

Breeding biology and conservation of hawk-eagles (*Spizaetus* spp.) Aves, Accipitridae) in southern Atlantic Forest, Brazil

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ABSTRACT. Neotropical hawk-eagles (*Spizaetus* spp.) are large forest raptors, having low population densities and high sensitivity to human disturbance. The three species of Brazil's Atlantic forest (*S. ornatus*, *S. melanoleucus*, *S. tyrannus*) are threatened and little is known of many aspects of their biology, such habitat requirements, nesting behavior, and food habits. Here I present data about the breeding biology, diet and behavior of the Ornate Hawk-Eagle (*S. ornatus*; OHE) and the Black-and-white Hawk-Eagle (*S. melanoleucus*; BWHW), and estimations of distribution - extent of occurrence (EOO) - and population sizes for the three hawk-eagles of the southern Atlantic Forest. I compiled data from nine years of field studies done in Rio Grande do Sul and Santa Catarina combined with data from the literature ($n = 191$ records). I calculated the total amount of forest available for each species by GIS analyses and estimated population sizes based on species density data from the literature. The EOO was 123,551 km² for BWHW, 92,512 km² for OHE, and 67,824 km² for Black Hawk-Eagle (*S. tyrannus*; BHE). All species experienced more than 30% shrinkage in their historical distribution (before the year 2000). Forest remnants comprise 32% of BHE's EOO and around 20% for other hawk-eagle species. Population sizes estimated for the southern region were 869 pairs for BHE (1,684 individuals), 1,532 pairs for BWHW (2,849 individuals), and 2,020 pairs for OHE (1,192 individuals). Population size estimates based only on forest patches larger than 10 km² were 542 pairs for BHE (RS = 48 pairs; SC = 494 pairs), 818 pairs for BWHW (RS = 67 pairs; SC = 751 pairs), and 1,178 pairs for OHE (RS = 67 pairs; SC = 1,111 pairs). I recorded displays and copulation of BWHW in July; the nest was built in an inaccessible, emergent tree in the hillside of a valley. Two nests of OHE were found in emergent trees (20 m and 30 m height) measured 138 x 115 x 45 cm and 132 x 100 x 100 cm; one egg was found (64.5 x 51.1 mm). *Spizaetus* seems to have very variable breeding cycles and begin breeding in the austral winter. I estimated egg laying occurs from July to September with fledging happening 3-4 months later. Diet of OHE consisted mostly of birds (90%) but also some mammals. Individuals of *Spizaetus* require large, unbroken forest areas to live, and my data reinforce the critical situation of hawk-eagles in southern Atlantic forest. All three species have lost habitat and their distributions have shrunk over the past decades. The estimated population sizes suggest concern and a need for conservation actions. Conservation of large raptors in the Atlantic Forest is not a simple task, requiring the need to preserve and limit the disturbance of remaining forests, establish connectivity among fragments and reduce direct threats to raptors (e.g., persecution). We also need to better understand the ecological requirements of hawk-eagles and establish public policies to protect both species and their habitats.

KEYWORDS. Distribution, diet, nest, population estimate, threatening status.

RESUMO. **Biologia reprodutiva e conservação de *Spizaetus* spp. (Aves, Accipitridae) na porção sul da Mata Atlântica, Brasil.** Os gaviões do gênero *Spizaetus* são espécies florestais de grande porte, que possuem baixas densidades populacionais e são sensíveis a alterações geradas pelo homem. As três espécies que ocorrem na Mata Atlântica (*S. ornatus*, *S. melanoleucus*, *S. tyrannus*) estão ameaçadas de extinção e o conhecimento sobre muitos aspectos de sua biologia, como habitat, comportamento reprodutivo e dieta, são pouco conhecidos. Neste trabalho eu apresento dados sobre a biologia reprodutiva, dieta e comportamento do gavião-de-penacho (*S. ornatus*, SORN) e do gavião-pato (*S. melanoleucus*, SMEL), bem como estimativas da distribuição – extensão de ocorrência (EOO) – e estimativas de tamanho populacional para as três espécies de *Spizaetus* na porção sul da Mata Atlântica. Foram compilados os registros das três espécies oriundos de nove anos de estudos realizados no Rio Grande do Sul e em Santa Catarina e somados com registros da literatura ($n = 191$ registros). O total de remanescente de área florestal na área de distribuição de cada espécie foi calculado por análise espacial (SIG). O tamanho das populações foi estimado para cada espécie utilizando dados de tamanho de território e densidade de indivíduos existentes na literatura. A EOO resultante foi 123.551 km² para SMEL, 92.512 km² para SORN e 67.824 km² para o gavião-pegamaco (*S. tyrannus*, STYR). A área de distribuição atual das três espécies apresentou uma redução superior a 30% em relação à distribuição histórica (anterior ao ano 2000). Os remanescentes florestais representaram 32% da EOO de STYR e cerca de 20% da EOO de SMEL e SORN. As populações estimadas foram 869 pares para STYR (1.684 indivíduos), 1.532 pares para SMEL (2.849 ind.), e 2.020 pares para SORN (1.192 ind.). Considerando apenas remanescentes florestais com mais de 10 km², as estimativas resultaram em 542 pares para STYR (RS = 48 pares; SC = 494 pares), 818 pares para SMEL (RS = 67 pares; SC = 751 pares), e 1.178 pares para SORN (RS = 67 pares; SC = 1.111 pares). Em julho/2009 eu observei um ninho de gavião-pato, construído em uma árvore emergente na encosta do vale do rio Vacas Gordas e que não pode ser acessado. Comportamento de corte e cópula foi observado na ocasião. Eu encontrei dois ninhos de gavião-de-penacho, construídos em árvores emergentes (20 e 30 metros de altura) que mediram 138 x 115 x 45 cm e 132 x 100 x 100 cm; um ninho continha um ovo (64,5 x 51,1 mm). Indivíduos do gênero *Spizaetus* aparentam ter um ciclo reprodutivo flexível, iniciando a reprodução durante o inverno austral. A postura foi estimada ocorrendo entre julho e setembro. A saída do filhote do ninho ocorre cerca de 3-4 meses após a postura. O gavião-de-penacho consumiu principalmente aves (90%) e mamíferos. Os gaviões do gênero *Spizaetus* necessitam de grandes áreas de floresta preservada e as estimativas aqui apresentadas reforçam a situação crítica das populações na porção sul da Mata Atlântica. As três espécies apresentaram redução nas áreas de distribuição, com acentuada perda de habitat nas últimas décadas. Os tamanhos populacionais estimados atingiram limiares de risco, que enquadram as espécies nas categorias de ameaça de extinção da IUCN. A conservação de grandes gaviões florestais na Mata Atlântica não é

alço simples; é preciso, além de preservar os remanescentes florestais existentes, reduzir a degradação dos mesmos e estabelecer conectividade entre os fragmentos. Além disso, é necessário que as ameaças diretas às aves de rapina sejam controladas (e.g., caça furtiva). Também é urgente que entendamos melhor as necessidades ecológicas estas espécies e que se estabeleçam políticas públicas para a proteção tanto das aves de rapinas quanto de seus habitats.

PALAVRAS-CHAVE. Distribuição, dieta, ninho, tamanho populacional, status de ameaça.

