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Authors: de J. Vargas González, José, and Vargas, F. Hernán

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NESTING DENSITY OF HARPY EAGLES IN DARIEN WITH POPULATION SIZE ESTIMATES FOR PANAMA

JOSÉ DE J. VARGAS GONZÁLEZ¹ AND F. HERNÁN VARGAS
The Peregrine Fund, 5668 West Flying Hawk Lane, Boise, ID 83709 U.S.A.

ABSTRACT.—Between October 2000 and December 2006, we located 30 nests of 25 breeding pairs of Harpy Eagle (*Harpia harpyja*) in the province of Darien, Panama. Most nests were in primary tropical rain forest at a mean altitude of 132 m (range = 50–305 m). Applying the Polygon and the Maximum Packed Nest Density (MPN) methods, we estimated nest densities of 4 and 6 nests/100 km², with each breeding pair occupying 24 and 16 km² of forest, respectively. This nesting density is the highest reported for the species throughout its breeding range. Although most nests ($n = 25$) were in primary forest, the average distance from small parcels (<2 ha) of agricultural fields was 2.5 km. By extrapolating the nesting density results from the selected study area in Darien to the entire area of Panama with suitable forest cover at altitudes below 350 m, we estimated that the Harpy Eagle population size could range between 806 and 1208 pairs. Greater conservation effort should be placed on potentially suitable Harpy Eagle habitat. We also suggest that educational outreach measures should be an important part of conservation efforts throughout Panama.

KEY WORDS: *Harpy Eagle*, *Harpia harpyja*; *conservation*; *density*; *neotropics*; *population*.

DENSIDAD DE ANIDACIÓN DEL ÁGUILA *HARPIA HARPYJA* EN DARIÉN CON ESTIMACIÓN DEL TAMAÑO POBLACIONAL PARA PANAMÁ

RESUMEN.—Entre octubre 2000 y diciembre 2006 localizamos 30 nidos, pertenecientes a 25 parejas de Águilas Arpías (*Harpia harpyja*) en la Provincia de Darién, Panamá. Los nidos fueron localizados en su mayoría en bosque primario húmedo tropical a una altitud promedio de 132 m (rango = 50–305 m). Aplicando los métodos de Polígono y de Densidad Máxima de Nidos (DMN), estimamos entre 4 y 6 nidos/100 km² y que cada pareja reproductora requiere entre 24 y 16 km² de bosque, respectivamente. Esta densidad de parejas reproductoras es la más alta registrada para la especie en su rango de distribución. Aunque la mayoría de los nidos ($n = 25$) se ubicaron en bosque primario, la distancia promedio a las parcelas de cultivos o áreas alteradas fue de 2,5 km. Extrapolando los resultados de densidad de nidos en Darién al área con hábitat adecuado debajo de los 350 m de altitud, estimamos que el tamaño de la población de *H. harpyja* en todo el territorio Panameño puede estar entre 806 y 1208 parejas. Recomendamos realizar mayores esfuerzos de conservación en los hábitats potencialmente idóneos para *H. harpyja*. Además, sugerimos realizar acciones educativas en todo Panamá como parte esencial de estos esfuerzos de conservación.

[Traducción de los autores editada]

Estimating density of nesting pairs is important for understanding the population dynamics and conservation of territorial birds (Newton 1979, Newton 1994a, Bierregaard 1998, Wilkin et al. 2006), but

in tropical forests this parameter is often understudied. Ecological theory predicts that tropical top predators occur at low densities (Holling 1973, Bruno et al. 2003) and range over large areas (Caselli de Azevedo and Murray 2007). These characteristics make raptors ideal umbrella species, such

¹ Email address: jvargas.gonz@gmail.com

that density estimates can be used to evaluate the impact of tropical forest fragmentation (Thiollay 1985, Whitacre and Thorstrom 1992). Forest degradation contributes to rapid declines of large raptors because habitat and area requirements conflict with those of humans. Consequently, raptors have been persecuted in most regions of the world (Whitfield et al. 2004, Sarasola and Maceda 2006, Thiollay 2007). Among these are Harpy Eagles (Curti and Valdez 2009) whose range extends from southern Mexico to northeastern Argentina between 0 to 800 m (Ferguson-Lees and Christie 2001). Harpy Eagles have been extirpated from several locations, and are currently declining in various countries (Vargas et al. 2006a). At the global scale, the Harpy Eagle is listed as Near Threatened (BirdLife International 2010, IUCN 2010), and it is considered Vulnerable in South America and Critically Endangered in Central America (GRIN 2010a). Deforestation rates are known to be particularly high in lowlands (Murphy and Lugo 1986, Armenteras et al. 2003, Linkie et al. 2004) which severely affects the breeding and foraging habitat of Harpy Eagles (Ferguson-Lees and Christie 2001).

Research on the Harpy Eagle began in the late 1960s and has included investigations on nesting behavior (Fowler and Cope 1964, Rettig 1978), distribution and identification of threats (Vargas et al. 2006a), foraging ecology (Touchton et al. 2002), interaction with other large raptors (Vargas et al. 2006b), diet (Álvarez-Cordero 1996, Piana 2007, Muñoz-López 2008), and foraging behavior (Eason 1989, Peres 1990). Some researchers have reported on area requirements for breeding pairs of Harpy Eagles (Álvarez-Cordero 1996, Piana 2007, Muñoz-López 2008), but this is the first analysis that provides estimates of nesting density and population size using a relatively large sample of adjacent pairs from an extensive and continuous (2000–06) study of the Harpy Eagle in the Darien region, Republic of Panama.

STUDY AREA AND METHODS

Study Area. Darien is a province in the eastern part of the Republic of Panama (8°42'N, 78°12'W) near the border with Colombia (Fig. 1). Altitude in the study area ranges from 0–1800 m. Darien is mostly covered by lowland moist tropical forest with annual precipitation of 1700–2000 mm. There are distinct dry (January–April) and wet (May–December) seasons with temperatures of 17–35°C (PNUD-MEF 2003). Darien represents 22% of the

Panamanian national territory and is characterized by a high diversity of flora, fauna, and landscapes (Myers et al. 2000, PNUD-MEF 2003). Thirteen of Holdridge's life zones, as described by Tosi (1971) for Panama, are found in Darien (PNUD-MEF 2003).

Darien is inhabited by three distinct ethnic groups (Fig. 1), each with different attitudes toward the conservation of Harpy Eagles. These groups include (1) the *colonos*, of Spanish origin; (2) the Afro-Antillean, of African origin; and (3) the native Embera and Wounaan peoples, who are indigenous to the Choco region of Panama and Colombia (Fig. 2). The Embera and Wounaan people were instrumental in locating Harpy Eagle nests for this study, because they know the forest and the historical nesting sites of Harpy Eagles around their villages in Darien. The study site has an area of approximately 5743 km² (35.3% of the Darien province).

