat over that of mammals (Mena et al., 2000; Santos-Fita et al., 2012). Most ethnozoological studies on the use of birds have additionally focused on their use as pets or on their cultural importance (Haenn, Schmook, Reyes, & Calmé, 2014; Nascimento Rodrigues, Czaban, & Nóbrega Alves, 2015; Nóbrega Alves, De Farias Lima, & Araujo, 2012; Roldán-Clarà, López-Medellín, Espejel, & Arellano, 2014), and not their role as game. Hunting is considered to be a particularly serious threat to several species belonging to the Cracidae (including guans, curassows, and chachalacas), as a result of their large body size (which increases their appeal to hunters) and their slow rate of population recovery (Brooks & Fuller, 2006; Thiollay, 2005). Of the 56 neotropical species of Cracid, 41% are in a threatened IUCN category, whereas an additional 9% are considered near threatened (IUCN Galliform Specialist Group, 2017). Hunting is believed to be a significant threat to all six Cracid species classed as critically endangered and is considered to have exacerbated the decline of the Alagoas currasow (*Crax mitu*), now extinct in the wild, as a result of habitat loss (Bianchi, 2006; BirdLife International, 2017b). Other avian groups with large bodied-taxa, such as parrots (Psittacidae) and toucans (Rhamphastidae), have also experienced local extinctions in areas with high hunting pressure (Thiollay, 2005).

The decline or extirpation of these large, frugivorous species is likely to have knock-on effects on the ecology of tropical forests (Peres, Thaise, Schietti, Desmoulieres, & Levi, 2016; Wright, Hernandéz, & Condit, 2007). Toucans, for example, are the most important seed dispersers of some species of *Virola*, and comparisons between hunted and nonhunted sites have found that fewer seeds were removed in places where the group was targeted by hunters (Holbrook & Loiselle, 2009). Similarly, frugivory by Cracids can disperse the seeds of preferred species (Sedaghatkish, Galetti, & Denny, 1999) or prevent the spread of others as a result of seed predation (Brooks & Fuller, 2006). Their preferences for certain flower species (e.g., *Tabebuia* spp.) may also alter forest demography by preventing the formation of fruit (Brooks & Fuller, 2006). In the long term, models projecting the impacts of arboreal frugivore declines have predicted substantial losses in above-ground biomass (Peres, Emilio, Schietti, Desmoulière, & Levi, 2016), with important consequences for the ecological processes and biotic interactions associated with frugivore-dispersed trees, as well as global carbon stocks.

The diversity of avian species that are targeted by hunters in each particular community will be the product of two influences: (a) how easy each species is to hunt (itself influenced by the abundance and behavior of that species in a particular area) and (b) its perceived value, in terms of its taste or cultural prestige. Although the outcome of this balance has been recorded in detail for a number of communities, we lack an understanding of how variable avian hunting profiles are on a cross-continental scale. The first aim of this article is therefore to assess the variability of bird hunting profiles across Latin America and to investigate whether an easy-to-obtain attribute of communities—their geographical location—is a good predictor of hunter preferences. Understanding the extent to which profiles are universal and the extent to which they vary on a case-by-case basis is important if we are to develop management plans that address the taxa most likely to be impacted; understanding the predictive power of geography alone will also allow us to assess whether we are able to accurately predict the likely preferences of communities that have not received research attention.

The second part of this article aims to assess whether avian hunting profiles change in a predictable way in response to high or prolonged of hunting pressure. Hunters in each community are principally assumed to act in a way that tries to maximize the amount of meat harvested for a given amount of hunting effort (although the cultural value of different prey species is expected to introduce small levels of skew; Jerozolimski & Peres, 2003). They may therefore be initially expected to focus on species that are both large and relatively abundant, which has been shown to be the case in multiple studies (e.g., Franzen, 2006; Mena et al., 2000; Ohl-Schacherer et al., 2007; Sirén, 2004). However, if larger species become scarce through overexploitation and the effort involved to hunt them becomes uneconomic, hunters may be expected to shift to a wider range of smaller prey species. We might therefore expect the prey items of settlements that are larger (and thus would be expected to exert a higher hunting pressure on their surrounding forest) or have been hunting for a longer amount of time to have a lower mean biomass. Although this phenomenon has been widely observed in fisheries data (Friedlander & DeMartini, 2002; Pauly, Christensen, Dalsgaard, Froese, & Torres Jr, 1998; Pauly & Palomares, 2005), evidence of it occurring in terrestrial systems remains more tentative. In the neotropics, Jerozolimski and Peres (2003) found that the mean

biomass of mammalian prey hunted declined as the age of settlements increased but not as their populations increased. Similarly, a study by Ingram et al. (2015) on hunting profiles from Central and West Africa found that the mean body mass of mammalian prey hunted had decreased significantly between 1966 and 2010. Contrary to expectations, however, the mean body mass of birds harvested increased between 1975 and 2010; possibly as a result of changes in demand for large birds and their bills such as the black-casqued hornbill. The authors suggest that an indicator based on the mean body mass of prey hunted (the mean body mass index) could be used as part of a suite of measures to monitor hunting pressure in the absence of comprehensive monitoring systems. Whether patterns such as these can be detected in neotropical bird hunting data remains untested. In this article, we therefore explore whether the age and size of communities can be used to predict a decline in the mean biomass of birds hunted; we also investigate the relationship between the mean body mass of prey and the year in which the study monitoring hunting activity took place in order to allow comparison of our data to the Ingram et al.'s (2015) study. We expect the mean biomass of prey items to decrease as settlements get older, larger, or had their hunting study conducted in later years.

Finally, it is important to consider the interactions between harvests of avian prey and the harvest of other taxa including mammals and reptiles, as shortages in preferred species belonging to one taxon might well be compensated for by increasingly targeting large species in a different group of animals. We briefly assess whether communities that hunt a large total biomass of birds hunt a lower biomass of mammals or reptiles. Through our analyses, we hope to (a) better characterize the variability of neotropical hunting profiles across space and time, (b) assess whether high or prolonged hunting pressure has a predictable impact on the mean biomass of birds hunted, and (c) identify data gaps that could better inform these assessments.

Methods

Literature Search and Data Compilation

We performed a literature search for studies listing hunting records of neotropical birds, using papers returned from the standard search terms: *hunting*, *neotropics*, *Amazon*, *wild meat*, *mammals*, and *birds* (in English, Spanish, and Portuguese) as starting points for a reference list-based search strategy. Our criteria for inclusion were as follows: (a) the study site must be located in Central America, Amazonia, or the Guianan shield, (2) its surrounding area must be principally covered by moist tropical forest, and (c) the study must include the type and number or biomass of birds hunted over a defined time period. Several studies only listed the common names of birds hunted, in which case we assigned them to the lowest possible taxonomic group (e.g., all toucans were put into Rhamphastidae). In cases where this could not be done with high confidence, we assigned birds to an *unknown* category. We examined data for synonyms and assigned species current names using the taxonomy in the Clements checklist of the birds of the world (2016). By analyzing these data sets together, we make a number of assumptions. We assume that our hunting data reflect the true relative contribution of each species to a community's total harvest, despite the fact that not every study recorded the activity of all hunters, a variety of methodologies were used for collecting offtake data, and studies can be prone to underreporting catches of smaller animals (Koster, 2007; Santos-Fita et al., 2012; Smith, 1976). We also assume that studies which did not run for a full year were unaffected by seasonal variation in the availability and abundance of preferred prey species. Lastly, we assume that hunting lists reflect all birds hunted for all purposes, rather than just those that are eaten. We did not find any list that explicitly said it included only species that were consumed (rather than hunted for tools or adornments, for example), although animals harvested for reasons other than consumption may be underreported depending on a participant's understanding of the purpose of the hunting data being collected. Finally, we note that the list of species hunted in any particular locality reflects the preferences of a community under the specific conditions of the hunting catchment and not those in an undepleted, pristine forest.