Spizaetus hawk-eagles are large top predators in the forests of the Neotropics. Three of the four species of *Spizaetus* occur in Brazil: the Black Hawk-Eagle [*Spizaetus tyrannus* (Wied, 1820)], the Ornate Hawk-Eagle [*Spizatus ornatus* (Daudin, 1800)] and the Black-and-white Hawk-Eagle [*Spizaetus melanoleucus* (Vieillot, 1816)]. All species are widespread over both lowland and montane Neotropical forests from Mexico to northern Argentina and southern Brazil (FERGUSON-LEES & CHRISTIE, 2001). Except for the Black-and-white Hawk-Eagle, *Spizaetus* populations of the Atlantic Forest are disconnected from those of the Amazon forest (FERGUSON-LEES & CHRISTIE, 2001). None of these species are nationally or globally threatened (MMA, 2014; IUCN, 2015 – although the Ornate Hawk-Eagle is Near Threatened and all species have decreasing population trends), but all species are regionally threatened – or near threatened – in the Atlantic Forest (BERGALLO *et al.*, 2000; MIKICH & BÉRNILS, 2004; ESPÍRITO SANTO, 2005; BRESSAN *et al.*, 2009; COPAM-MG, 2010; CONSEMA-SC, 2011; RIO GRANDE DO SUL, 2014), meaning that Atlantic Forest populations might be neglected by conservation policies that assume that the Amazon forest does support healthy populations.

The three hawk-eagles are syntopic for most of their distribution, but segregate themselves by nesting habitats, food and hunting behavior (ROBINSON, 1994; FERGUSON-LEES & CHRISTIE, 2001; THIOLLAY, 2007; WHITACRE *et al.*, 2012a,b).

Black Hawk-Eagles have a density estimated at 1.29 pairs/20 km² in French Guiana (THIOLLAY, 2007), 1 pair/25 km² in the Tikal Forest (around 20 pair in 576 km² of forest habitats in Belize and Guatemala; WHITACRE & BURNHAM, 2012) and 1 pair/29.6 km² in Panamá (CANUTO, 2008a). It feeds mainly upon mammals, hunting from perches in the lower canopy and captures prey mostly on trees or diurnal retreats or by making long attacks through the forest. Black Hawk-Eagles nest on small branches – covered by vegetation (e.g., vines tangles) – far from the trunk (ROBINSON, 1994; WHITACRE *et al.*, 2012a).

Ornate Hawk-Eagles are apparently more abundant with densities estimated to be 1.32 pairs/20 km² in French Guiana (THIOLLAY, 2007), 1 pair/10.8 km² in Tikal Forest (around 50 pairs in the study area; WHITACRE & BURNHAM, 2012) and 1 pair/44.4 km² in Panamá (CANUTO, 2008a). It differs from other hawk-eagles by its hunting tactics being mainly stalk-and-ambush strategy, food being mostly birds and squirrels and selecting more exposed trees for nesting and locating the nest on large branches near the trunk (WHITACRE *et al.*, 2012b).

The Black-and-white Hawk-Eagle is the least known of these three species. It is rare or at least uncommon (FERGUSON-LEES & CHRISTIE, 2001), although it could be underestimated because usually soars high (WILLIS, 1988; MENQ, 2015) and vocalizes less often than other hawk-eagles. In French Guiana, THIOLLAY (2007) found 29 pairs in 25 sites (1.16 pair/20 km²) from among 32 surveyed areas. Diet and hunting tactics are poorly described, but it is known to feed mainly upon reptiles and birds caught in the canopy by long flights from perches or by stooping from the sky (WILLIS, 1988; ROBINSON, 1994). Its breeding behavior is known only by observation of few nests (BROWN & AMADON, 1968; STRAUCH, 1975; ANDERSON *et al.*, 2004; CANUTO, 2008b; PHILLIPS, 2009; CANUTO *et al.*, 2012).

Despite hawk-eagles being relatively easy to observe because of their flight displays and conspicuous vocalizations, being sought after by birdwatchers and ornithologists, and having a widespread distribution, much of the biological information about these species are scarce (e.g., diet, breeding biology, habitat requirements), especially for Atlantic Forest populations for which information on breeding and nesting biology are basically anecdotal. There is only one description of a nest of the Black-and-white Hawk-Eagle (CANUTO, 2008b) and one of the Ornate Hawk-Eagle (JOENCK *et al.*, 2011). The Black Hawk-Eagle and Ornate Hawk-Eagle were extensively studied during the Maya Project, which was developed by The Peregrine Fund in Belize and Guatemala during the 1980s and 1990s, and which acquired much information about their diet, breeding biology, habitat requirements, territory size, and so on (WHITACRE *et al.*, 2012a,b). Most of the biology of Black-and-white Hawk-Eagle is basically unknown (STRAUCH, 1975; WILLIS, 1988; ROBINSON, 1994; CANUTO, 2008b; KOHLER & REZINNI, 2013; MENQ, 2015).

My objective in this paper is to present novel information about these three species of hawk-eagles at the southern limits of their distribution in the Atlantic Forest in southern Brazil. Here I present estimates of the distribution and abundance of these three hawk-eagles in the states of Rio Grande do Sul and Santa Catarina, and report observations about the breeding biology, diet and behavior of Ornate and Black-and-white Hawk-Eagles.

METHODS

Distribution and abundance. The abundance of hawk-eagles was estimated using field records, data from the literature and from sound/images libraries. Field records were collected for the nine years from 2004 to 2012, mostly from two projects: the Barra Grande Hydroelectric Power

Station (BGHPS) monitoring program from 2004 to 2010; and the raptor diversity in grasslands of Uruguayan Savanas ecoregion from 2009 to 2012. The field records included both anecdotal observations and standardized sampling methods. Most records were from surveys done from 2007 to 2010 using Fixed point count methods (*i.e.*, five hours count per point) from elevated points above the forest canopy in northern Rio Grande do Sul and southern Santa Catarina (eight point counts sampled each season, $n = 44$).

The literature survey included searching in digital data bases (Google Scholar, Web of Science, Sora, GBIF, SpeciesLink, Taxeus) and image and sound sources/libraries (xeno-canto, wikiaves), using a combination of scientific or common name (Portuguese and English names) of the species plus “Atlantic Forest”, “Santa Catarina” or “Rio Grande do Sul”. I limited my search for published data from 1990 to 2015 because older data for Rio Grande do Sul (before 2013) had already been compiled to evaluate the threatened status of these species in the Rio Grande do Sul (BENCKE *et al.*, 2003; RIO GRANDE DO SUL, 2014), and data before the 1990s for Santa Catarina were available from ROSÁRIO (1996). Records before the year 2000 were assumed as historical. This cutoff point was the same used for the Red List for Rio Grande do Sul (RIO GRANDE DO SUL, 2014). Data were processed to eliminate duplicate records. All records associated with a geographical coordinate as identified by the record’s author were considered valid. In cases where the name of the municipality was the only geographical information available, I used the coordinates of the municipality’s city hall.

The abundance of each species was estimated based on the area of forest available (using GIS analysis) and the mean territory size of each species. Data of home range for estimating the number of individuals and territory for estimating the number of pairs were taken from the literature (THIOLLAY, 1989, 2007; WHITACRE & BURNHAM, 2012): 1) Ornate Hawk-Eagle, 18.3 km²/ind and 10.8 km²/pair; 2) Black Hawk-Eagle, 12.9 km²/ind and 25 km²/pair; and 3) Black-and-white Hawk-Eagle, 9.25 km²/ind and 17.24 km²/pair. The extent of occurrence (EOO) of each species was calculated based on a minimum convex polygon (MCP) but excluding historical data, and overlaid data of Atlantic Forest remnants (available at Fundação SOS Mata Atlântica – www.sosma.org.br) to estimate the area of forest available for the species’ EOO. Atlantic Forest remnants were defined as forest patches larger than 100 ha (FUNDAÇÃO SOS MATA ATLÂNTICA & INPE, 2014) resulting in an optimistic estimate of the area available since these species need large areas of continuous forest (THIOLLAY, 1989, 2007; WHITACRE *et al.*, 2012a) and the Atlantic Forest is extremely fragmented (around 97% of Atlantic Forest are patches < 250 ha which represent 42% of the forest remnants; RIBEIRO *et al.*, 2009). I also did a more conservative evaluation to estimate population size by excluding patches of forest smaller than 1000 ha (10 km²). I performed GIS analyses with SAGA software (CONRAD *et al.*, 2015). Maps of species distribution were built using R (R DEVELOPMENT CORE TEAM, 2015).