Nest Searches. Harpy Eagles build large stick nests placed 20–30 m high in emergent trees, primarily Cuipo (*Cavanillesia platanifolia*), and Bonga (*Ceiba pentandra*) trees (J. de J. Vargas unpubl. data). Nest searches and verification were conducted by biologists and local Embera and Wounaan field assistants, on 10 d/mo from 06:30–17:00 H from October 2000 to December 2006 using two methods: (1) opportunistic searches, carried out by local hunters and farmers during hunting expeditions and farming activities, respectively, and (2) annual systematic searches conducted by two observers walking on foot through selected transects with apparent suitable forest cover (assessed visually) where no nests had been previously reported during the dry season (between January and April). We considered as Harpy Eagle nests those structures where we observed adults incubating, nestlings present, or fledglings nearby in at least one year. Nest position was recorded with a hand-held GPS and plotted on a land cover map from 2008 provided by the National Environmental Authority of Panama (ANAM). We classified nests within 1.24 km from each other as alternate nests of the same nesting territory, based on our 10 yr of breeding data.

Nesting Density. Eighteen of the 30 occupied Harpy Eagle nests found in this study were used to estimate nesting density after excluding five alternate nests <1.24 km from old nests, and seven isolated nests >15 km from the “core group” of nests (Figs. 1, 3). We estimated nesting density using the Maximum Packed Nest Density method (Selás 1998, Thorstrom and Quixchán 2000, Thorstrom 2001)

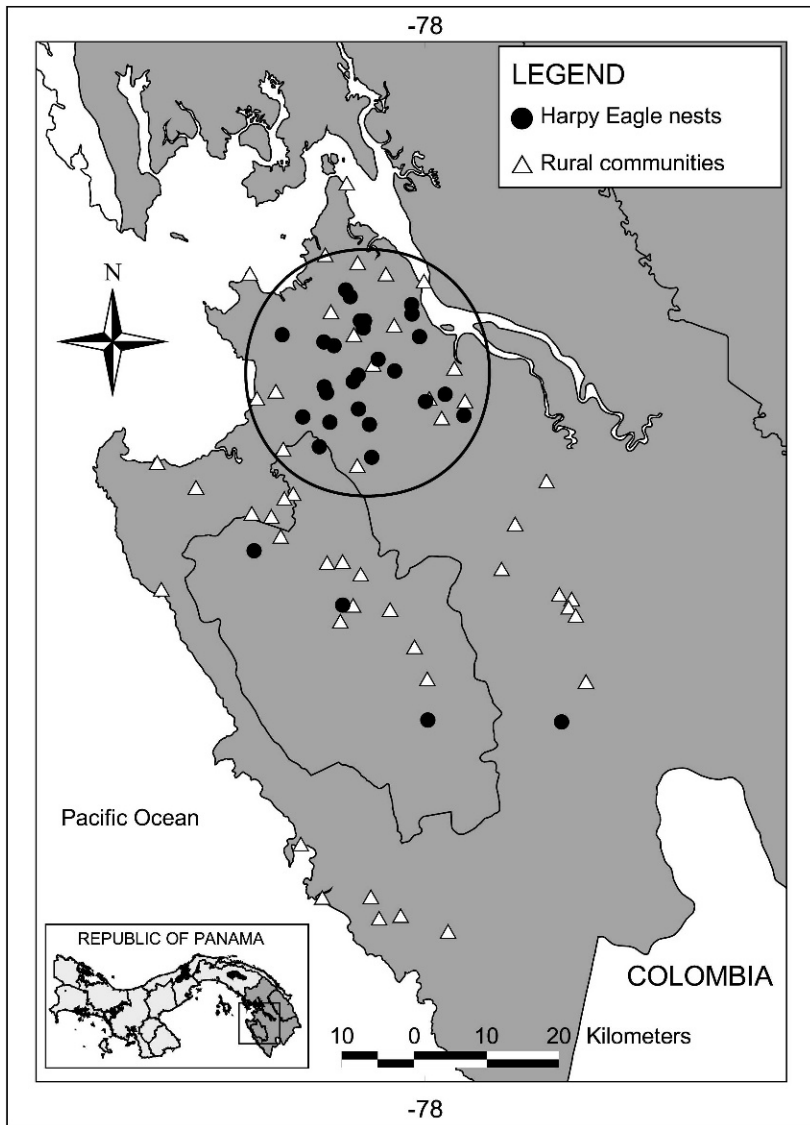


Figure 1. Location of study area in Darien, Republic of Panama. Nests within circle were used to estimate nesting density.

and the polygon method (Thorstrom and Quixchán 2000, Fig. 3). The Maximum Packed Nest Density method uses the mean distance of the nearest nest to estimate total area required for each pair using the equation $A = \pi r^2 * 1.158$, where 1.158 is a constant that includes the portion of the nonoverlapping area between neighboring territories (Brown 1975). The polygon method uses the radius of the mean distance of the nearest neighboring nest and peripheral nests to estimate a polygon which in-

cludes all the nests and adjacent areas of potential occupancy as nest sites. In other words, nesting density estimated by the polygon method equaled total number of nests divided by the area of potential habitat ($d = \text{nests}/100 \text{ km}^2$). Our selected habitat included only areas with secondary or primary forest where Harpy Eagles could potentially nest, and excluded fields used for agricultural purposes. We used ArcView 3.2 to plot nest locations and measure inter-nest distances.