Geographic Variability

For each community, we calculated the percentage of total kills and percentage of total biomass accounted for by each avian order. In cases where the biomass of a particular species was not recorded, we averaged their recorded biomass across all studies that had actively measured weights (i.e., did not rely on literature values), and multiplied by the number of individuals harvested. If information on the biomass of species was not available (because it had not been hunted elsewhere or because it was only included as part of a large species grouping such as *toucans* or *parrots*), we excluded that community's data from our analysis. We then used ArcGIS to visualize community preferences according to the number ($N = 64$) and biomass ($N = 54$) of birds hunted by order, using maps to estimate coordinates for communities whose precise location was not included in studies.

By using such a high taxonomic level to measure similarity, we will inevitably be losing resolution and the ability to detect preferences for different families. However, because not all families occur across all study locations (Phasianidae, for example are only represented

by a single species [*Meleagris ocellata*], whose distribution is limited to the Mexican Yucatán Peninsula, Guatemala, and northern Belize; McRoberts et al., 2012), this method minimizes any bias that may be introduced as a result of family absences. The approach, however, is still subject to the caveat that we do not know the starting relative abundance of each order in each particular hunting catchment.

To test whether communities that were closer together geographically had similar hunting profiles, we used our data set to generate two distance matrices: one based on the similarity of hunting profiles as defined by the percentage of individuals hunted belonging to each avian order, and one based on geographical proximity using the latitude and longitude coordinates of each settlement. The hunting similarity matrix was calculated using a Bray-Curtis dissimilarity index in the *vegan* package (Oksanen et al., 2016) in R version 3.3.2 on untransformed percentages, whereas the geographical similarity matrix was calculated using the Vincenty's ellipsoid method in the package *geosphere* (Hijmans, 2016). We excluded any communities whose location we had estimated using maps, leaving only those whose location could be assigned with high certainty ($N = 56$ communities). We then tested whether the two matrices were correlated using a Mantel test with 999 permutations in the R package *vegan* and used hierarchical clustering (Ward method) to visualize each of the matrices as trees. Because the studies included in our analysis took place over such a wide time period, during which the Amazon has experienced considerable cultural changes (Roosevelt, 2013), we also performed a partial Mantel test that included the starting year in which the hunting study was conducted as a third matrix, calculated using Euclidean distances. We had to use a reduced data set ($N = 50$) for this as a result of missing data.

Correlates of Average Biomass

We used Spearman's rank correlations, as in, Spearman's rank correlations to investigate the relationship between the mean biomass of birds hunted and (a) the age of communities, (b) the population size of communities, and (c) the year in which each hunting study was carried out. Average biomass was calculated by dividing the total biomass of birds hunted by the total number of individuals recorded in the profile. Information on the population of communities at the time of study was available for $N = 47$ settlements, on the age of communities for $N = 27$ settlements, and the year of study for $N = 47$ settlements.

Interactions Between Bird, Mammal, and Reptile Hunting

We investigated whether the total biomass of birds in each profile was correlated to the total biomass of mammals and reptiles recorded using a linear model with $N = 54$ studies where the required data were available. Bird, reptile, and mammal biomasses were transformed using $\log(x + 1)$ in order to meet the assumptions of the parametric model. We excluded any studies that only listed mammal species unless we could be sure that bird and reptile kills were also being recorded in tandem.

Results

Overview

Our literature search yielded hunting data for 65 communities from 34 articles, spanning studies conducted from 1968 to 2010 (Supplementary Table 1). We recorded a total of 92 named bird species belonging to 62 different genera and 18 orders (Table 1). In lists where the names of all hunted genera were recorded ($N = 38$), profiles contained significantly fewer bird genera than mammal genera (paired Wilcoxon test, $Z = 5.64$, $p < .01$; Figure 1), although the potential for the underreporting of small birds should be considered a caveat. Bird lists were also more likely than mammal lists to contain a category of unclassified carcasses, or groupings like *pigeons* or *toucans* that did not allow identification to genus level.

Table 1. Number of Species Belonging to Each Order Recorded Across $N = 65$ Studies and Percentage of Lists in Which Each Order Was Recorded.

Order	Number of species recorded	Lists (%)
Accipitriformes	4	12
Anseriformes	3	12
Cathartiformes	2	3
Ciconiiformes	3	5
Columbiformes	4	25
Cuculiformes	1	2
Falconiformes	2	5
Galliformes	25	97
Gruiformes	5	51
Opisthocomiformes	1	5
Passeriformes	6	9
Pelecaniformes	5	9
Piciformes	13	51
Psittaciformes	8	58
Strigiformes	2	8
Struthioniformes	1	2
Suliformes	2	5
Tinamiformes	7	71

Galliformes was the dominant order hunted by both the number of animals harvested and by biomass (Figure 2) and appeared in the highest proportion of lists (97%). They accounted for an average of 57% of the total number of individuals harvested in the profiles of communities where at least one member of the order was hunted and were the only order of birds targeted in six communities (Figure 2). Within the Galliformes, in communities where it is included in prey lists, *Meleagris* accounted for the highest percentage of kills on average (54%) although recorded percentages range from 17% (in Chankaj Veracruz, a Mayan settlement in Quintana Roo, Mexico) to 84% (in Los Petenes, also a Mayan settlement in Campeche, Mexico). *Crax*, *Penelope*, *Mitu*, and *Pipile* were the most commonly hunted genera (i.e., they appeared on the highest proportions of lists) and accounted for an average of 28%, 20%, 18%, and 14% of kills, respectively, in communities that hunt them (Figure 2). Two genera, *Pauxi* and *Colinus*, very rarely appeared on lists but accounted for a large percentage of kills when they did. After Galliformes, the most commonly hunted orders were Tinamiformes, Psittaciformes, Gruiformes, Piciformes, and Columbiformes, occurring in in 71%, 58%, 51%, 51%, and 25% of lists, respectively, (Table 1). Toucans (Piciformes) were more prevalent in the hunting profiles of communities in Nicaragua, Ecuador, southern Venezuela, and northern Brazil, whereas parrots (Psittaciformes) were prevalent in hunting profiles across the continent.