Breeding biology. Breeding behavior of the Black-and-white Hawk-Eagle was derived from observations at a single nest. To Ornate Hawk-Eagle breeding data was collected by monitoring one nest during an entire breeding season, and with additional information from another two nests. The nest was monitored one or twice every month until laying, once a week in the first month after hatching (November 2008), and twice a month after that until April 2009. Monitoring consisted of climbing to access the nest and taking notes and photos about breeding behavior, nestling development, and prey remains. Afterwards I visited the local in July 2009 and January 2010 after the raptor monitoring at the BGHPS reservoir had stopped.

Diet. Diet of Ornate Hawk-Eagles was described based on prey remains and pellets collected in the nests and from a direct observation of one adult carrying prey to the nest. Most samples were identified to species level by comparing the remains (*i.e.*, bones and feathers) with vouchers from collections of the Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN/FZB) and Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCT/PUCRS). Weights of prey species were taken from DUNNING (2008) and SILVA (2014).

RESULTS

Distribution and abundance. I compiled 161 records after year 2000 and 30 historical records: 65 records of Ornate Hawk-Eagle (nine historical), 69 of Black Hawk-Eagle (14 historical), and 57 of Black-and-white Hawk-Eagle (seven historical). The extent of occurrence (EOO) was 123,551 km² for Black-and-white Hawk-Eagle (Fig. 1), 92,512 km² Ornate Hawk-Eagle (Fig. 2), and 67,824 km² for Black Hawk-Eagle (Fig. 3). EOO of Ornate Hawk-Eagle was almost entirely overlaid with the EOO of Black-and-white Hawk-Eagle, while the current distribution of Black Hawk-Eagle was restricted to the eastern Atlantic Forest (Fig. 3). The area of potential sympatry of the three species totaled 46,235 km². All species showed more than 30% shrinkage from their historical distributions. Black and Ornate Hawk-Eagle showed greater reduction in their area of occurrence (*i.e.*, 55% and 37% respectively), and had practically vanished from the central forests of Rio Grande do Sul (das Antas, Taquari, Pardo and Jacuí river basins) (Figs 2, 3). The Black-and-white Hawk-Eagle showed 31% reduction and had also disappeared from the central forests of Rio Grande do Sul (Fig. 1).

Despite the small EOO of the Black Hawk-Eagle, forest remnants correspond to 32% of the area, or about 21.7 thousand km². Forest remnants comprise 23.6% of the Ornate Hawk-Eagle’s EOO (around 21.8 thousand km²) and 21.3% of the Black-and-white Hawk-Eagle’s EOO (around 26.3 thousand km²) (Tab. I). Estimated population sizes for the southern region was 869 pairs for the Black Hawk-Eagle (1,684 individuals), 1,532 pairs for the Black-and-white Hawk-Eagle (2,849 individuals), and 2,020 pairs for the

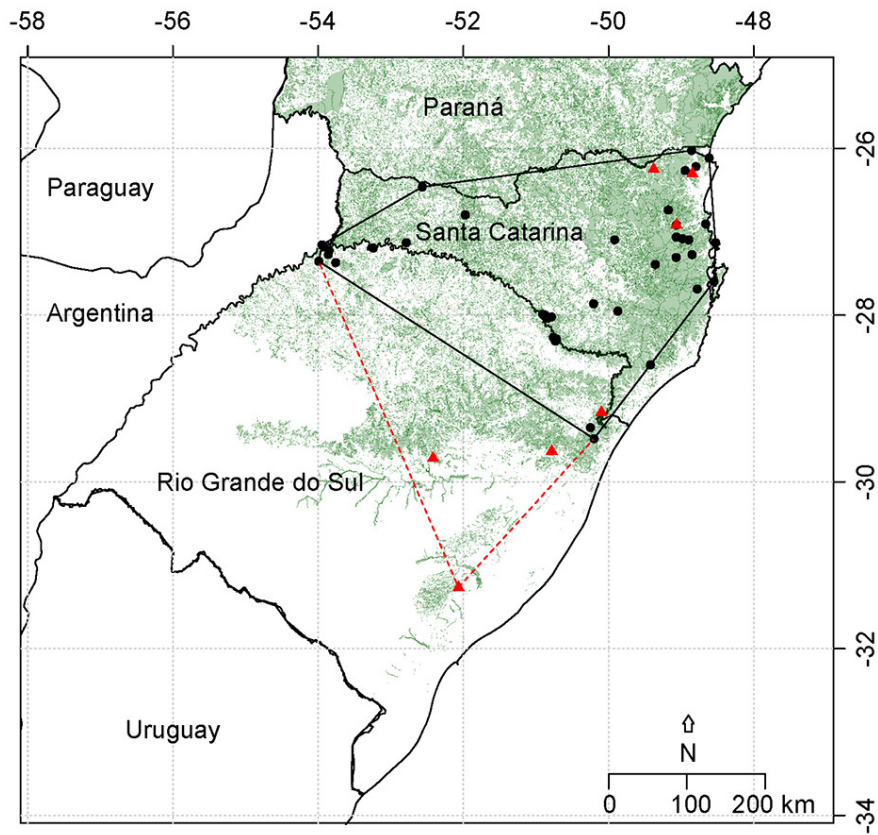


Fig. 1. Extent of occurrence of the Black-and-white Hawk-Eagle in the southern Atlantic Forest, Brazil based on historical (before 2000s; red triangles and red dashed line) and current records (after 2000s; black dots and line). Atlantic Forest remnants are showed in light green.

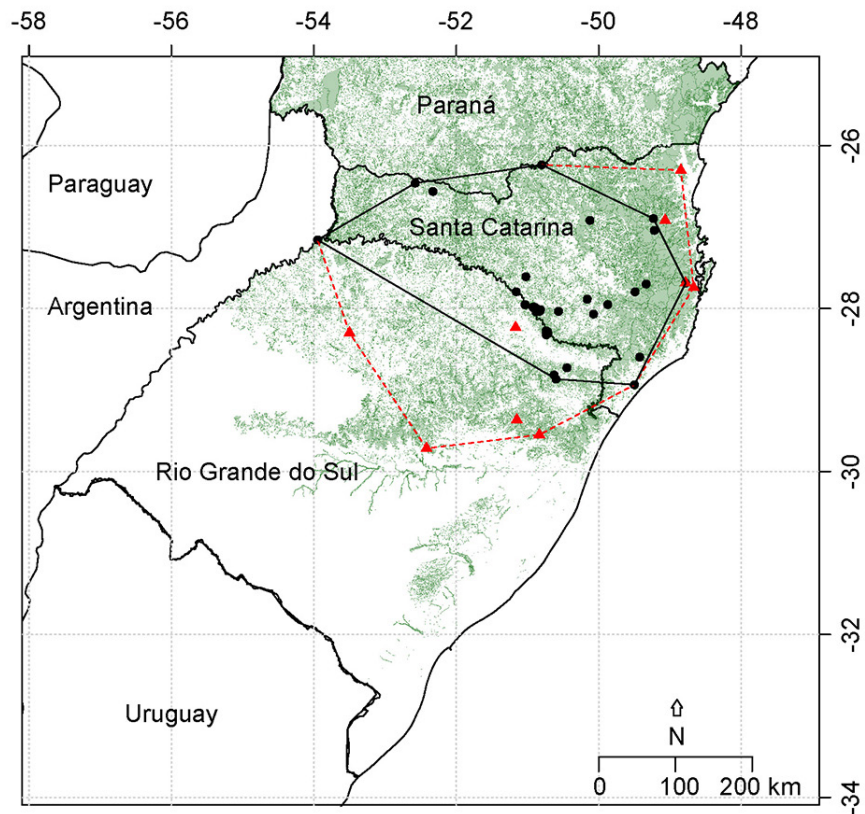


Fig. 2. Extent of occurrence of the Ornate Hawk-Eagle in the southern Atlantic Forest, Brazil based on historical (before 2000s; red triangles and red dashed line) and current records (after 2000s; black dots and line). Atlantic Forest remnants are showed in light green.