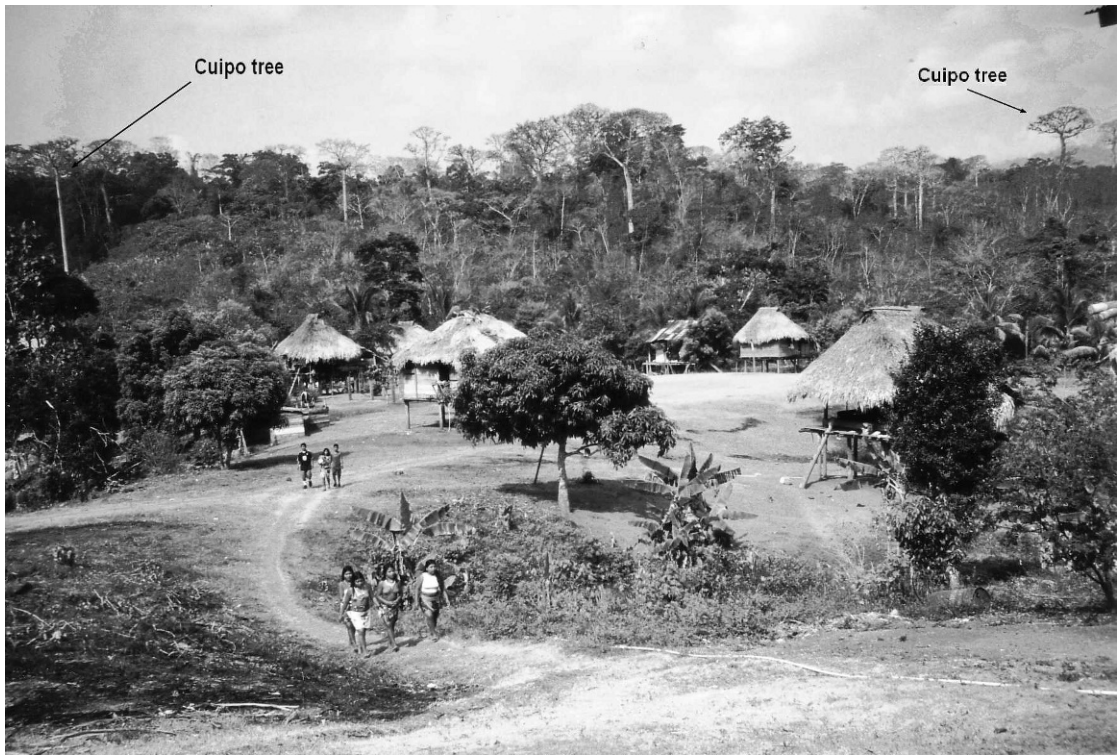


Figure 2. Typical small Embera indigenous community in Darien showing fast-growing, emergent Cuipo trees (*Cavendishia platanifolia*) nearby and available for nesting by Harpy Eagles.

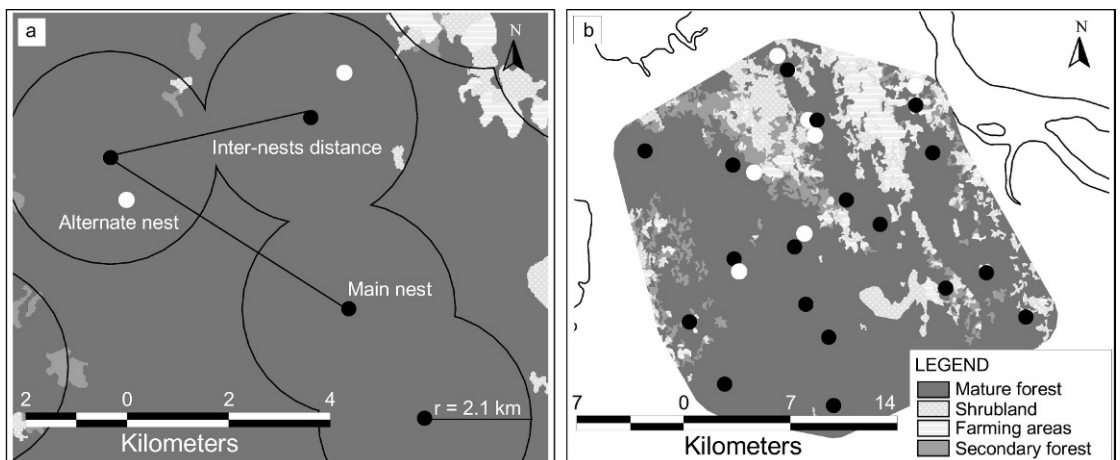


Figure 3. The Maximum Packed Nest Density (a), and the polygon methods (b). Methods are illustrated with forest types and Harpy Eagle nesting data from Darien. Alternate nests are depicted as white circles (○).

Population Size Estimates for Panama. The nesting density values, vegetation types (primary and secondary forest), and altitudinal ranges selected by breeding pairs in Darien were used to estimate the population size (Harpy Eagle pairs) in the entire Republic of Panama. In addition to our findings on altitudinal ranges selected by Harpy Eagles in Darien, we considered suitable breeding habitat as those areas with primary or secondary forest below 350 m, because other studies suggest that Harpy Eagles breed successfully below this altitude (Piana 2007, Muñoz-López 2008) and in these forest types (Vargas 2008). The National Environmental Authority of Panama (ANAM) provided a forest cover map of Panama, updated in 2008, and we downloaded the Digital Elevation Model from the Shuttle Radar Topography Mission (<http://www2.jpl.nasa.gov/srtm/>). We overlaid GPS locations of nests to estimate their altitude. The forest cover map provided by ANAM was prepared using geo-referenced satellite images from the sensors Aster (bands v1, v2, v3 and v4; spatial resolution of 15×15 m pixel) and Landsat ETM (bands 2, 3, 4 and 5; spatial resolution of 30×30 m pixel). We used nonsupervised classification using ERDAS Image software and direct visual interactive interpretations to process these images (ANAM 2009) and classify areas of suitable (primary and secondary forest) and non-suitable habitat for the Harpy Eagle in Panama. We edited and combined both cartographic inputs using ArcView 3.2 software to estimate areas of primary and secondary forest and relate them to Harpy Eagle density and population size in Panama.

RESULTS

Nest Searches. From 2000–06, we located 30 occupied nests of 25 nesting pairs of Harpy Eagles in the Darien province. Twenty-nine nests were in Cuipo trees (*Cavanillesia platanifolia*), and one was in a Bonga tree (*Ceiba pentandra*). All were found below 310 m; the mean altitude was 132 m, and most ($n = 22$ nests) were located at 50–150 m (Fig. 4). Of the 30 nests, 25 were in primary forest, and five were in areas of human use (agriculture or fallow farmland <2 ha where agriculture had ceased less than 10 yr ago). Mean distance between alternate nests was 1.1 km (± 0.3 km, range = 0.6–1.2 km; $n = 5$ inter-nest distances).

Nesting Density. Applying the Maximum Packed Nesting Density method, the mean distance between nests of neighboring pairs was 4.1 km (± 1.2 km; range = 2.6–6.2 km; $n = 13$ inter-nest

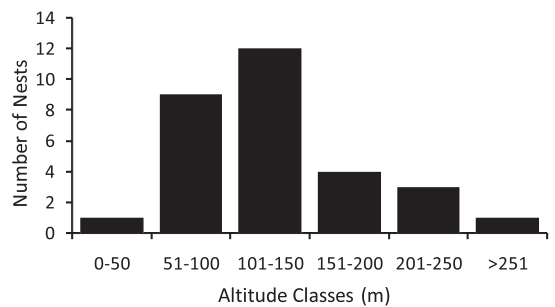


Figure 4. Altitudinal distribution of 30 Harpy Eagle nests located in Darien, Panama, between 2000 and 2006.

distances) and nesting density was estimated at 6 nests/100 km² with a breeding area of 16 km² per pair. Using this method, we also identified 120 km² of presumably unoccupied areas that might provide space for about seven more breeding pairs. Applying the polygon method, the total area estimated from calculations based on 18 nests was 440 km², the resulting nesting density was 4 nests/100 km², and the size of each breeding area was 24 km².

Population Size Estimates for Panama. Based on the minimum and maximum nesting density of Harpy Eagles in our study area in Darien, we estimated between 806 and 1208 Harpy Eagle pairs in the entire Republic of Panama (Table 1). The remnant forests below 200 m would support about 70% of the population, with Harpy Eagle numbers decreasing at higher altitudes. We estimated that less than 26% of the Panamanian forested area provides suitable forest cover for Harpy Eagles (Table 1).