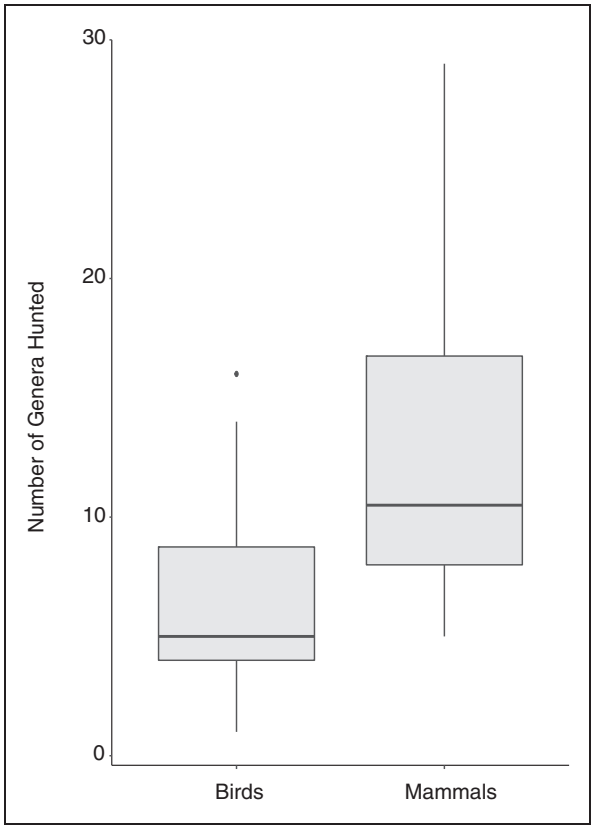

Figure 1. Number of mammal and bird genera reported in $N = 38$ communities where all genera were named.

Geographic Variability

The geographic proximity of settlements and the shape of their hunting profile (in terms of the percentage of kills accounted for by different avian orders) were significantly but weakly correlated (Mantel test, $r = .1108$, $p = .006$, $N = 56$). Including the year of study as an additional matrix made little difference to the outcome of the analysis (partial Mantel test, $r = .1136$, $p = .015$, $N = 50$). Figure 4 shows the trees generated using hierarchical clustering of the two distance matrices based on the geographic proximity and hunting profile similarity of settlements. Both the map and geographic tree reflect a high degree of clustering in areas where multiple communities were included as part of one study (e.g., all data points in Nicaragua come from Williams-Guillén, Griffith, Polisar, Camilo, & Bauman, 2006) and areas that have received a high level of research interest. The cluster of settlements in the Ecuadorian Oriente, for example, includes data from eight different sources.

Several clusters of settlements that are geographically close have similar hunting profiles. Settlements in Yucatán and Quintana Roo, for example, almost solely hunt Galliformes, which is reflected in their tight clustering in the hunting profile similarity tree. Settlements in the Ecuadorian Oriente tend to have more diverse profiles that are principally composed of Galliformes and Piciformes, and most of them grouped together in our profile similarity tree. However, there are also several groups of communities that are geographically close but have very different profiles. Notably the Nicaraguan communities in our sample, though clustered tightly geographically, are scattered throughout the hunting offtake similarity tree; indicating that in certain cases, preferences can change rapidly over short distances.

Correlates of Avian Prey Biomass

Figure 5 shows the average biomass of bird kills versus (a) the age of communities, (b) the size of communities, and (c) the starting year of each hunting study. We found no significant relationship between any of the three variables and the average biomass of birds hunted (Table 2). There was a significant positive relationship between the biomass of mammals and the biomass of birds harvested across communities but not between the biomass of birds and reptiles (Table 3, Figure 6).

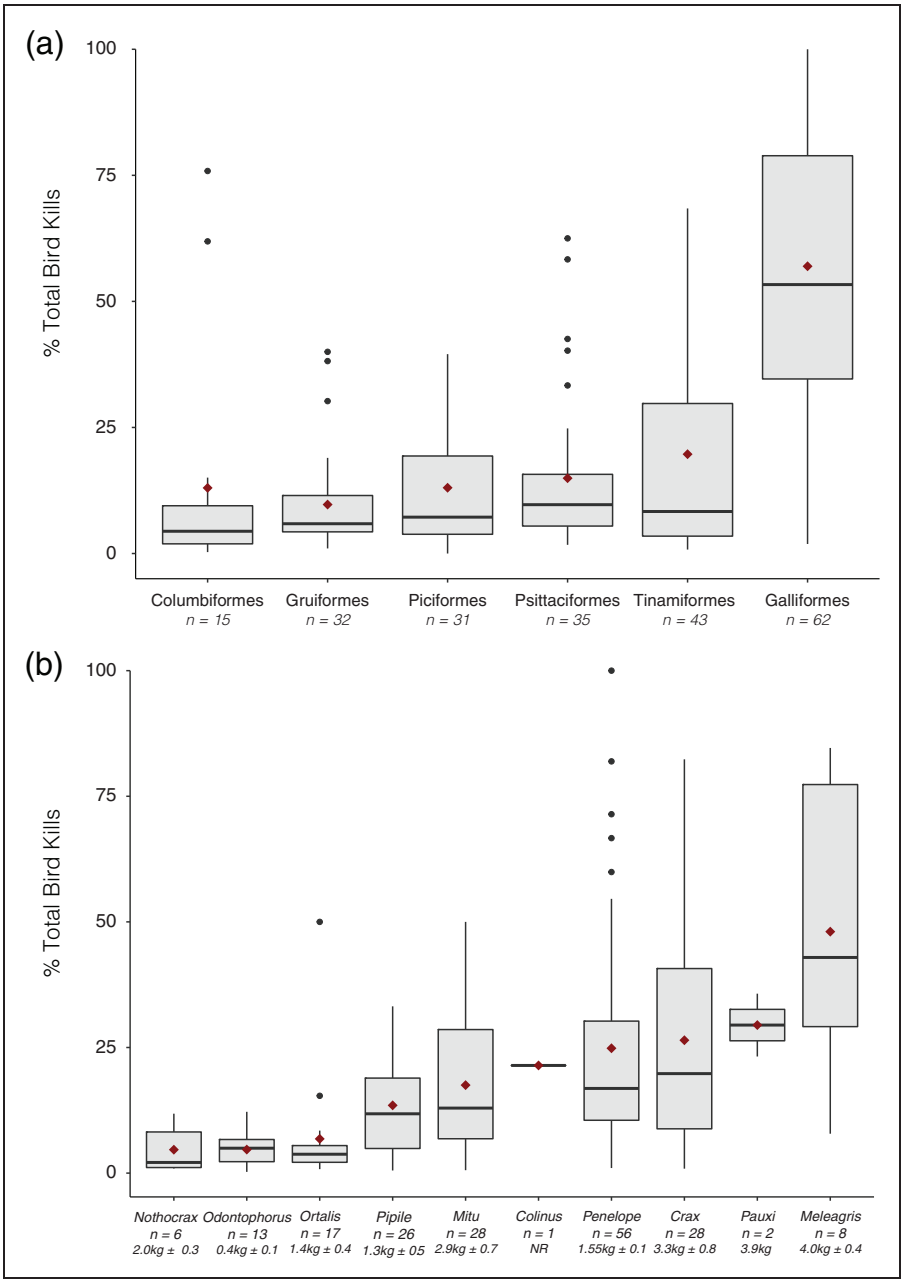

Figure 2. (a) Percentage of kills accounted for by the top six avian orders reported in offtake lists using only communities where a member of that order is listed as being hunted and (b) percentage of kills accounted for by all Galliform genera, using only those where a genus is included in an offtake list. The number of prey profiles featuring each genus is given below the genus name, alongside its average biomass (± standard error), calculated from all studies which weighed carcasses and did not use literature values. Red diamonds show the average percentage kills for each order or genus. Whiskers extend to the largest value no further than 1.5*IQR (inter-quartile range) from each hinge.