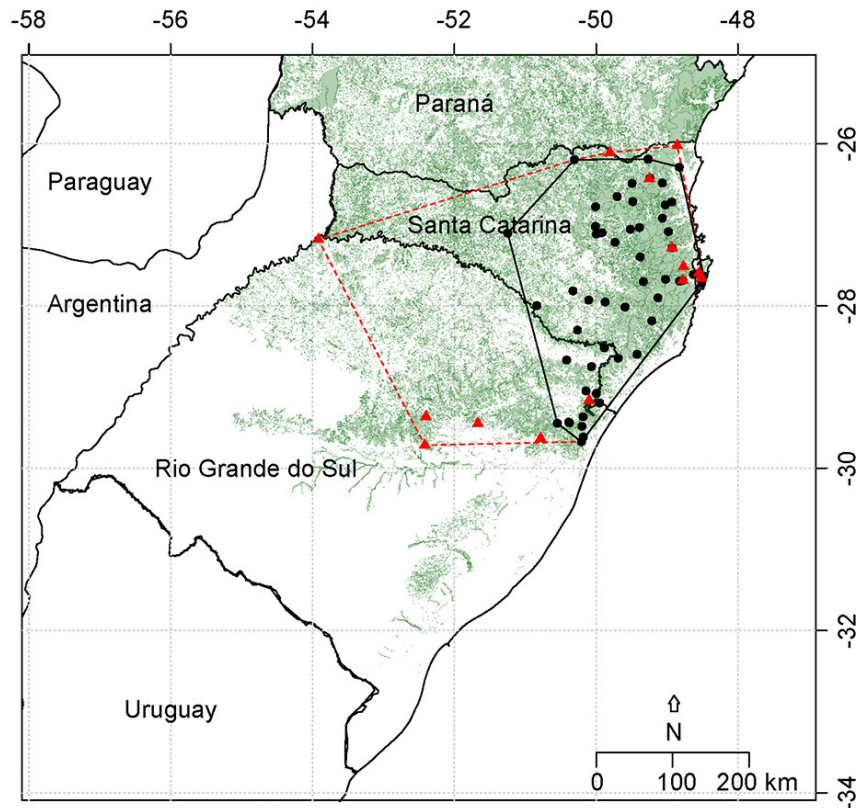


Fig. 3. Extent of occurrence of the Black Hawk-Eagle in the southern Atlantic Forest, Brazil based on historical (before 2000s; red triangles and red dashed line) and current records (after 2000s; black dots and line). Atlantic Forest remnants are showed in light green.

Tab. I. Extent of forest remaining within the Extent of Occurrence (EOO) of hawk-eagles' species in the southern Atlantic Forest, Brazil. The amount of forest for Santa Catarina (SC) and Rio Grande do Sul (RS), considering patches larger than 1 km² and 10 km².

<i>Spizaetus</i> species		Forest Remaining (km ²)					
		patches > 1 km ²			patches > 10 km ²		
		EOO	SC	RS	EOO	SC	RS
Black Hawk-Eagle	<i>S. tyrannus</i>	21,727.26	19,478.05	2,249.21	13,539.73	12,348.75	1,190.99
Ornate Hawk-Eagle	<i>S. ornatus</i>	21,816.63	19,640.11	2,176.53	12,726.78	11,998.52	728.27
Black-and-white Hawk-Eagle	<i>S. melanoleucus</i>	26,353.09	22,657.84	3,695.26	14,069.53	12,915.45	1,154.08

Ornate Hawk-Eagle (1,192 individuals; estimated territory size for a pair is smaller than for an individual; WHITACRE & BURNHAM, 2012). Estimates for each state, which are important for regional evaluation (*e.g.*, state red list), are as follows: Rio Grande do Sul (RS) have an estimated population of 90 pairs for the Black Hawk-Eagle (174 individuals), 214 pairs for the Black-and-white Hawk-Eagle (399 individuals), and 201 pairs for the Ornate Hawk-Eagle (119 individuals); and Santa Catarina (SC) of 779 pairs for the Black Hawk-Eagle (1,510 individuals), 1,317 pairs for the Black-and-white Hawk-Eagle (2,449 individuals), and 1,818 pairs for the Ornate Hawk-Eagle (1,073 individuals) (Tab. II).

Considering only forest patches larger than 10 km², regardless of the isolation of the patch, the forest available to hawk-eagles has been reduced to less than 20% of the EOO (Tab. I). Using this criteria, I estimated population sizes to be 542 pairs for the Black Hawk-Eagle (RS = 48 pairs; SC

= 494 pairs), 818 pairs for the Black-and-white Hawk-Eagle (RS = 67 pairs; SC = 751 pairs), and 1178 pairs for the Ornate Hawk-Eagle (RS = 67 pairs; SC = 1,111 pairs) (number of individuals showed on Tab. II).

Breeding biology

Black-and-white Hawk-Eagle. On 15 July 2009, I found a nest of the Black-and-white Hawk-Eagle built in an emergent tree (unknown species) in the valley of the Vacas Gordas river (28°2.23'S; 50°50.37'W). Around 09:30 AM, one individual (later identified as the male) was observed perched on a branch near the nest. Around 10:30 AM the male flew out, disappearing into the valley. Few minutes later it came back and perched on the nest with an unidentified prey item. At this moment, the female flew out the forest and took the prey and the male moved to a nearby tree. After a while, the female flew out and was not observed until 02:00

Tab. II. Population estimates of hawk-eagles' species in southern Atlantic Forest, Brazil: a) number of individuals, and b) number of pairs (based in THIOLLAY, 1989, 2007; WHITACRE & BURNHAM, 2012).

a)		Estimated number of individuals					
		patches > 1 km ²			patches > 10 km ²		
<i>Spizaetus</i> species		EOO	SC	RS	EOO	SC	RS
Black Hawk-Eagle	<i>S. tyrannus</i>	1,684.28	1,509.93	174.36	1,049.59	957.27	92.32
Ornate Hawk-Eagle	<i>S. ornatus</i>	1,192.17	1,073.23	118.94	695.45	655.66	39.80
Black-and-white Hawk-Eagle	<i>S. melanoleucus</i>	2,848.98	2,449.50	399.49	1,521.03	1,396.26	124.77

b)		Estimated number of pairs					
		patches > 1 km ²			patches > 10 km ²		
<i>Spizaetus</i> species		EOO	SC	RS	EOO	SC	RS
Black Hawk-Eagle	<i>S. tyrannus</i>	869.09	779.12	89.97	541.59	493.95	47.64
Ornate Hawk-Eagle	<i>S. ornatus</i>	2,020.06	1,818.53	201.53	1,178.41	1,110.97	67.43
Black-and-white Hawk-Eagle	<i>S. melanoleucus</i>	1,532.16	1,317.32	214.84	818.00	750.90	67.10

PM, when she returned to the nest. During this period, the male was observed perched or flying high above the forest, apparently foraging, and sometimes diving into the valley. Few minutes after the female came back to nest, the male flew to the nest and copulated with her. After copulating, the male flew away, and was immediately followed by the female. They flew together, gliding and rising above the valley, chasing each other and, sometimes grasping onto the back of the other. After a while, they separated and I did not see them during the rest of the day (I ended my observations at 03:00 PM). I tried to access the nest later, but was not successful.