DISCUSSION

We found 30 occupied Harpy Eagle nests in six years: 25 were located in primary forests and five in disturbed forest. Our findings indicate that Harpy Eagles prefer fairly pristine habitats for breeding, with little human disturbance. All nests were in emergent trees at altitudes below 310 m, as was found by other researchers in Ecuador (Muñoz-López 2008), Perú (Piana 2007), Panamá (Aparicio 2003) and Venezuela (Álvarez-Cordero 1996). Our estimate of nesting density in the Darien is the highest known for the species along its distributional range, and also represents one of the highest among the species of forest eagles. The extrapolated population size estimates for Panama, at between 806 and 1208 pairs, suggest that the population status of Harpy Eagles might be better than previously assumed (Aparicio 2003) and raise hopes for the

Table 1. Estimated number of Harpy Eagle pairs and areas of suitable habitat in Panama. The numbers of pairs were derived from the two density estimators applied to the selected study area in Darien and extrapolated to the total suitable forest remaining at altitudes below 350 m in the whole country.

ALTITUDINAL RANGE (m)	ESTIMATED AVAILABLE HABITAT (km ²)				ESTIMATED NUMBER OF PAIRS	
	SELECTED STUDY AREA IN DARIEN	REMAINING FOREST IN DARIEN, OUTSIDE STUDY AREA	REMAINING FOREST OUTSIDE DARIEN	TOTAL FOREST REMAINING IN PANAMA	EACH PAIR REQUIRES 16 km ² (MPN METHOD)	EACH PAIR REQUIRES 24 km ² (POLYGON METHOD)
0–50	621.6	893.8	1633.6	3148.9	197	131
51–100	509.8	1571.3	2276.3	4357.4	272	182
101–150	510.5	914.8	2226.5	3651.8	228	152
151–200	533	531.1	1577.5	2641.6	165	110
201–250	418.9	434.6	1284.6	2138.1	134	89
251–300	309.5	388.5	1118.2	1816.2	114	76
301–350	246.1	337.3	997.6	1580.9	99	66
Total	3149.4	5071.2	11 114.3	19 334.9	1208	806

long-term conservation of the species and associated forest in Panama (Fig. 5).

Nest Searches. The presence of 30 occupied nests indicates that Panama, and specifically, the Pacific region of the Darien Province, currently supports the largest known nesting population of Harpy Eagles in Central America. Panama has the third largest total number of confirmed nests (Vargas et al. 2006a) and is surpassed only by the Guayana region in Venezuela with 76 (Álvarez-Cordero 1996) and Brazilian Amazon basin in Brazil with 53 nests (Sanaïotti 2002). Although Embera and Wounaan peoples have established a network of paths within the forest up to 1000 m altitude, they only reported finding nests below 310 m, and 73% of these nests were between 50–150 m (Fig. 4). Nesting altitudes in our study area in Darien were similar to those reported by Muñiz-López (2008) for Ecuador (range = 206–241 m, $n = 7$ nests), Piana (2007) and Giudice (2005) for Peru (mean = 146 m, range = 85–202, $n = 9$ nests) and Rettig (1978) for southwestern Guyana (135 m, $n = 1$). These results suggest that Harpy Eagles may prefer to nest at altitudes below 300 m, but more nest searches covering higher altitudinal ranges are needed to verify this. To date no Harpy Eagle nests have been found above 400 m in the Neotropics (Aparicio 2003, Giudice 2005). Knowing that Harpy Eagles are able to visit sites up to 2000 m (Stiles and Skutch 1989), it is difficult to explain why they usually nest below 300 m. Potential limiting factors at higher altitudes might include climatic factors, food and nest tree availability, and interspecific competition.

Food may be more available at lower elevations. Although there are few data comparing mammal abundance along altitudinal gradients in Central and South America, lowland tropical moist forests are known as one of the most diverse ecosystems in the Neotropics (Ojasti 2000) and provide good habitat for sloths (*Choloepus hoffmani*, *Bradypus variegatus*) monkeys (*Saguinus geoffroyi*, *Cebus capucinus*, *Alouatta palliata*) and kinkajous (*Potos flavus*; Molina et al. 1986, Reid 1997) which constitute the main prey of Harpy Eagles (Piana 2007, Muñiz-López 2008). However, the distribution of these prey species extends to altitudes of 3300, 2500, and 2200 m, respectively (Reid 1997).

The abundance of Cuipo trees and of other emergent trees used for nesting may diminish with increasing altitude. Although Cuipo trees have been recorded up to 2700 m, herbarium data indicate that most specimens were collected below 350 m (Tropicos.org 2010). In Darien, Cuipos occur up to 520 m (Tropicos.org 2010), and their abundance is higher than in other areas of Panama (FAO and PNUMA 1981, Murawski et al. 1990) such as the Canal Area, Veraguas, Colón and Kuna Yala (Carrasquilla 2006), where our forest cover map predicts suitable forests for Harpy Eagles.

Harpy Eagles may experience competition from other large forest eagles at higher elevations. The Crested Eagle (*Morphnus guianensis*), Black-and-white Hawk-Eagle (*Spizaetus melanoleucus*), Black Hawk-Eagle (*S. tyrannus*), and Ornate Hawk-Eagle (*S. ornatus*) were observed in the nesting areas of the Harpy Eagle in Darien. We were unable to de-