Discussion

This article aimed to give an overview of the variability of bird hunting profiles on a pan-continental scale and to investigate whether different aspects of a community's hunting profile could be predicted by four variables: its location, its age, its population size, and the year in which the hunting survey was conducted. We found that there was a significant but weak correlation between a community's location and the structure of its hunting profile in terms of the proportion of kills belonging to each avian order. In addition, there was no correlation between the age of a community, its population size, or the year in which the hunting study was conducted and the average biomass of individual birds hunted. Our results raise

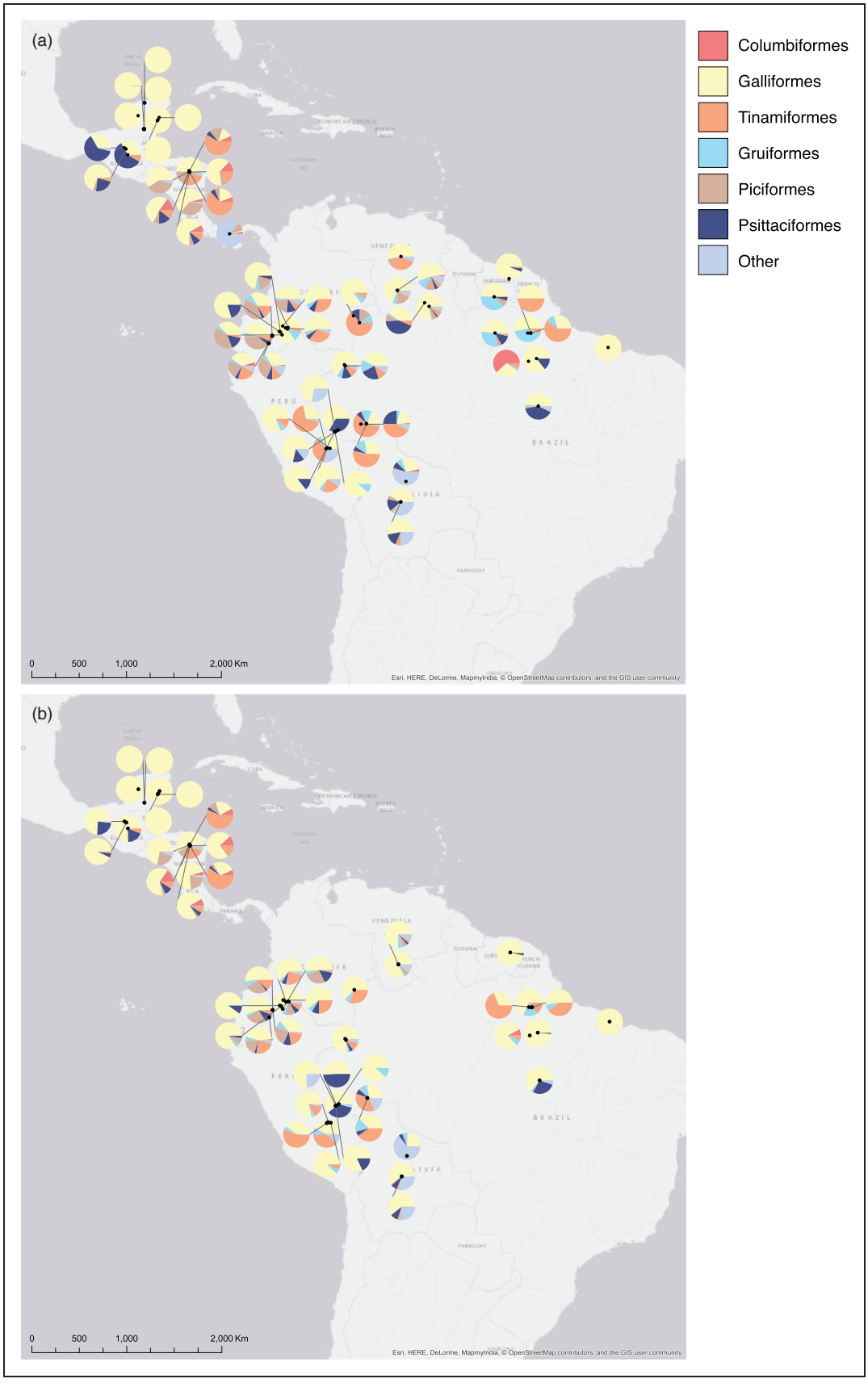

Figure 3. Proportion of (a) kills and (b) biomass belonging to each order, from $N = 63$ and $N = 54$ communities, respectively (data on the biomass of each order were either not recorded or not available for certain settlements). Black dots show the precise location of each community.

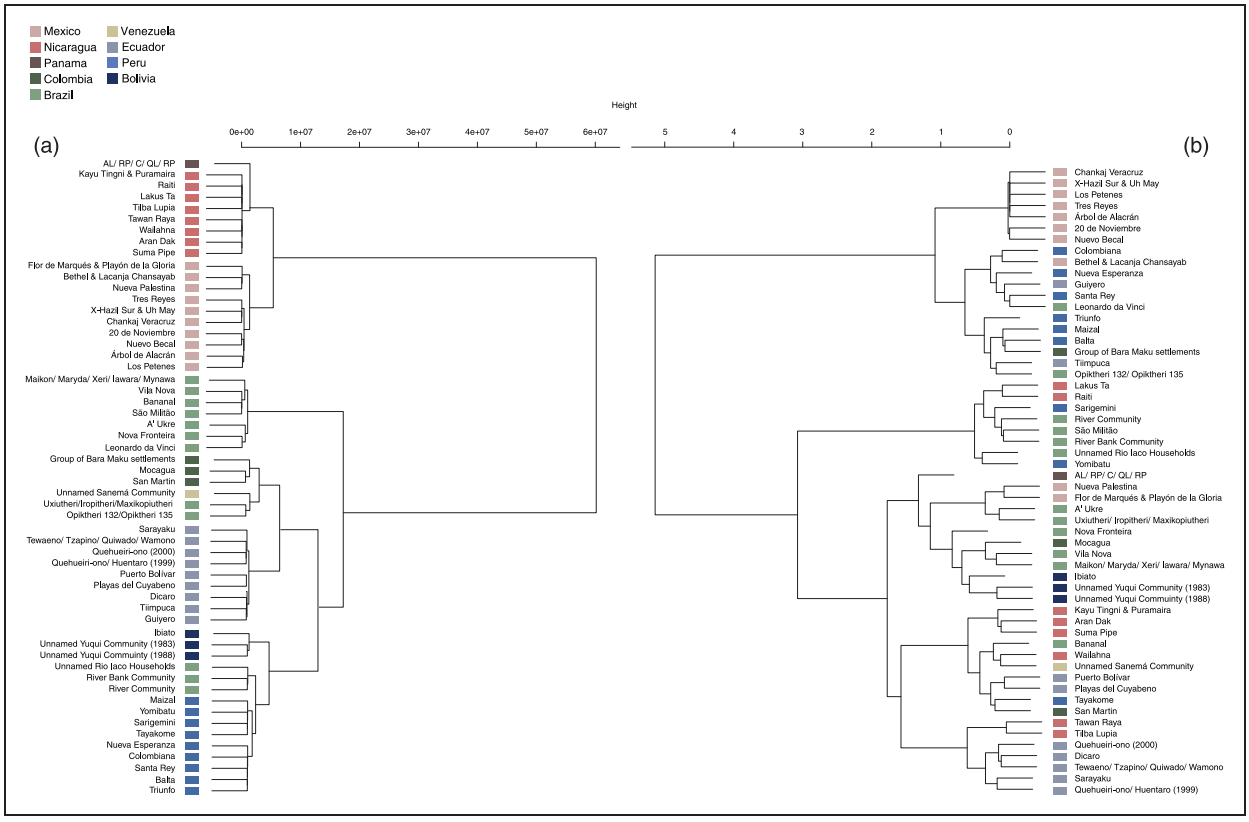

Figure 4. Comparison of trees generated using the Ward method of hierarchical clustering, showing the relationship of settlements according to (a) their geographical proximity and (b) the similarity of their hunting profile according to the percentage of kills belonging to each avian order.