Ornate Hawk-Eagle. The first nest of Ornate Hawk-Eagle (nest A) was found in 2005. It was rescued and translocated during the flooding of the Barra Grande UHE reservoir (data available in JOENCK *et al.*, 2011). In February 2008, I observed a pair of Ornate Hawk-Eagles performing courtship displays in this general area; the pair flew together with intense vocalization, the male was performing an undulating display (series of loops and dives) and chasing the female which turned over touching his feet. On 29 September 2008, another nest in a Myrtaceae tree (DBH = 78.94 cm; nest B; Fig. 4) was found about 350 m from the translocated nest (27°57.2'S; 51°2.3'W) and about 300 m from the edge of the reservoir in second-growth forest. I first climbed to the nest on 17 December 2008. The nest was 15 m above ground in a secondary crotch amongst two large (diameter = 25 cm) and three medium branches (diameter = 4.5 – 6 cm). The nest was 132 cm long, 100 cm wide with an external depth of 100 cm, built with dry branches having diameters around 0.5 to 1.5 cm. The chamber no longer existed, but a flat depression about 80 x 84 cm remained in the center with a few green leaves and sticks. The presence of prey remains, faeces and feather of Ornate Hawk-Eagle suggested that the nest was still active, at least as a feeding location for a juvenile. This impression was reinforced by the observation of a juvenile Ornate Hawk-Eagle around 300 m from the nest location (Fig. 5).

The third nest (nest C; Fig. 6) was found in 06 May 2008, at a site where adults and juveniles had been observed since April 2007. The nest was found after I observed an adult carrying a green stick to an *Araucaria* tree (*Araucaria angustifolia* (Bertol.) Kuntze), close to border of the BGHPS

reservoir in second-growth forest near *Pinus* sp. plots (27°59.2'S; 50°54.5'W). At 12:15 PM, the female left the tree and joined the male which was flying nearby. At about 01:00 PM, I observed the same pair gliding together, the male above the female and trying several times to scratch the female's back. Twice I observed foot-touching, although without complete claw bonding, and only for a few seconds. I lost visual contact when the female dived into the valley, followed by the male.

I climbed to the nest for the first time on 1 September 2008. The nest was built 30 m in a 31 m *Araucaria* (DBH = 132 cm) and 73.5 cm from the main trunk on three branches (diameter around 10 cm). External measures of the nest were 138 cm long, 115 cm wide with an external height of 45 cm, built of dry sticks with diameters around 0.95 to 2.3 cm. The nest chamber was 49 cm long, 47 cm wide and 17 cm deep and decorated with green sticks and leaves of *Lithraea brasiliensis* Marchand. On 27 September I found a white egg measuring 64.5 mm x 51.1 mm (Fig. 7). On 21 October, before climbing to the nest, I observed one adult perched on the hill side near the nest. When it flew to and perched on the nest, other adult (smaller, probably the male) left the nest, started gliding above the *Araucaria* tree for a while and flew out along the river valley. During visits before hatching, the adults were noted to have continued to bring green leaves to the nest and rotate the egg. On 08 November I observed a nestling (Fig. 7) that had likely hatched between 05 and 07 November. For the first time, the adults were very aggressive and attacked me several times, both while climbing and when at the nest. Such aggressive behavior continued until fledging and I kept all visits short in order to reduce stress on the adults. Consequently I did not take any measurements of the nestling nor did I band it. Based on the estimated hatching date, laying probably occurred between 20 and 24 September since incubation is reported to be 44–46 days (WHITACRE *et al.*, 2012b). On 23 January 2009 the nestling flew from nest as I was climbing the tree. This was the first time I observed it outside the nest although its rectrices were not completely developed and it had not fully developed flight capability. On 7 and 24 March, I observed the juvenile about 50 m and 200 m from the nest. In April and May, the juvenile (Fig. 7) was still within its parents' territory. I found prey remains in the

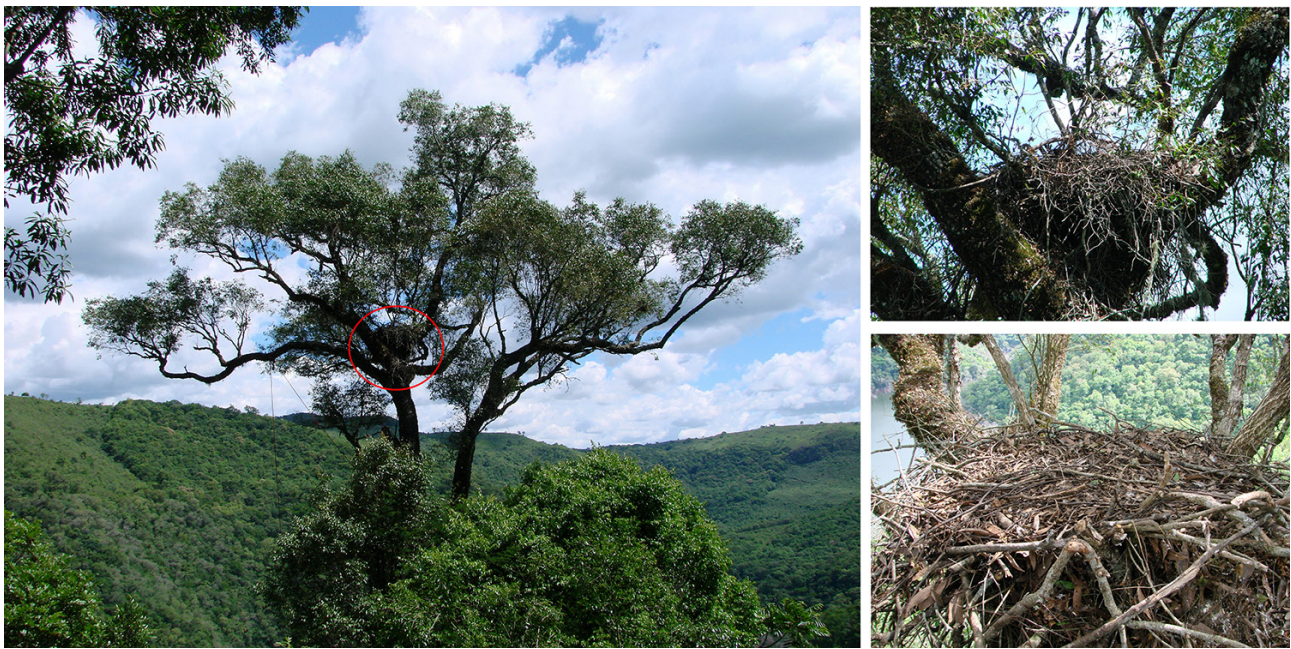


Fig. 4. Nest of an Ornate Hawk-Eagle built 20 m in a Myrtaceae tree (DBH = 78.94 cm) (red circle). Lateral view (upper right) and view from above (bottom right) of the nest.



Fig. 5. Juvenile Ornate Hawk-Eagle (probably a fledgling) observed about 300 m from nest B.

nest in late April, but did not see the juvenile when I came back in January 2010.