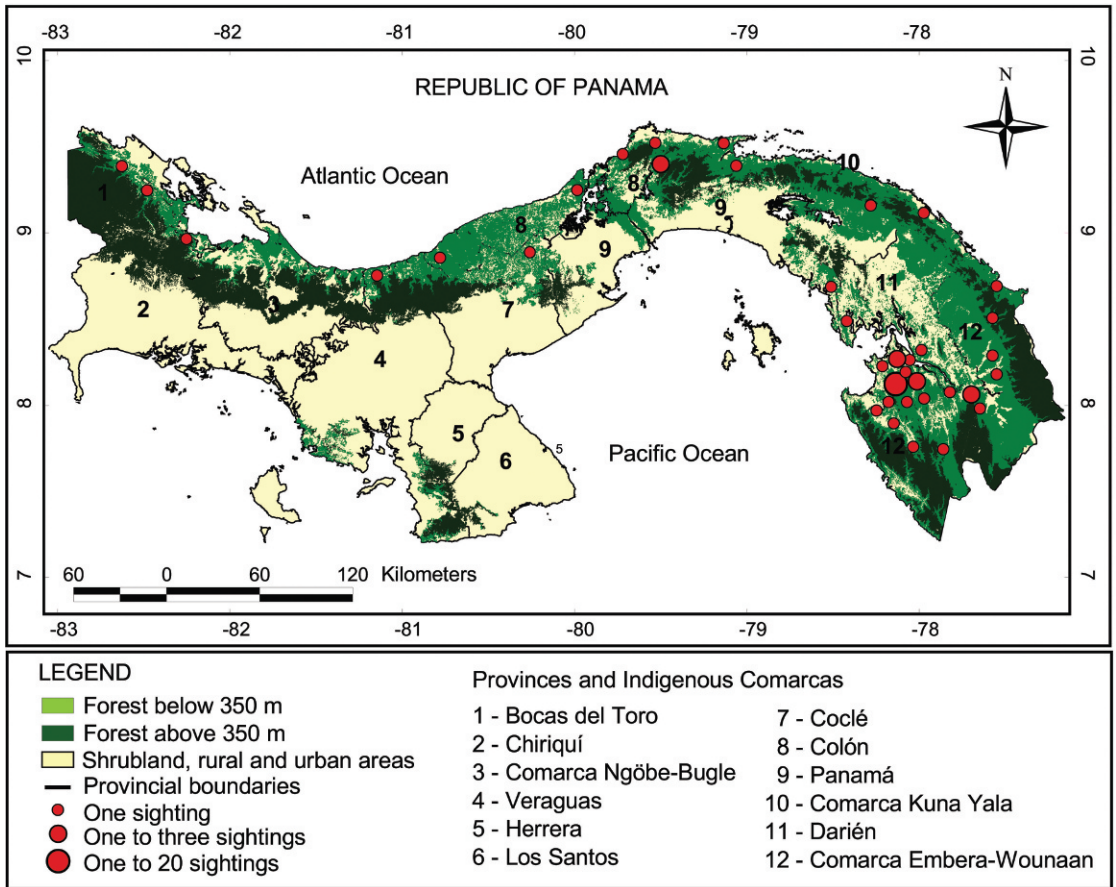


Figure 5. Harpy Eagle sightings in the Republic of Panama between 1980 and 2010 (Updated from Vargas et al. 2006a).

tect altitudinal segregation for these species as reported in French Guiana (Thiollay 1989a). For instance, we recorded Crested Eagles ($n = 3$ nests), Black-and-white Hawk-Eagles ($n = 2$ nests) and Ornate Hawk-Eagles ($n = 2$ nests) nesting within 2 km of Harpy Eagle nests and we detected no agonistic interactions between them. Interestingly, we documented an unusual relationship in which an adult female Crested Eagle frequently fed a post-fledged young Harpy Eagle (Vargas et al. 2006b). Our observations and diet differences documented for large neotropical forest raptors (listed above) suggest that competitive exclusion may not play a strong influential role at higher altitudes (Bierregaard 1984, Funes et al. 1992, Madrid et al. 1992).

Nesting Density. Estimates of nesting density varied to some extent as a function of the methods

used. The polygon method probably provides the most realistic estimate because it excludes areas of unsuitable nesting habitat unlikely to be occupied by Harpy Eagles.

Our estimated area requirements for breeding pairs derived from the Maximum Pack Density Method for Panama are similar to the 10–20 km² ($n = 6$ nests) areas reported by Álvarez-Cordero (1996) in his study of the Harpy Eagle population of southern Darién in 1989–96, but our estimates of 24 km² using the polygon method are higher than those reported by Álvarez-Cordero (1996).

Comparisons between Panamanian and South American populations suggest that the area required by each pair of Harpy Eagles in Darién is smaller than that in Ecuador (47.8 km²; $n = 6$ nests, Muniz-López 2008, study period 2002–06), Peru

(43 km²; $n = 3$ nests, Piana 2007, study period 1996–2001), and Venezuela (range 45–79 km²; $n = 9$ nests, Álvarez-Cordero 1996, study period 1989–96), and much lower than in French Guiana (100 km², Thiollay 1989a, 1989b, study period 1981–86 over a total period of nine months, based on observations of three individuals and no nests). Estimates from other countries except French Guiana were based on inter-nest distances, as in our study.

Our results raise the question: why is Harpy Eagle density higher in the Pacific region of Darien, Panama, than in South America? One possible reason is that South America, by virtue of its larger size, has more species of raptors (Ferguson-Lees and Christie 2001, GRIN 2010b) and mammalian predators (Ruggiero 1994, Nowak 1999). More competitors for food in South America (Emmons 1987, 1988, Moreno et al. 2006) and probably low prey availability (Redford 1992) may require Harpy Eagles to forage in larger areas, as in other species of raptors (Jaksić 1983, Korpimäki 1985, Jaksić 1988). Fewer survey efforts in South America, more intense human persecution of Harpy Eagles (Vargas et al. 2006b) and higher hunting pressure on prey resources (Redford 1992, Galetti et al. 2009, Endo et al. 2010) also might account for differences in Harpy Eagle nesting density. Vegetation structure is another important factor that may affect the Harpy Eagle nesting density because it directly influences the distribution of prey species, the presence of suitable trees for nesting, and good quality microhabitat for refuge (Patton 1992, Thiollay 1992, Berg et al. 1994, Newton 1994b). It would be valuable to learn what types and levels of human activities are positively associated with high Harpy Eagle nesting densities. The sympatry of indigenous people and Harpy Eagles has probably existed for thousands of years, and one wonders how many other places in the lowlands of South America replicate the same human-eagle-habitat relationship found in Darien, Panama. Traditional small-scale slash-and-burn shifting cultivation with land reused after 20–30 yr may be a sustainable method of farming and may even provide appropriate conditions for fast-growing secondary tree species such as *Cavanillesia platanifolia* (Condit et al. 1993) for Harpy Eagle nesting, and *Cecropia* spp. (D'Oliveira et al. 2011), a key food source for sloths (Urbani and Bosque 2007) which are the Harpy Eagle's primary prey in Darien. Embera and Wounaan indigenous communities in Darien subsist primarily on fish from rivers, and on large ground-dwelling mammals such as deer (*Ma-*

zama americana), wild pigs (*Tajasu tajasu*, *T. pecari*), agoutis (*Dasyprocta punctata*), and native birds. They do not eat sloths. Their subsistence hunting and small-scale shifting cultivation would not appear to diminish the long-term persistence of this top predator, and may improve it. However, contemporary human impacts, including urban development, agriculture, and cattle ranching, will continue to affect lowland tropical rain forests in Panama and other countries of Latin America (FAO 1995, ANAM 2004).

The most probable reason for high Harpy Eagle density in the Darien region is the low level of human persecution due to the ancestral cultural values of the local indigenous communities, as well as the recent educational efforts carried out by The Peregrine Fund in this region (Curti and Valdez 2009). Additionally, the diverse ecosystem of the Darien offers an abundance of prey resources, nesting trees, and climatic factors that favor the persistence of Harpy Eagles (see Montañez and Angehr 2007). Advances of the agricultural frontier in Darien, however, will likely affect Harpy Eagle habitat. We still do not know how much forest fragmentation can be tolerated by Harpy Eagles, but our findings suggest they can tolerate some habitat modification and human activity as long as prey species and nesting trees remain available and they are not persecuted.