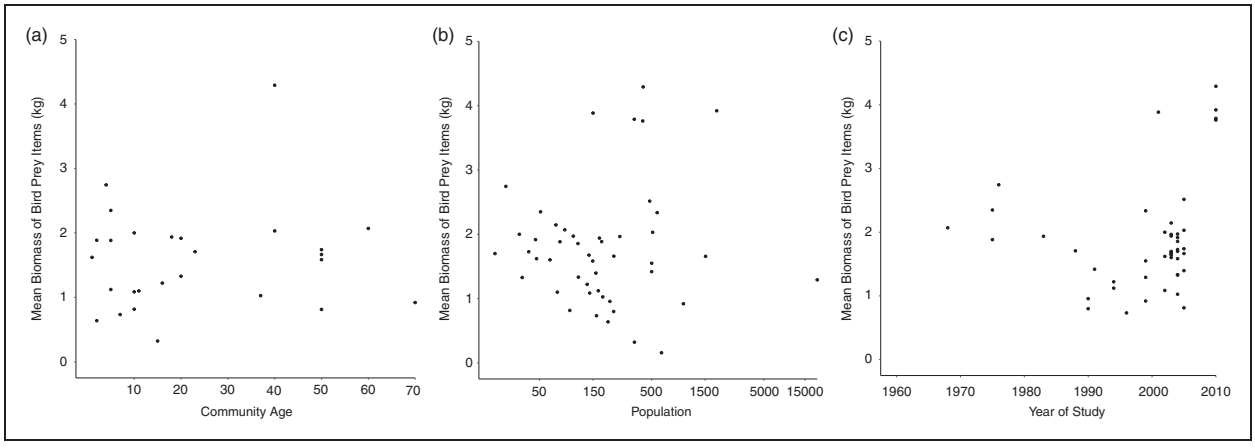

Figure 5. Average biomass of bird kills versus (a) settlement age ($N = 27$), (b) settlement population size ($N = 47$), and (c) starting year of study ($N = 47$). Note the *x*-axis on (b) uses a logarithmic scale.

several interesting questions for further research but also highlight important gaps in the literature pertaining to bird hunting which, if filled, could allow more sophisticated analysis of its causes and impacts.

Although the data sets included in this study covered a wide geographical area, they were tightly clustered and revealed sizeable gaps in the availability of avian hunting offtake data for large regions of Central America, the Amazon, and the Guianan shield. We did not find any published data for studies carried out in the state of Amazonas, Brazil, or Loreto, Peru, despite them covering a significant proportion of their respective country's

Table 2. Spearman's Rank Correlation Coefficients (Probability, Sample Size) for the Age of Communities, Size of Communities, and Year of Study Versus the Mean Undressed Biomass of Bird Prey Included in Their Offtake List.

Age vs. average biomass of birds hunted	.04 ($p = .83$, $N = 27$)
Population size vs. average biomass of birds hunted	−.07 ($p = .60$, $N = 47$)
Year of study vs. average biomass of birds hunted	.22 ($p = .13$, $N = 47$)

Table 3. Linear Model of Bird Biomass Hunted Versus Mammal and Reptile Biomass Hunted (Number of Observations = 54, $r^2 = .2452$).

	Estimate	Standard error	t	$p(>\|t\|)$
(Intercept)	−0.60663	0.6863	−0.884	.3809
Log(Mammal Biomass+1)	0.74706	0.21946	3.404	.0013**
Log(Reptile Biomass+1)	0.05913	0.10554	0.56	.5778

Note. **$p = 0.01$.

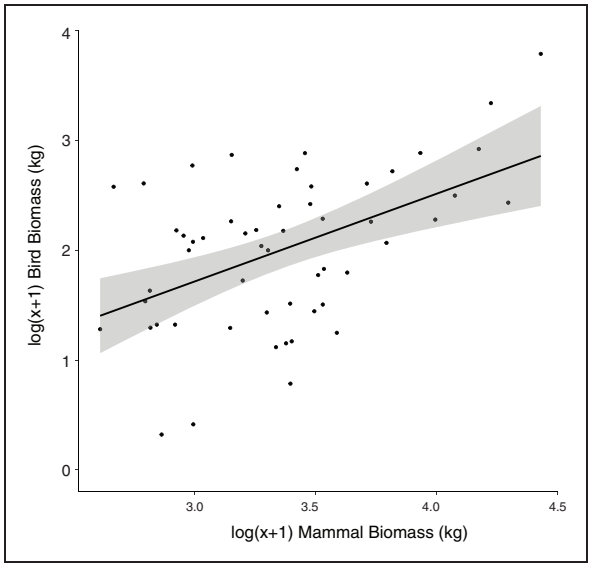

Figure 6. Biomass of birds hunted versus the biomass of mammals hunted in $N = 54$ communities. Regression line, with 95% confidence interval, shows the results of a generalized linear model where log(x+1) Bird Biomass ~ log(x+1) Mammal Biomass ($t = 4.0$, $r^2 = .22$, $p < .01$).

Amazonian territory. Likewise, we were unable to find hunting offtake lists from any communities in Costa Rica, Guatemala, Honduras, Belize, or Guyana. Nevertheless, our data showed that neotropical bird offtake lists tend to be less diverse (in terms of genera) than mammal lists, and that they are dominated by five orders which were recorded in over 50% of profiles (Galliformes, Tinamiformes, Psittaciformes, Gruiformes, and Piciformes). This narrower scope could potentially reflect the smaller selection of bird genera that reach a size where hunting them is considered worthwhile. Carcasses of relatively large genera such as *Meleagris*, *Crax*, and *Mitu*, for example, weighed an average of 4.0 kg (±0.4), 3.3 kg (±0.8), and 2.9 kg (±0.7), respectively. By comparison, even relatively small mammals like paca (*Cuniculus* sp.) and agouti (*Dasyprocta* sp.) weigh a comparable average of 3.44 kg (±0.22) and 5.15 kg (±0.22) (C. A. Stafford, Preziosi, & Sellers, 2017). A focus on targeting smaller species would only be expected if a particular one was hyper-abundant, but we could not find an example among our communities where this appeared to be the case.