Diet – Ornate Hawk-Eagle. I collected bones, feathers and hair of several prey remains and two pellets at nest B during two visits and during several visits over seven-months checking nest C. I identified at least 30 prey items, 90% of them Aves. Twelve taxa were identified at least to genus (Tab. III) with the most abundant prey being

Brown Tinamou [*Crypturellus obsoletus* (Temminck, 1815): Tinamidae; n = 8]. Mammal remains (n = 3) could not be identified, except one Ingram's squirrel [*Guerlinguetus ingrami* (Thomas, 1901); mean weight = 150 g], which an adult Ornate Hawk-Eagle carried to the nest. Mean weight of prey items was 417 g and ranged from 115 g [Ruddy quail-dove; *Geotrygon montana* (Linnaeus, 1758)] to 1,770 g (Dusky-legged guan; *Penelope obscura* Temminck, 1815).



Fig. 6. Nest of an Ornate Hawk-Eagle located 31 m in an *Araucaria* tree (DBH = 132 cm). Lateral view (upper right) and view from above (bottom right) with details of the chamber (with green leaves and sticks).



Fig. 7. Nesting phenology of Ornate Hawk-Eagle (nest C). Chronological sequence from upper left to bottom right: nest with an egg (27 Sep 2008); egg; (27 Sep 2008); nestling – few days old (08 Nov 2008); adult on nest (16 Nov 2008); nestling about 10 days old (19 Nov 2008); nestling about 20 days old (28 Nov 2008); nestling about 40 days old (Dec 2008); Fledging (Apr 2009); Nest without chamber or traces of use (Apr 2009).

Tab. III. Diet of Ornate Hawk-Eagle at the nest in southern Atlantic Forest, Brazil. Number of individuals and frequency (%). Prey weights were from DUNNING (2008) and SILVA (2014) [*; prey not identified; #, probably *Patagioenas cayennensis* (Bonnaterre, 1792); mean weight = 254 g].

Prey species	Weight (g)	Number of items (%)		
		Nest B	Nest C	Total
Tinamidae				
<i>Crypturellus obsoletus</i> (Temminck, 1815)	444	2 (28.56)	8 (34.78)	10 (33.33)
Cracidae				
<i>Penelope obscura</i> Temminck, 1815	1770	1 (14.29)	1 (4.35)	2 (6.67)
Phasianidae				
<i>Gallus gallus</i> (Linnaeus, 1758)	904	-	1 (4.35)	1 (3.33)
Columbidae				
<i>Patagioenas picazuro</i> (Temminck, 1813)	279	1 (14.29)	-	1 (3.33)
<i>Patagioenas</i> sp.#	254	-	1 (4.35)	1 (3.33)
<i>Leptotila</i> sp.	159	-	3 (13.04)	3 (10.0)
<i>Geotrygon montana</i> (Linnaeus, 1758)	115	-	1 (4.35)	1 (3.33)
Ramphastidae				
<i>Ramphastos dicolorus</i> Linnaeus, 1766	331	-	1 (4.35)	1 (3.33)
Picidae				
<i>Colaptes melanochloros</i> (Gmelin, 1788)	137	1 (14.29)	1 (4.35)	2 (6.67)
Psittacidae				
<i>Pionus maximilliani</i> (Kuhl, 1820)	293	-	3 (13.04)	3 (10.0)
Corvidae				
<i>Cyanocorax chrysops</i> (Vieillot, 1818)	166	1 (14.29)	-	1 (3.33)
Aves N.I.*		-	1 (4.35)	1 (3.33)
Total Aves		6 (85.71)	21 (91.3)	27 (90.0)
Sciuridae				
<i>Guerlinguetus ingrami</i> (Thomas, 1901)	150	-	1 (4.35)	1 (3.33)
Mammalia N.I.*		1 (14.29)	1 (4.35)	2 (6.67)
Total Mammalia		1 (14.29)	2 (8.70)	3 (10.0)
Total		7	23	30

DISCUSSION

Distribution and abundance. Hawk-eagles are threatened in southern Brazil (MIKICH & BÉRNILS, 2004; CONSEMA-SC, 2011; RIO GRANDE DO SUL, 2014), mostly because of habitat loss (SOARES *et al.*, 2008). Although the rate of deforestation has been reduced in recent decades, remaining forests are extremely fragmented (RIBEIRO *et al.*, 2009; FUNDAÇÃO SOS MATA ATLÂNTICA & INPE, 2014), and the reduction of 30% of their historical distribution suggests that they are declining. I did not estimate vegetation available for historical records, so the real loss is probably overestimated since species distributions were calculated which included inappropriate habitats for hawk-eagles (*e.g.*, grasslands). The past distribution of the Black Hawk-Eagle, for example, is probably overestimated. In spite of its occurrence in Misiones, Argentina (BODRATI & COCKLE, 2006; BODRATI *et al.*, 2012; MARTÍNEZ, 2016; although there are few recent records, BODRATI *et al.*, 2012) and western Paraná, Brazil (SOARES *et al.*, 2008), Black Hawk-Eagles have never been recorded in western Rio Grande do Sul and Santa Catarina (Fig. 3) excepting a single record in Turvo State Park (MÄHLER, 1996).

Despite the increasing popularity of bird watching in Brazil during this century – denoted by posts in websites like WikiAves (www.wikiaves.com.br) – hawk-eagles have not been recorded at several places at which they occurred

in the past, suggesting true local extinction rather than lack of surveys. I'd highlight the lack of recent records of Black Hawk-Eagle in Turvo State Park, northwest of Rio Grande do Sul, where both Ornate and Black-and-white Hawk-Eagles, and even a Harpy Eagle [*Harpia harpyja* (Linnaeus, 1758)], have been recorded (D. A. Meller, pers. comun.; MELLER & GUADAGNIN, 2016), suggesting that this species has vanished from the western portion of the state (last record in 1996; MÄHLER, 1996). Also, all hawk-eagle species have disappeared from the central and southern forests of Rio Grande do Sul which are regions extensively disturbed by urban and agricultural expansion. The Black-and-white Hawk-Eagle, for instance, which historically has occurred in southern and central Rio Grande do Sul (São Lourenço do Sul – Ihering, 1899 mentioned in BELTON, 1984; Santa Cruz do Sul – BENCKE, 1997; and Taquara – Berlepsch & Ihering, 1885 also informed in BELTON, 1984), now has its southernmost records in the Serra Geral, in northeastern of the state.

I have estimated population size based on data from Amazon and Tikal forests, areas which are better preserved than the southern Atlantic Forest. CANUTO *et al.* (2012) summarized data on *Spizaetus* from the Atlantic Forest and estimated 1 pair/53.75 km² for the Ornate and Black Hawk-Eagle, and 1 pair/42.85 km² for the Black-and-white Hawk-Eagle, estimations that are smaller than those of THIOLLAY (1989, 2007) and WHITACRE & BURNHAM (2012). Assuming

the same situation is true for southern Brazil, where most fragments are less than 250 ha and are separated by 8 km (RIBEIRO *et al.*, 2009), population size can be estimated as 252 pairs for the Black Hawk-Eagle (RS = 22 pairs; SC = 230 pairs), 328 pairs for the Black-and-white Hawk-Eagle (RS = 27 pairs; SC = 301 pairs), and 237 pairs for the Ornate Hawk-Eagle (RS = 14 pairs; SC = 223 pairs). These are less than half of the estimation based on Amazon and Tikal forests data (THIOLLAY, 1989, 2007; WHITACRE & BURNHAM, 2012), and probably more accurate, since the highly fragmented condition of the Atlantic Forest (RIBEIRO *et al.*, 2009).