Our estimates of high nesting density are unusual for a raptor with a large body mass that depends on large, scattered prey (Newton 1979). Except for the Crowned Hawk-Eagle (*Stephanoaetus coronatus*) in Ivory Coast, Africa, which is found at a higher density (6.5 km² per pair, Shultz 2002), the Harpy Eagle in Darien has a higher nesting density than that of other forest eagles with smaller body mass such as the Ornate Hawk-Eagle (Flatten et al. 1990) the Javan Hawk-Eagle (*Nisaetus bartelsi*; Kaneda et al. 2007), and the Philippine Eagle (*Pithecophaga jefferyi*; Bueser et al. 2003). This may be explained by the difference in foraging behavior of these eagles, and the size and behavior of their main prey. The Harpy Eagle is truly a forest eagle (e.g., not soaring above the forest canopy), using a sit-and-wait hunting strategy within the forest to capture their large and slow-moving prey, such as sloths.

Population Size Estimates for Panama. Our estimate of about 1000 pairs of Harpy Eagles in Panama is probably an overestimate. Forest suitability for Harpy Eagles probably varies with prey density (see Chiarello 1999), emergent tree density (see Berg et al. 1994, Aleixo 1999), and hunting pressure

adjacent to forest tracts (see Laurance et al. 2009), which cannot be evaluated through satellite imagery. Additionally, the forest connectivity and size of forest patches were not included in our analysis and some of the forest patches may be too small to support sustainable populations of Harpy Eagles.

Conservation Implications. Our results have implications for conservation of the Harpy Eagle, not only in Panama but also throughout Central America. First, the species is listed as “Critically Endangered” in Panama (República de Panamá 2008) which assumes that the population size is fewer than 250 mature individuals. Our higher estimates indicate that the listing should be reassessed. Second, our results show that protected areas in Darien such as the Reserva Forestal de Chepigana, Corredor Biológico Serranía del Bagre, and Darien National Park are very important conservation sites for Harpy Eagles. However, the long-term conservation of the Darien forest is not assured. Between 2000 and 2008, Darien was the province with the highest deforestation rate (ANAM 2009). Additionally, plans are currently under discussion to construct roads in Darien, including completion of the “missing link”—the Darien Gap—of the Pan-American Highway. We recommend that the Panamanian government take firmer conservation action both within and outside Darien. Third, our results illustrate the importance of Panama as a “source population” for other forested areas in the Mesoamerican Biological Corridor. Successful conservation of the Harpy Eagle in Panama could have implications for the conservation of the species in other countries of Central America where it has severely declined or has become extinct (e.g., El Salvador). By conserving the Harpy Eagle in Panama, other areas of Central America could be repopulated by means of the proposed Mesoamerican Biological Corridor (see Miller et al. 2001).

The conservation status of the other Harpy Eagle populations and associated habitats outside Darien (e.g., in Bocas del Toro, Veraguas, Kuna Yala, and East of Panama province) should be evaluated to validate our population estimates. A concerted commitment of governmental and nongovernmental organizations, the private sector, and local communities is required to mitigate the deterioration of the available breeding habitat for Harpy Eagles in Panama. Therefore, careful strategic planning is essential to achieve biodiversity conservation goals, including the long-term persistence of the Harpy Eagle, which is Panama’s national bird.

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LITERATURE CITED

- ALEIXO, A. 1999. Effects of selective logging on a bird community in the Brazilian Atlantic forest. *Condor* 101:537–548.
- ÁLVAREZ-CORDERO, E. 1996. Biology and conservation of the Harpy Eagle in Venezuela and Panama. Ph.D. thesis. Univ. of Florida, Gainesville, FL U.S.A.
- ANAM. 2004. Informe del estado del ambiente. Autoridad Nacional del Ambiente (ANAM). Ciudad de Panamá, República de Panamá.
- ANAM. 2009. Informe del estado del ambiente. Autoridad Nacional del Ambiente y Gobierno Nacional de la República de Panamá. Ciudad Panamá, República de Panamá.
- APARICIO, K. 2003. Ecología, participación comunitaria y conservación del Águila Harpía (*Harpyia harpyja*) en la República de Panamá. M.S. thesis. Universidad Nacional, Heredia, Costa Rica.
- ARMENTERAS, D., F. GAST, AND H. VILLAREAL. 2003. Andean forest fragmentation and the representativeness of protected natural areas in the eastern Andes, Colombia. *Biological Conservation* 113:245–256.
- BERG, A., B. EHNSTRÖM, L. GUSTAFSSON, T. HALLINGBÄCK, M. JONSELL, AND J. WESLIEN. 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. *Conservation Biology* 8:718–731.
- BIERREGAARD, R.O., JR. 1984. Observations on the nesting biology of the Guiana Crested Eagle (*Morphnus guianensis*). *Wilson Bulletin* 96:1–5.
- . 1998. Conservation status of birds of prey in the South American tropics. *Journal of Raptor Research* 32:19–27.
- BIRDLIFE INTERNATIONAL. 2010. Species factsheet: *Harpyia harpyja*. <http://www.birdlife.org> (last accessed 10 March 2010).
- BROWN, D. 1975. A test of randomness of nest spacing. *Wildfowl* 26:102–103.