Geographic Variation

Several studies have shown that what a community hunts will not only be influenced by the efficiency of harvesting different species in that particular community's catchment but also the cultural and personal considerations of the *value* of those species (Jerozolimski & Peres, 2003; Koster, Hodgen, Venegas, & Copeland, 2010; Zapata-Ríos, Urgilés, & Suárez, 2009). We initially expected communities that were close together geographically to have similar hunting profiles, reasoning that their surrounding forest was likely to have a similar degree of productivity, and that communities that were closer together would foster higher rates of cultural exchange. In addition, their hunting catchments would be expected to hold a comparable diversity of bird species and be more likely to contain species that are particularly sought after, such as the ocellated turkey (*Meleagris ocellata*) in Quintana Roo and the Yucatán peninsula. Our analysis, however, found that geographic distance and hunting profile similarity were significantly but weakly correlated. Some geographic clusters generally corresponded to hunting profile similarity clusters; the Mexican communities, for example, grouped closely together to the exclusion of Bethel and Lacanja Chansayab, Nueva Palestina, and Flor de Marqués and Playón de la Gloria, whereas seven of the nine Ecuadorian communities were all found on the same side of the hunting similarity tree's principal division. However, most clusters of hunting similarity were made up of sets of communities that were geographically disparate. In particular, the Nicaraguan communities were spread throughout the hunting profile similarity tree, with sister groups from Ecuador, Peru, Brazil, Colombia, and Venezuela. Two possibilities that explain our observed patterns are that (a) cultural differences in the perceived value of species are changing rapidly over short distances or (b) there are rapid shifts in the

abundance of prey species that are large enough to alter the economics of hunting each particular species. Changes in abundance could themselves be driven by intrinsic differences in forest productivity, or by the particular hunting history of each area. Disentangling these two possibilities, however, would require contemporary measures of the density of each species, which were not available for the majority of studies included herein. Nevertheless, our data suggest that little generalization can be made about the shape of hunting profiles (in terms of what orders are hunted in what percentages) across the continent and highlight the fact that settlements may not necessarily hunt in a similar way to their neighbors.

A third confounding factor to consider is the wide time span over which the data included in this study were gathered. The 42 years over which the data included in this study were collected have seen many communities undergo considerable cultural and technological changes (Roosevelt, 2013). Many communities have become better connected to market towns and cities (Apaza et al., 2002; Stafford, Alarcon-Valenzuela, Patiño, Preziosi, & Sellers, 2016; Suárez et al., 2009), new technologies such as guns, outboard motors, and lamps have become more widely available (Hames & Vickers, 1982; Yost & Kelley, 1983), new laws have been passed that modify the legality and cost of different practices (e.g., Sirén & Wilkie, 2014), and many communities are experiencing population growth (Holt, 2005). This raises important questions about the validity of comparing community preferences that may well have changed in the intervening years. Controlling for year of study in our analysis testing whether communities that were closer together had similar hunting profiles made little difference to the outcome of the analysis. Nevertheless, more longitudinal data sets are needed to search for trends and to assess the comparability of data sets covering a wide time span.

Correlates of Prey Profiles

We found no evidence that the mean biomass of individual birds hunted decreased as settlements get older or larger, or of decreased mean biomass in studies that were conducted in later years. Taken at face value, our findings indicate either (a) that larger, preferred bird species are, in general, being hunted at sustainable rates or (b) that it is not worth switching to smaller species of birds once the larger ones become scarce, and a better economic choice may be to switch to other sources of wild meat such as mammals or fish. The former explanation is not supported by data from studies which have found a lower abundance of Cracids, macaws, and toucans in hunted forests (Begazo & Bodmer, 1998; Peres & Nascimento, 2006; Thiollay, 2005), although some studies suggest that the availability of nearby unhunted areas to act as a source of migration to replenish stocks may be enough to protect some bird species from depletion (Ohl-Schacherer et al., 2007), and not all species hunted in these studies were harvested unsustainably. Investigating the second possibility is difficult because hunting profiles are rarely accompanied by a full inventory of species that were theoretically available to hunt, and we could not find any studies that explicitly tested how preferences may switch between groups. Longitudinal data sets that track preferences of all groups (including fish) as well as the abundance of different species through time may present a better avenue under which to investigate these patterns.

A third possibility is that the three proxies that we selected for our analysis—the age of settlements, size of settlements, and year of the hunting study—are not sufficiently informative of actual hunting pressure. The true hunting pressure an area experiences will be influenced by several factors, including the proportion of a settlement's population that actively hunts, the availability of alternative protein sources such as domestic animals and fish, the size of hunting catchments, and their governance. In addition, the ability of each particular species to persist in a catchment will be influenced by the productivity of forests (which is known to vary across the continent; Emmons, 1984; Haugaasen & Peres, 2005) and the availability of nearby unhunted areas that can replenish hunted stocks (Ohl-Schacherer et al., 2007). Although previous studies found that decreases in biomass could be detected without adjusting for these different sources of variation (Jerozolimski & Peres, 2003), the discord between our failure to find a pattern and the declines of large species documented in the literature suggests a need to investigate whether accounting for these factors can give a better picture of the impacts of hunting in cross-sectional (as opposed to longitudinal) data. However, even simple measures such as the age and population size of communities were only available for 41% and 72% of settlements, respectively. Restricting our analysis further to include only studies where these additional variables were available would have significantly reduced the available pool of hunting profiles.

Finally, our data suggest that communities that hunt large quantities of mammal biomass also hunt high quantities of bird biomass, suggesting that they do not tend to specialize in either one or the other. It would be interesting to investigate whether a similar relationship exists with the diversity of species hunted (i.e., whether communities that hunt a wide diversity of mammal species hunt a wide diversity of bird species), but the lack of identification to species or genus level that was commonly observed in our bird offtake lists meant we were not able to investigate this possibility.

Implications for Conservation

Our finding that geography is a significant but weak predictor of the relative proportions in which avian orders are hunted suggests that profiles in communities that have not been monitored will not necessarily follow the same patterns as their neighbors. This stresses the need for management plans or conservation interventions (if they are deemed necessary) to carefully consider the particulars of each individual community without assuming it will follow a similar pattern to communities nearby. In addition, our analysis suggests that the mean biomass of bird prey hunted does not decrease as settlements get older or larger. Assuming that the age and size of communities are good proxies for hunting pressure (which may not be the case), better data are needed to understand how mammal, bird, reptile, and fish hunting interact with each other, in order to assess whether our observed pattern is indicative of sustainable practices or likely to be caused by diminishing returns of one prey type (birds) being compensated for by an increased focus on other taxa such as reptiles, mammals, and fish.

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Supplementary Material

Supplementary material for this article is available online.

References

Apaza, L., Wilkie, D., Byron, E., Huanca, T., Leonard, W., Pérez, E., . . . Godoy, R. (2002). Meat prices influence the consumption of wildlife by the Tsimane' Amerindians of Bolivia. *Oryx*, *36*(4): 382–388. Retrieved from https://doi.org/10.1017/S003060530200073X.

Begazo, A. J., & Bodmer, R. E. (1998). Use and conservation of Cracidae (Aves: Galliformes) in the Peruvian Amazon. *Oryx*, *32*(4): 301–309. Retrieved from https://doi.org/10.1017/S0030605300030106.

Benítez-López, A., Alkemade, J. R. M., Schipper, A. M., Ingram, D. J., Verweij, P. A., Eikelboom, J., . . . Huijbregts, M. (2017). The impact of hunting on tropical mammal and bird populations. *Science*, *356*, 180–183. Retrieved from https://doi.org/10.1126/science.aaj1891.