Considering both states (Rio Grande do Sul and Santa Catarina), the three hawk-eagles meet the IUCN criteria C (Population Size) to be classified as Endangered (less than 2,500 mature individuals, IUCN 2012a). Although there are no data about population structure and trends in southern Brazil, it is reasonable to assume that each possible subpopulation has less than 250 individuals. Consequently, based on BIRDLIFE INTERNATIONAL (2016) trends, the Black and Ornate Hawk-Eagle meet the IUCN criteria C2ii as Endangered species in the southern Atlantic Forest. BIRDLIFE INTERNATIONAL (2016) also assumes declining trends for the Black-and-white Hawk-Eagle, which seems to be in a similar situation to that of the Ornate Hawk-Eagle in terms of EOO, population estimation, and habitat use. So, both species should be classified similarly.

The current species risk evaluation for hawk-eagles of Santa Catarina and Rio Grande do Sul, using C2a(i) and C2a(ii) criteria, classified the Black Hawk-Eagle as Vulnerable, Black-and-white Hawk-Eagle as Endangered and Ornate Hawk-Eagle as Critically Endangered in Santa Catarina (CONSEMA-SC, 2011) and classified both Black and Black-and-white Hawk-Eagle as Endangered and the Ornate Hawk-Eagle as Critically Endangered in Rio Grande do Sul (RIO GRANDE DO SUL, 2014). My estimates suggest that the Black Hawk-Eagle has the smallest population of the three species and it is possible that the regional risk evaluation underestimates the risk to this species. Both Black and Ornate Hawk-Eagle depend on mature forests (WHITACRE *et al.*, 2012a,b) and, despite the supposed tolerance that the Black Hawk-Eagle has for second-growth and forest edge (BIERREGARD & KIRWAN, 2016), it is not clear how sensitive the species is to disturbed landscapes (WHITACRE *et al.*, 2012a). In Rio Grande do Sul, the three species could be classified as Critically Endangered (CR) by C2a(ii) criteria. Indeed, all species were classified as CR, but both Black and Black-and-white Hawk-Eagle were downlisted to Endangered due to regional adjustments (according to IUCN, 2012b recommendations; pers. obs). In Santa Catarina, using the same criteria above, my data suggest that all species should be considered Endangered. Santa Catarina has one of the largest fragments of Atlantic Forest (3,824 km²; RIBEIRO *et al.*, 2009), which contributed to a higher estimation of population size for all species. Although my evaluations are in disagreement with the current classifications for Black Hawk-Eagle (Vulnerable) and Ornate Hawk-Eagle (Critically Endangered) for Santa Catarina (CONSEMA-SC, 2011),

they should be treated with caution, and I would suggest maintaining the current classification for the Ornate Hawk-Eagle until there is more accurate data. My estimates were based only on the potential habitat available and probably overestimate the real population size. Populations of the Black Hawk-Eagle also need to be monitored, but risk evaluation for this species could be more conservative for Santa Catarina, classifying the species as Endangered. For Rio Grande do Sul, my data agreed with the current classification (RIO GRANDE DO SUL, 2014).

Breeding biology. Individuals of *Spizaetus* seems to have high plasticity in their breeding cycle. The Black-and-white Hawk-Eagle is the least known species of these three species of *Spizaetus*, and the nest reported here is only the second known for the Atlantic Forest. In southeastern Brazil, CANUTO (2008b) observed a fledging in early October, which suggests laying in June or July (assuming a 3 - 4 months span between laying and fledging for *Spizaetus* spp.; WHITACRE *et al.*, 2012a, b). The copulation observed in mid-July at BGHPS fits with CANUTO's (2008b) observation, suggesting that Black-and-white Hawk-Eagle starts its breeding cycle during the winter in the Southern Hemisphere. Also fits with observations in Central America, where breeding starts at the end of the rainy season (September; STRAUCH, 1975) and beginning of the dry season (January and February; ANDERSON *et al.*, 2004, PHILLIPS, 2009), since winter corresponds with the dry season for most of Brazil.

In Central America, Ornate and Black Hawk-Eagle start egg laying between January and April (LYON & KUHNIGK, 1985; PHILLIPS & HATTEN, 2012; WHITACRE *et al.*, 2012a, b), although for the Ornate Hawk-Eagle egg dates also exist for November, December and May (WHITACRE *et al.*, 2012a,b). There are little data for South America, but Ornate Hawk-Eagles seems to have the same pattern in the Amazon basin: nesting in March in Ecuador (GREENEY *et al.*, 2004) and during May in Venezuela (NAVEDA-RODRIGUEZ, 2004), but KLEIN *et al.* (1988) observed copulation in July in Manaus, Brazil. In the Atlantic Forest, egg laying by the Ornate Hawk-Eagle has been reported, or estimated, to be during June and July (JOENCK *et al.*, 2011) and September (this study). It is unclear why the Ornate Hawk-Eagle and also the Black-and-white Hawk-Eagle start breeding in the middle of the winter in southern Brazil. Large raptors, with long breeding cycles, are less influenced by food supplies when starting to breeding; "it is more a matter of avoiding the worst months" (NEWTON, 1979: p. 98). Growth to maturity takes 12 to 21 months for *Spizaetus* species (WHITACRE *et al.*, 2012a,b), and some variation in laying dates can be expected among different years or even different pairs in order to avoid the worst months.

Most nest characteristics and breeding behavior I observed follow what has been reported for hawk-eagles or for raptors in general (BROWN & AMADON, 1968; NEWTON, 1979; WHITACRE *et al.*, 2012a,b). *Spizaetus* species nest in tall trees (DBH = 92.23 cm, range 66 - 178 cm, n = 29) above the canopy, with nest heights averaging 33.4 m (21 to 51 m; n = 36; Appendix 1). Nest trees and nest features of both

Black and Ornate Hawk-Eagles are similar (WHITACRE *et al.*, 2012), but the Black-and-white Hawk-Eagle seems to use taller trees (nest tree mean height: Black = 30 m, n=4; Ornate = 30.3 m, n = 27; Black-and-white = 40.2 m; n = 5) (Appendix 1). Nests are large, with mean dimensions of 125.9 cm length x 114.8 cm (n = 34) and 67.1 cm external depth (n = 31) (Appendix 1). The Ornate Hawk-Eagle's egg I measured was similar to values of eggs measured in Guatemala and Venezuela (mean = 63.6 cm x 47.3 cm; n = 3) (NAVEDA-RODRIGUEZ, 2004; WHITACRE *et al.*, 2012b), and larger than eggs of captive hawk-eagles (mean = 57.9 cm x 43.8 cm; n = 2; KIFF & CUNNINGHAM, 1980). My observation of nestling development seems similar to the accounts reported by KLEIN *et al.* (1988) and NAVEDA-RODRIGUEZ (2004).

The Black-and-white Hawk-Eagle seems to have a less elaborated courtship display than other species of *Spizaetus*. While both Ornate and Black Hawk-Eagle performs elaborated flight displays including intense vocalization, diving, looping, grasping, food-touching and rolling-over (VANNINI, 1989; FERGUSON-LEES & CHRISTIE, 2001; pers. obs.), observations of courtship of the Black-and-white Hawk-Eagle report pairs gliding together, low vocal activity, chasing and diving culminating with grasping (FERGUSON-LEES & CHRISTIE, 2001; CANUTO, 2008b; KOHLER & REZINI, 2013; this study). WHITACRE *et al.* (2012a,b) mentioned only one observation of an elaborate courtship by Ornate Hawk-Eagles and none for the Black Hawk-Eagle in Tikal Forest.

Behavior by the pair before and during copulation of the Black-and-white Hawk-Eagle also differed from the reported behavior of both Black and Ornate Hawk-Eagle. While WHITACRE *et al.* (2012a,b) reported vocal communication between the pair before copulation for both Black and Ornate Hawk-Eagle, I did not hear any call from Black-and-white Hawk-Eagle before or after copulation. Indeed, the Black-and-white Hawk-Eagle seems to be a very shy species, detected rather by visualization than vocalization (pers. obs.). I did not see the female bringing sticks or green leaves materials to the nest before copulation, as has been reported for other hawk-eagles (WHITACRE *et al.* 2012a,b); the prey items brought by the male might represent a gift to reinforce pair bonding or stimulates copulation, as reported to other raptors (BROWN & AMADON, 1968; WREGE & CADE, 1977). My observation of Black-and-white Hawk-Eagle copulating on the nest is more similar to the behavior shown by Black Hawk-Eagles than by Ornate Hawk-Eagles (WHITACRE *et al.*, 2012b).