- BRUNO, J.F., J.J. STACHOWICZ, AND M.D. BERTNESS. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18:119–125.
- BUESER, G.L.L., K.G. BUESER, D.S. AFAN, D.I. SALVADOR, J.W. GRIER, R.S. KENNEDY, AND H. MIRANDA, JR. 2003. Distribution and nesting density of the Philippine Eagle *Pithecophaga jefferyi* on Mindanao Island, Philippines: what do we know after 100 years? *Ibis* 145:130–135.
- CARRASQUILLA, R.L. 2006. Árboles y arbustos de Panamá. Editora Novo Art, S.A. Ciudad de Panamá, República de Panamá.
- CASCELLI DE AZEVEDO, F.C. AND D.L. MURRAY. 2007. Spatial organization and food habits of jaguars (*Panthera onca*) in a floodplain forest. *Biological Conservation* 137: 391–402.
- CHIARELLO, A. 1999. Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. *Biological Conservation* 89:71–82.
- CONDIT, R., S.P. HUBBELL, AND R.B. FOSTER. 1993. Identifying fast-growing native trees from the neotropics using data from a large, permanent census plot. *Forest Ecology and Management* 62:123–143.
- CURTI, M. AND U. VALDEZ. 2009. Incorporating community education in the strategy for Harpy Eagle conservation in Panama. *Journal of Environmental Education* 40:3–15.
- D'OLIVEIRA, M.V.N., E.C. ALVARADO, J.C. SANTOS, AND J.A. CARVALHO. 2011. Forest natural regeneration and biomass production after slash and burn in a seasonally dry forest in the Southern Brazilian Amazon. *Forest Ecology and Management* 261:1490–1498.
- EASON, P. 1989. Harpy Eagle attempts predation on adult howler monkey. *Condor* 91:469–470.
- EMMONS, L.H. 1987. Comparative feeding ecology of felids in a neotropical rainforest. *Behavioral Ecology and Sociobiology* 20:217–283.
- . 1988. A field study of ocelots in Peru. *Revue d'Ecologie la Terre et la Vie* 43:133–157.
- ENDO, W., C.A. PERES, E. SALAS, S. MORI, J.L. SANCHEZ-VEGA, G.H. SHEPARD, V. PACHECO, AND D.W. YU. 2010. Game vertebrate densities in hunted and nonhunted forests sites in Manu National Park, Peru. *Biotropica* 42: 251–261.
- FAO AND PNUMA. 1981. Proyecto de evaluación de los recursos forestales tropicales – Los recursos de la América Tropical. Informe Técnico UN 32/6.1301-78-04, Organización de las Naciones Unidas para la agricultura y la alimentación, Roma. <http://www.fao.org> (last accessed 07 March 2010).
- FAO. 1995. Evaluación de los recursos forestales 1990. Países tropicales. *Estudio FAO Montes* (Roma) 112:43–63.
- FERGUSON-LEES, J. AND D.A. CHRISTIE. 2001. Raptors of the world. Houghton Mifflin Company, Boston, MA and New York, NY U.S.A.
- FLATTEN, C.J., J.A. MADRID, H.D. MADRID, S.H. FUNES, A.E. HERNANDEZ, AND R.R. BOTZOC. 1990. Biology of the Ornate Hawk-Eagle (*Spizaetus ornatus*). Pages 129–144 in W. Burnham, D. Whitacre, and J. Jenny [EDS.], Progress report III, 1990, Maya Project: use of raptors as environmental indices for design and management of protected areas and for building local capacity for conservation in Latin America. The Peregrine Fund, Boise, ID U.S.A.
- FOWLER, J.M. AND J.B. COPE. 1964. Notes on the Harpy Eagle in British Guiana. *Auk* 81:257–273.
- FUNES, S.H., J. LOPEZ A., AND G. LOPEZ A. 1992. Reproductive biology, food habits, and behavior of the Black Hawk-Eagle in Tikal National Park. Pages 173–178 in D.F. Whitacre and R.K. Thorstrom [EDS.], Maya Project progress report V, 1992. The Peregrine Fund, Inc., Boise, ID U.S.A.
- GALETTI, M., H.C. GIACOMINI, R.S. BUENO, CH.S.S. BERNARDO, R.M. MARQUES, R.S. BOVENDORP, C.E. STEFFLER, P. RUBIM, S.K. GOBBO, C.I. DONATTI, R.A. BEGOTTI, F. MEIRELLES, R.DEA. NOBRE, A.G. CHIARELLO, AND C.A. PERES. 2009. Priority areas for the conservation of Atlantic forest large mammals. *Biological Conservation* 142:1229–1241.
- GIUDICE, R. 2005. Arquitectura de árboles y estructura de la vegetación del bosque como factores determinantes en la anidación del Águila Arpía (*Harpia harpyja* Linnaeus 1878) en la cuenca baja del Río Tambopata. B.S. thesis. Universidad Nacional Agraria La Molina, Lima, Perú.
- GLOBAL RAPTOR INFORMATION NETWORK (GRIN). 2010a. Species account: Harpy Eagle *Harpia harpyja*. <http://www.globalraptors.org> (last accessed 8 June 2010).
- . 2010b. Neotropical zoogeographic region. <http://www.globalraptors.org> (last accessed 21 November 2010).
- HOLLING, C.S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1–23.
- IUCN. 2010. *Harpia harpyja*. Red List of Threatened Species. <http://www.iucnredlist.org> (last accessed 10 March 2010).
- JAKSIĆ, F.M. 1983. The trophic structure of sympatric assemblages of diurnal and nocturnal birds of prey. *American Midland Naturalist* 109:152–162.
- . 1988. Trophic structure of some nearctic, neotropical and palearctic owl assemblages: potential roles of diet opportunism, interspecific interference and resource depression. *Journal of Raptor Research* 22: 44–52.
- KANEDA, H., D.M. PRAWIRADILAGA, AND S. YAMAGISHI. 2007. Home range and habitat use for an individual Javan Hawk-Eagle (*Spizaetus bartelsi*). *Journal of Raptor Research* 41:68–71.
- KORPIMÄKI, E. 1985. Prey choice strategies of the kestrel *Falco tinnunculus* in relation to available small mammals and other Finnish birds of prey. *Annual Zoology Fennici* 22:91–104.
- LAURANCE, W., M. GOOSEM, AND S.F.W. LAURANCE. 2009. Impacts of roads and linear clearings on tropical forests. *Trends in Ecology and Evolution* 24:659–669.
- LINKIE, M., R.J. SMITH, AND N.L. LEADER-WILLIAMS. 2004. Mapping and predicting deforestation patterns in the