Bezerra, D. M. M., de Araujo, H. F. P., Alves, A. G. C., & Alves, R. R. N. (2013). Birds and people in semiarid northeastern Brazil: Symbolic and medicinal relationships. *Journal of Ethnobiology and Ethnomedicine*, *9*, 3. Retrieved from https://doi.org/10.1186/1746-4269-9-3.

Bianchi, C. A. (2006). Alagoas Currasow (*Mitu mitu*). In: D. M. Brooks (ed.) *Conserving Cracids: The most threatened family of birds in the Americas* (pp. 27–29). Houston, TX: Miscellaneous Publications of The Houston Museum of Natural Science, No. 6.

BirdLife International. (2017a). *IUCN red list for birds*. Retrieved from http://www.birdlife.org.

BirdLife International. (2017b). *Species factsheet: Mitu mitu.* Retrieved from http://datazone.birdlife.org/species/factsheet/22678486.

Brooks, D. M., & Fuller, R. A. (2006). Biology and Conservation of Cracids. In D. M. Brooks (Ed.), *Conserving Cracids: The most threatened family of birds in the Americas* (pp. 10–22). Houston, TX: Miscellaneous Publications of The Houston Museum of Natural Science, No. 6.

Brooks, D. M., & Strahl, S. D. (2000). *Curassows, Guans and Chachalacas. Status survey and conservation action plan for Cracids 2000–2004.* Oxford, England: IUCN/SSC Cracid Specialist Group.

Cullen, L., Bodmer, R. E., & Valladares Pádua, C. (2000). Effects of hunting in habitat fragments of the Atlantic forests, Brazil. *Biological Conservation*, *95*(1): 49–56. Retrieved from https://doi.org/10.1016/S0006-3207(00)00011-2.

Emmons, L. H. (1984). Geographic variation in densities and diversities of non-flying mammals in Amazonia. *Biotropica*, *16*(3): 210–222.

Fernandes-Ferreira, H., Mendonça, S. V., Albano, C., Ferreira, F. S., & Alves, R. R. N. (2012). Hunting, use and conservation of birds in Northeast Brazil. *Biodiversity and Conservation*, *21*(1): 221–244. Retrieved from https://doi.org/10.1007/s10531-011-0179-9.

Franzen, M. (2006). Evaluating the sustainability of hunting: A comparison of harvest profiles across three Huaorani communities. *Environmental Conservation*, *33*(1): 36–45. Retrieved from https://doi.org/10.1017/S0376892906002712.

Fraser, B. (2014). Carving up the Amazon. *Nature*, *509*, 418–419.

Friedlander, A. M., & DeMartini, E. E. (2002). Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: The effects of fishing down apex predators. *Marine Ecology Progress Series*, *230*, 253–264. Retrieved from https://doi.org/10.3354/meps230253.

Galetti, M., Martuscelli, P., Olmos, F., & Aleixo, A. (1997). Ecology and conservation of the jacutinga *Pipile jacutinga* in the Atlantic Forest of Brazil. *Biological Conservation*, *82*(1): 31–39. Retrieved from https://doi.org/10.1016/S0006-3207(97)00004-9.

Haenn, N., Schmook, B., Reyes, Y. M., & Calmé, S. (2014). A cultural consensus regarding the king vulture?: Preliminary findings and their application to Mexican conservation.

Ethnobiology and Conservation, *3*(1): 1–22. Retrieved from https://doi.org/10.15451/ec2014-1-3.1-1-15.

Hames, R. B., & Vickers, W. T. (1982). Optimal diet breadth theory as a model to explain variability in Amazonian hunting. *American Ethnologist*, *9*(2): 358–378. Retrieved from https://doi.org/10.1525/ae.1982.9.2.02a00090.

Haugaasen, T., & Peres, C. A. (2005). Mammal assemblage structure in Amazonian flooded and unflooded forests. *Journal of Tropical Ecology*, *21*(2): 133–145. Retrieved from https://doi.org/10.1017/S026646740400207X.

Hijmans, R. J. (2016). *Geosphere: Spherical trigonometry (R package version 1.5-5)*. Retrieved from https://CRAN.R-project.org/package=geosphere.

Holbrook, K. M., & Loiselle, B. A. (2009). Dispersal in a neotropical tree, *Virola flexuosa* (Myristicaceae): Does hunting of large vertebrates limit seed removal? *Ecology*, *90*(6): 1449–1455.

Holt, F. L. (2005). The catch-22 of conservation: Indigenous peoples, biologists, and cultural change. *Human Ecology*, *33*(2): 199–215. Retrieved from https://doi.org/10.1007/s10745-005-2432-X.

Ingram, D., Coad, L., Collen, B., Kümpel, N. F., Breuer, T., Fa, J. E., . . . Charlemann, J. P. W. (2015). Indicators for wild animal offtake: Methods and case study for African mammals and birds. *Ecology and Society*, *20*(3). Retrieved from https://doi.org/10.5751/ES-07823-200340.

IUCN Galliform Specialist Group. (2017). *Cracids*. Retrieved from http://galliformes.org/subgroup/cracids.

Jerozolimski, A., & Peres, C. A. (2003). Bringing home the biggest bacon: A cross-site analysis of the structure of hunter-kill profiles in Neotropical forests. *Biological Conservation*, *111*, 415–425.

Koster, J. M. (2007). *Hunting and subsistence among the Mayangna and Miskito of Nicaragua's Bosawas Biosphere Reserve* (Doctoral dissertation). Pennsylvania State University. Retrieved from https://etda.libraries.psu.edu/catalog/7423.

Koster, J. M., Hodgen, J. J., Venegas, M. D., & Copeland, T. J. (2010). Is meat flavor a factor in hunters' prey choice decisions? *Human Nature, 21*(3), 219–242. Retrieved from https://doi.org/10.1007/s12110-010-9093-1.

Lenselink, J. (1972). De Jachtopbrengst in een Surinaams Trio-dorp [The hunting yield of a Trio settlement in Suriname]. *De Surinaamse Landbouw, Paramaribo*, *20*, 37–41.

McRoberts, J. T., Terrell, D. R., Rodríguez-Flores, C. I., Soberanes-González, C. A., & del Coro Arizmendi, M. (2012). Ocellated Turkey (*Meleagris ocellata*). In T.S. Schulenberg (Ed.), *Neotropical birds online*. Ithaca: Cornell Lab of Ornithology. Retrieved from https://neotropical.birds.cornell.edu/Species-Account/nb/species/ocetur1.

Mena, P., Stallings, J., Regalado, J., & Cueva, R. (2000). The sustainability of current hunting practices by the Huaorani. In: J. G. Robinson, & E. L. Bennett (Eds.). *Hunting for sustainability in tropical forests* (pp. 57–78). New York, NY: Columbia University Press.

Nascimento Rodrigues, C. A., Czaban, R. E., & Nóbrega Alves, R. R. (2015). Trends in illegal trade of wild birds in Amazonas state, Brazil. *Tropical Conservation Science*, *8*(4): 1098–1113.

Nóbrega Alves, R. R., De Farias Lima, J. R., & Araujo, H. F. P. (2012). The live bird trade in Brazil and its conservation implications: An overview. *Bird Conservation International*, 1–13. Retrieved from https://doi.org/10.1017/S095927091200010X.