CONCLUSION

WHITACRE & BURNHAM (2012) suggested 500 individuals or 250 pairs as a viable population to forest raptors, meaning that an area of 6,250 km² is required to maintain a viable population of Black Hawk-Eagle or any other raptors including the Ornate Hawk-Eagle that have small home ranges (WHITACRE & BURNHAM, 2012). Applying this requirement to the Atlantic Forest, there is only one patch of continuous forest able to support viable populations of these three species of *Spizaetus*: Serra do Mar in São Paulo

and Rio de Janeiro, a fragment of 11,095.46 km² (RIBEIRO *et al.*, 2009). Two other large patches are also located in the Serra do Mar region: Paraná, 5,085.71 km², and Santa Catarina, 3,842.22 km². Other forested areas are fragments of less than 2,500 km² (around 87% of the forest area; RIBEIRO *et al.*, 2009). Also, the smallest forest fragment known to harbor a breeding pair of *Spizaetus* in the Atlantic Forests was 840 ha (CANUTO *et al.*, 2012), meaning that, according estimates of RIBEIRO *et al.* (2009), only 0.38% of the remaining Atlantic Forest fragments might have a breeding pair of hawk-eagle.

In addition to deforestation, fragment isolation adds to the threat to large raptors. According to RIBEIRO *et al.* (2009), the mean amount of isolation among Atlantic Forest fragments is 8 km if considering only patches larger than 200 ha. This is a greater distance than the 6.9 ± 1.5 km average distance between territories of *Spizaetus* (CANUTO *et al.*, 2012). If considering only fragments with more than 500 – 1,000 ha, the mean isolation increases to more than 10 km (RIBEIRO *et al.*, 2009). Consequently, the fragmentation and isolation of Atlantic Forest remnants suggest a patchy distribution for *Spizaetus*, with single birds or pairs limited to isolated patches of forest.

The conservation of large raptors such as *Spizaetus*, *Morphnus* and *Harpyia* in the Atlantic Forest it is not a simple task. Their conservation requires preservation not only of the best remaining forest fragments, but also halting deforestation and disturbance of the remained forest fragments, establishing connectivity among fragments and reducing direct threats to raptors (*e.g.*, persecution). We also need to better understand the ecological requirements of the species in terms of habitat requirements, diet, and breeding biology, as well as establish public policies to protect both species and their habitats, as stated in the Brazilian Action Plan for the Conservation of Birds of Prey (Plano de Ação Nacional para a Conservação de Aves de Rapina; SOARES *et al.*, 2008). Without this information we always will be just guessing about the conservation status of the species, and barely able for formulate a conservation plan.

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Appendix 1. Characteristics of the nest and nest trees used by hawk-eagle (SMEL, Black-and-white Hawk-Eagle; SORN, Ornate Hawk-Eagle; STYR, Black Hawk-Eagle).

Reference	Raptor species	Tree species or family	Tree height (m)	DBH (cm)	Nest height (m)	Nest external dimensions (length x wide x height)(cm)	Chamber (cm)
ANDERSON <i>et al.</i> , 2004	Smel	<i>Metoxylon balsamum</i> (L.) Harms	40		Tree crown	150 x 100	
CANUTO, 2008b	Smel	<i>Cariniana legalis</i> (Mart.) Kuntze	40	86	37	102x85.5x60	62x50x5 cm
STRAUCH, 1975	Smel	<i>Cavanillesia platanifolia</i> (H.& B.) H.B.K.	50		40	>1 m diameter	
CANUTO <i>et al.</i> , 2012	Smel	<i>Joannesia</i> sp.	30				
	Smel	<i>Zeyheria cf. tuberculosa</i> Burman	51	86			
JONECK <i>et al.</i> , 2011	Sorn	<i>Myrocarpus frondosus</i> Fr. Allem	30			170x140x120	
CANUTO <i>et al.</i> , 2012	Sorn	<i>Copaifera langsdorffii</i> Desf.	23	66			
This study	Sorn	Myrtaceae	20	78.94	15	132x100x100	80 x 84 ^D
	Sorn	<i>Araucaria angustifolia</i> (Bertol.) Kuntze	31	132	30	138x115x45	49x47x17
		<i>Swietenia macrophylla</i> King, <i>Ceiba pentandra</i> (L.) Gaertn., <i>Bucida buceras</i> L., <i>Ficus</i> sp., <i>Piscidia piscipula</i> (L.) Sarg., <i>Cedrela odorata</i> L., <i>Pouteria amygdalina</i> (Standl.) Baehni, <i>Calophyllum brasiliensis</i> Cambess	29.9 ± 4.8 m (21 – 40 m) ^A	107 ± 33 cm (larger = 178 cm) ^C	22.9 ± 3.9 m (16 – 30 m) ^A	102±14 cm x 49±11 cm (depth) ^E ; n=16	44±8 cm x 22±13 cm (deep) ^E ; n = 4
PHILLIPS & HATTEN, 2012	Sorn	<i>Manilkara zapota</i> (L.) P.Royen	35.1	71.8	24.4	100x100x80	
	Sorn	<i>Bucida buceras</i> L.	34.8	92.6	23.1	150x100x50	
	Sorn	<i>Ceiba pentandra</i> (L.) Gaertn.	29.2	115.5	21.9	170x150x120	
	Sorn	<i>Bucida buceras</i> L.	27.4	79.7	17.7m	100x200x30	
LYON & KUHNIGK, 1985	Sorn		30		20		
	Sorn		30		26	125x85x50	
KLEIN <i>et al.</i> , 1988	Sorn		40		37	170 (diameter)	
NAVEDA-RODRIGUEZ, 2004	Sorn				29	109x92x56	
GREENEY <i>et al.</i> , 2004	Sorn				30	100 (diameter)	
WHITACRE <i>et al.</i> , 2012a	Styr	<i>Bucida buceras</i> L., <i>Brosimum alicastrum</i> Sw., <i>Rehdera penninervia</i> Standl. & Moldenke	30 ± 3 m (28 – 30 m) ^B	98 ± 35 cm (70 - 150 cm) ^B	25.5 m (23 – 28 m) ^B	97±9 cm (89-115 cm) x 46 (38 – 56 cm; depth) ^F ; n = 4	59 cm (41 - 74 cm) x 5.1 cm (3.4 – 8 cm; deep) ^F ; n = 4
Means	Smel		42.2	86	38.5	117.3x95.2x60	62x50x5 cm
	Sorn		30.03	93.07	24.75	130.5x121.2x70	46.5 x 45.5 x 19.5
	Styr		30 ± 3 m (28 – 30 m)	98 ± 35 cm (70 - 150 cm)	25.5 m (23 – 28 m)	97±9 cm (89-115cm) x 46 (38 - 56 cm; depth) ^F	59cm (41 - 74 cm) x 5.1cm (3.4 – 8 cm; deep) ^F
		all species	33.41	92.23	26.6333	125.9x114.8x67.2	

^A mean ± standard deviation (range); n = 17 nests^B mean ± standard deviation (range); n = 4 nests^C mean ± standard deviation (larger DBH); n = 17 nests^D measure of the center depression on the nest^E mean diameter and depth ± standard deviation^F mean diameter and depth ± standard deviation (range)