- lowlands of Sumatra. *Biodiversity and Conservation* 13:1809–1818.
- MADRID M., H.D., J.A. MADRID M., J.R. CRUZ E., J.L. CORDOVA A., M. CASTILLO R., W.E. MARTINEZ A., AND A. RAMOS C. 1992. Behavior and breeding biology of the Ornate Hawk-Eagle. Pages 179–182 in D.F. Whitacre and R.K. Thorstrom [EDS.], *Maya Project progress report V*, 1992. The Peregrine Fund, Inc., Boise, ID U.S.A.
- MILLER, K., E. CHANG, AND N. JOHNSON. 2001. Defining common ground for the Mesoamerican Biological Corridor. Informe Técnico. World Resources Institute. Washington DC, U.S.A.
- MOLINA, U., C.C. ROLDAN, A. SANCHEZ, AND S. TORRES. 1986. Hallazgo de *Bradipus griseus* y *Choloepus hoffmanni* (Edentata: Bradypodidae) en tierras altas de Costa Rica. *Revista de Biología Tropical* 34:165–166.
- MONTAÑEZ, D. AND G.R. ANGEHR. 2007. Important Bird Areas of the neotropics: Panama. *Neotropical Birding* 2:12–19.
- MORENO, S.R., R.W. KAYS, AND R. SAMUDIO, JR. 2006. Competitive release in diets of ocelots (*Leopardus pardalis*) and Puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. *Journal of Mammalogy* 87:808–816.
- MUÑOZ-LÓPEZ, R. 2008. Revisión de la situación del Águila Harpía *Harpia harpyja* en Ecuador. *Cotinga* 29:42–47.
- MURAWSKI, D.A., J.L. HAMRICK, S.P. HUBBELL, AND R.B. FOSTER. 1990. Mating systems of two Bombacaceae trees of a neotropical moist forest. *Oecologia* 82:501–506.
- MURPHY, P.G. AND A.E. LUGO. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17:67–68.
- MYERS, N., R.A. MITTERMEIER, C.G. MITTERMEIER, G.A.B. DA FONSECA, AND J. KENT. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
- NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD U.S.A.
- . 1994a. Experiments on the limitation of breeding bird density: a review. *Ibis* 136:397–411.
- . 1994b. The role of nest sites in limiting the numbers of hole nesting birds: a review. *Biological Conservation* 70:265–276.
- NOWAK, R.M. 1999. Walker's mammals of the world, Vol. I and II. Sixth Ed. The Johns Hopkins Univ. Press, Baltimore, MD U.S.A.
- OJASTI, J. 2000. Manual de fauna silvestre neotropical., F. Dallmeier [Ed.], SIMAB Series No. 5. Smithsonian Institute/MAB Program, Washington, DC U.S.A.
- PATTON, D.R. 1992. Wildlife habitat relationships in forested ecosystems. Timber Press, Portland, OR U.S.A.
- PERES, C.A. 1990. A Harpy Eagle successfully captures an adult male red howler monkey. *Wilson Bulletin* 102:560–561.
- PIANA, R. 2007. Anidamiento y dieta de *Harpia harpyja* Linnaeus en la comunidad nativa de infierno, Madre de Dios, Perú. *Revista Peruana de Biología* 14:135–138.
- PNUD-MEF. 2003. Diversidad biológica de Darién: situación actual e indicadores para su integración al desarrollo de la región. Programa de las Naciones Unidas para el Desarrollo y Ministerio de Economía y Finanzas, PAN/01/03. Ciudad de Panamá, República de Panamá.
- REDFORD, K.H. 1992. The empty forest. *BioScience* 42: 412–422.
- REID, F.A. 1997. A field guide of the mammals of Central America and southeast Mexico. Oxford Univ. Press, New York, NY U.S.A.
- REPÚBLICA DE PANAMÁ. 2008. Listado de especies en peligro de extinción. Autoridad Nacional del Ambiente (ANAM), Resolución No. AG-0051-2008. http://www.anam.gob.pa/index.php?option=com_content&view=article&id=148%3Aespecies-en-peligro-de-extincion&catid=40%3Aaprotegidas&Itemid=147&lang=es (last accessed 10 January 2011).
- RETTIG, N.L. 1978. Breeding behavior of Harpy Eagle (*Harpia harpyja*). *Auk* 95:629–643.
- RUGGIERO, A. 1994. Latitudinal correlates of the size of mammals geographical ranges in South America. *Journal of Biogeography* 21:545–559.
- SANAIIOTTI, T.M. 2002. Ubicación geográfica y monitoreo de los nidos del Águila Arpía en la amazonía brasileña. Page 21 in The Peregrine Fund y Fondo Peregrino-Panamá [Eds.], Libro de resúmenes de la conferencia de rapaces neotropicales y simposio del Águila Arpía, Panamá. The Peregrine Fund, Ciudad de Panamá, República de Panamá.
- SARASOLA, J.H. AND J.J. MACEDA. 2006. Past and current evidence of persecution of the endangered Crowned Eagle *Harpialiaetus coronatus* in Argentina. *Oryx* 40:347–350.
- SELÁS, Y. 1998. Does food completion from red fox (*Vulpes vulpes*) influence the breeding density of goshawk (*Accipiter gentilis*)? Evidence from a natural experiment. *Journal of Zoology* 246:325–335.
- SHULTZ, S. 2002. Population density, breeding chronology and diet of Crowned Eagles *Stephanoaetus coronatus* in Taï National Park, Ivory Coast. *Ibis* 144:135–138.
- STILES, F.G. AND A.F. SKUTCH. 1989. A guide to the birds of Costa Rica. Comstock/Cornell Univ. Press, Ithaca, NY U.S.A.
- THIOLLAY, J.-M. 1985. Raptor community structure of a primary rain forest in French Guiana and effect of hunting pressure. *Journal of Raptor Research* 18:117–122.
- . 1989a. Area requirements for the conservation of rain forest raptor and game birds in French Guiana. *Conservation Biology* 3:128–137.
- . 1989b. Censusing of diurnal raptors in a primary rain forest: comparative methods and species detectability. *Journal of Raptor Research* 23:72–84.
- . 1992. Influence of selective logging on bird species diversity in Guianan rainforest. *Conservation Biology* 6:47–63.
- . 2007. Raptor declines in West Africa: comparisons between protected, buffer and cultivated areas. *Oryx* 41:322–329.

- THORSTROM, R. 2001. Nest-site characteristic and breeding density of two sympatric forest-falcons in Guatemala. *Ornitología Neotropical* 12:337–343.
- AND A.L. QUIXCHÁN. 2000. Breeding biology and nest site characteristic of the Bicolored Hawk in Guatemala. *Wilson Bulletin* 112:195–202.
- TOSI, J.A. 1971. Inventariación y demostraciones forestales, Panamá: zonas de vida. Organización de las Naciones Unidas para el Desarrollo, Roma, Italia.
- TOUGHTON, J.M., Y. HSU, AND A. PALLERONI. 2002. Foraging ecology of reintroduced captive bred subadult Harpy Eagle (*Harpia harpyja*) on Barro Colorado Island, Panama. *Ornitología Neotropical* 13:365–379.
- TROPICOS.ORG. 2010. Missouri Botanical Garden. <http://www.tropicos.org/Name/3900058> (last accessed 26 November 2010).
- URBANI, B. AND C. BOSQUE. 2007. Feeding ecology and postural behaviour of the three-toed sloth (*Bradypus variegatus flaccidus*) in northern Venezuela. *Mammalian Biology* 72:321–329.
- VARGAS, G.J. DE. J. 2008. Estrategia para la conservación del hábitat reproductivo del Águila Arpía (*Harpia harpyja*) en la región Darién, Panamá. M.S. thesis. Universidad Experimental de los Llanos Occidentales Ezequiel Zamora, UNELLEZ. Guanare, Portuguesa, República Bolivariana de Venezuela.
- , R. MOSQUERA, AND M. WATSON. 2006b. Crested Eagle (*Morphnus guianensis*) feeding a post-fledged young Harpy Eagle (*Harpia harpyja*) in Panama. *Ornitología Neotropical* 17:581–584.
- VARGAS, G.J.de.J., D. WHITACRE, R. MOSQUERA, J. ALBUQUERQUE, R. PIANA, J.-M. THIOLLAY, C. MÁRQUEZ, J. SÁNCHEZ, M. LEZAMA-LÓPEZ, S. MIDENCE, S. MATOLA, S. AGUILAR, N. RETTIG, AND T. SANAIOTTI. 2006a. Estado y distribución actual del Águila Arpía (*Harpia harpyja*) en Centro y Sur América. *Ornitología Neotropical* 17:39–55.
- WHITACRE, D.F. AND R.K. THORSTROM. 1992. Proyecto Maya: Uso de aves rapaces y otra fauna como indicadores del medio ambiente, para el diseño y manejo de áreas protegidas y para fortalecer la capacidad local para la conservación en América Latina. The Peregrine Fund, Inc., Boise, ID U.S.A.
- WHITFIELD, D.P., A.H. FIELDING, D.R.A. MCLEOD, AND P.F. HAWORTH. 2004. The effects of persecution on age of breeding and territory occupation in Golden Eagles in Scotland. *Biological Conservation* 118:249–259.
- WILKIN, T.A., D. GARANT, A.G. GOSLER, AND B.C. SHELDON. 2006. Density effects of life-history traits in a wild population of the Great Tit *Parus major*: analyses of long-term data with GIS techniques. *Journal of Animal Ecology* 75:604–615.

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