Nuñez-Iturri, G., & Howe, H. F. (2007). Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rain forest in western Amazonia. *Biotropica*, *39*(3): 348–354. Retrieved from https://doi.org/10.1111/j.1744-7429.2007.00276.x.

Ohl-Schacherer, J., Shepard, G. H., Kaplan, H., Peres, C. A., Levi, T., & Yu, D. W. (2007). The sustainability of subsistence hunting by Matsigenka native communities in Manu National Park, Peru. *Conservation Biology*, *21*(5): 1174–1185. Retrieved from https://doi.org/10.1111/j.1523-1739.2007.00759.x.

Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Wagner, H. (2016). *Vegan: Community ecology package (R package version 2.4-1)*. Retrieved from https://CRAN.R-project.org/package=vegan.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., & Torres, Jr F. (1998). Fishing down marine food webs. *Statewide Agricultural Land Use Baseline 2015*, *279*, 860–863. Retrieved from https://doi.org/10.1017/CBO9781107415324.004.

Pauly, D., & Palomares, M. (2005). Fishing down marine food web: It is far more persuasive than we thought. *Bulletin of Marine Science*, *76*(2): 197–211. Retrieved from https://doi.org/10.1126/science.279.5352.860.

Peres, C. A. (1990). Effects of hunting on western Amazonian primate communities. *Biological Conservation*, *54*(1): 47–59. Retrieved from https://doi.org/10.1016/0006-3207(90)90041-M.

Peres, C. A. (2000). Effects of subsistence hunting on vertebrate community structure in amazonian forests. *Conservation Biology*, *14*(1): 240–253. Retrieved from https://doi.org/10.1046/j.1523-1739.2000.98485.x.

Peres, C. A., Emilio, T., Schietti, J., Desmoulière, S. J. M., & Levi, T. (2016). Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(4): 892–897. Retrieved from https://doi.org/10.1073/pnas.1516525113.

Peres, C. A., & Nascimento, H. S. (2006). Impact of game hunting by the Kayapó of south-eastern Amazonia: Implications for wildlife conservation in tropical forest indigenous reserves. *Biodiversity and Conservation*, *15*, 2627–2653. Retrieved from https://doi.org/10.1007/s10531-005-5406-9.

Roldán-Clarà, B., López-Medellín, X., Espejel, I., & Arellano, E. (2014). Literature review of the use of birds as pets in Latin-America, with a detailed perspective on Mexico. *Ethnobiology and Conservation*, *3*(5): 1–18. Retrieved from https://doi.org/10.15451/ec2014-10-3.5-1-18.

Roosevelt, A. C. (2013). The Amazon and the Anthropocene: 13,000 years of human influence in a tropical rainforest. *Anthropocene*, *4*(2013): 69–87. Retrieved from https://doi.org/10.1016/j.ancene.2014.05.001.

Rosin, C., & Swamy, V. (2013). Variable density responses of primate communities to hunting pressure in a Western Amazonian river basin. *Neotropical Primates*, *20*(1): 25–31.

Santos-Fita, D., Naranjo, E. J., & Rangel-Salazar, J. L. (2012). Wildlife uses and hunting patterns in rural communities of the Yucatan Peninsula, Mexico. *Journal of Ethnobiology and*

Ethnomedicine, *8*(1 Retrieved from https://doi.org/10.1186/1746-4269-8-38.

Sedaghatkish, G., Galetti, M., & Denny, C. (1999). The importance of Pipile as a seed disperser of economically important plants. In D. M. Brooks, A. J. Begazo, & F. Olmos (Eds.), *Biology and conservation of the piping guans (Pipile)* (pp. 4–12). Houston, TX: Spec. Publ. CSG 1.

Sirén, A. (2004). *Changing interactions between humans and nature in Sarayaku, Ecuadorian Amazon* (Doctoral dissertation). Swedish University of Agricultural Sceinces, Uppsala. Retrieved from https://pub.epsilon.slu.se/498/1/Agraria447.pdf.

Sirén, A., & Machoa, J. (2008). Fish, wildlife, and human nutrition in tropical forests: A fat gap? *Interciencia*, *33*(3): 186–193.

Sirén, A. H., & Wilkie, D. S. (2014). The effects of ammunition price on subsistence hunting in an Amazonian village. *Oryx*, 1–9. Retrieved from https://doi.org/10.1017/S0030605314000026X.

Smith, N. J. H. (1976). Utilization of game along Brazil's transamazon highway. *Acta Amazonica*, *6*, 455–466.

Stafford, C. A., Alarcon-Valenzuela, J., Patiño, J., Preziosi, R. F., & Sellers, W. I. (2016). Know your monkey: Identifying primate conservation challenges in an indigenous kichwa community using an ethnoprimatological approach. *Folia Primatologica*, *87*(1): 31–47. Retrieved from https://doi.org/10.1159/000444414.

Stafford, C. A., Preziosi, R. F., & Sellers, W. I. (2017). A pan-neotropical analysis of hunting preferences. *Biodiversity and Conservation*. Retrieved from https://doi.org/10.1007/s10531-017-1334-8.

Suárez, E., Morales, M., Cueva, R., Utreras Bucheli, V., Zapata-Ríos, G., Toral, E., . . . Vargas Olalla, J. (2009). Oil industry, wild meat trade and roads: Indirect effects of oil extraction activities in a protected area in north-eastern Ecuador. *Animal Conservation*, *12*(4): 364–373. Retrieved from https://doi.org/10.1111/j.1469-1795.2009.00262.x.

Thiollay, J. M. (2005). Effects of hunting on guianan forest game birds. *Biodiversity and Conservation*, *14*(5): 1121–1135. Retrieved from https://doi.org/10.1007/s10531-004-8412-4.

Vickers, W. T. (1980). An analysis of Amazonian hunting yields as a function of settlement age. *Working Papers on South American Indians*, *2*, 7–29.

Williams-Guillén, K., Griffith, D., Polisar, J., Camilo, G., & Bauman, K. (2006). Abundancia de animales de caza y características de cacería en el territorio indígena de Kipla Sait Tasbaika, Reserva de Biosfera BOSAWAS [Abundance of game animals and characteristics of hunting in the indigenous territory of Kipla Sait Tasbaika, BOSAWAS Biosphere Reserve]. *Wani*, *46*, 37–61.

Wright, S. J., Hernandéz, A., & Condit, R. (2007). The bushmeat harvest alters seedling banks by favoring lianas, large seeds, and seeds dispersed by bats, birds, and wind. *Biotropica*, *39*(3): 363–371. Retrieved from https://doi.org/10.1111/j.1744-7429.2007.00289.x.

Yost, J. A., & Kelley, P. M. (1983). Shotguns, blowguns and spears: The analysis of technological efficiency. In: R. B. Hames, & E. T. Vickers (Eds.). *Adaptive responses of native Amazonians* (pp. 189–224). New York, NY: Academic Press.

Zapata-Ríos, G., Urgilés, C., & Suárez, E. (2009). Mammal hunting by the Shuar of the Ecuadorian Amazon: Is it sustainable? *Oryx*, *43*(3): 375–385. Retrieved from https://doi.org/10.1017/S0030605309001914.