

## **Nestling Sex Ratio in a Critically Endangered Dimorphic Raptor, Ridgway's Hawk (*Buteo ridgwayi*)**

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## NESTLING SEX RATIO IN A CRITICALLY ENDANGERED DIMORPHIC RAPTOR, RIDGWAY'S HAWK (*BUTEO RIDGWAYI*)

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**ABSTRACT.**—Variation in nestling sex ratio is an important concept in population ecology, and has particular implications for the conservation status of small populations. Research on species exhibiting Reversed Sexual Size Dimorphism (RSSD), in which females are larger than males, have shown that significant biases in nestling sex ratios can result from demographic and environmental conditions experienced by parents during the breeding episode. We collected morphometric measurements from the critically endangered Ridgway's Hawk (*Buteo ridgwayi*) over a 4-yr period, verifying that the species exhibits RSSD. Females weighed 25% more than males and were significantly larger for 7 of 12 body measurements. Nestling sex-ratios were determined by PCR amplification of the CHD1 gene. The results revealed a weak but consistent trend toward female-biased broods for the small remaining population. Parents may potentially be producing more females, the more costly sex, due to an ample food supply and adaptive allocation of parental care. A female-bias sex ratio may also signal management concern for the species if it is caused by inbreeding; however, currently the bias is not significant enough to warrant immediate intense nest intervention or nest management for this critically endangered species.

**KEY WORDS:** *Ridgway's Hawk*; *Buteo ridgwayi*; conservation; endangered species; nestling sex ratio; reversed sexual size dimorphism.

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### RELACIÓN DE SEXOS EN PICHONES DE *BUTEO RIDGWAYI*, UNA RAPAZ DIMÓRFICA EN PELIGRO CRÍTICO

**RESUMEN.**—La variación en la relación de sexos en pichones es un concepto importante en la ecología de poblaciones y tiene implicancias particulares para el estado de conservación de poblaciones pequeñas. Investigaciones en especies que presentan Dimorfismo Sexual Invertido (DSI), en el cual las hembras son más grandes que los machos, han demostrado que los sesgos significativos en la relación de sexos de los pichones pueden ser el resultado de condiciones demográficas y ambientales experimentadas por los padres durante el episodio de cría. Colectamos medidas morfométricas de individuos de *Buteo ridgwayi*, una especie en peligro crítico, durante un periodo de cuatro años, verificando que la especie presenta DSI. Las hembras pesaron 25% más que los machos y fueron significativamente más grandes en 7 de 12 medidas corporales. La relación de sexos de los pichones se determinó por amplificación de RCP del gen CHD1. Los resultados revelaron una tendencia débil pero consistente hacia nidadas sesgadas hacia las hembras para la pequeña población restante. Los padres pueden estar produciendo más hembras, que representa el sexo más costoso, debido a un amplio suministro de alimento y a una distribución flexible del cuidado parental. La relación de sexos sesgada hacia las hembras puede ser una señal de preocupación en el manejo de la especie, si es que ésta es causada por endogamia; sin embargo, actualmente el sesgo no es lo suficientemente significativo como para requerir intervención de nidos de forma inmediata o manejo de nidos para esta especie en peligro crítico.

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Variation in offspring sex ratio is an important concept in conservation and population ecology (Clutton-Brock 1986, Frankham and Wilcken 2006) and is an essential parameter for viability analyses of small populations (Ferrer et al. 2004, 2009, Rossmanith et al. 2006, 2007, Frankham 2010). This is particularly true for small isolated populations (Bro et al. 2000) where distortion of nestling sex ratios can accelerate extinction (Gabriel and Burger 1992, Brook et al. 2000, Ferrer et al. 2009). For some avian taxa which have recently gone extinct, including the Heath Hen (*Tympanuchus cupido cupido*) and Dusky Seaside Sparrow (*Ammodramus maritimus nigrescens*), the last breeding pairs produced single-sex broods after years of population decline and inbreeding (Awise and Nelson 1989, Simberloff 1988).

In birds, studies have provided evidence that parents can adjust the offspring sex ratio either at the egg-laying stage (primary sex ratio adjustment) or during the period of provisioning for the nestlings (secondary sex ratio adjustment; Ellegren and Sheldon 1997, Kilner 1998, Trnka et al. 2012). Patterns of sex ratio adjustment among raptors have been of particular interest because unlike other groups of birds, most diurnal raptors exhibit reversed sexual size dimorphism (RSSD) with females being larger than males (Snyder and Wiley 1976, Ferguson-Lees and Christie 2001). One consequence of this size difference may be that rearing daughters is more costly, because daughters require more parental investment in the form of food energy, compared to sons (Laaksonen et al. 2004). Research in species with RSSD has shown that significant biases in the sex ratio of nestlings are linked to demographic factors and environmental conditions experienced by the parents during breeding (Torres and Drummond 1997, Korpimäki et al. 2000, Arroyo 2002, Byholm et al. 2002, Hipkiss et al. 2002, Villegas et al. 2004, Magrath et al. 2007, Erikstad et al. 2009). Fisher's theory (1930) predicts that under poor conditions parents should favor the least costly sex to minimize parental investment. Evidence to support this hypothesis is mixed, with some research documenting male-biased broods when food is limited and/or weather conditions are adverse (Wiebe and Bortolotti 1992, Korpimäki et al. 2000, Ingraldi 2005) and others showing no sex-ratio distortions during adverse conditions (Genovart et al. 2008). In addition, demographic factors such as age of parents, laying date, and clutch size have been reported to influence brood sex ratios (Leroux and Bretag-

nolle 1996, Risch and Brinkhof 2002, Griggio et al. 2002, Ferrer et al. 2009, Wu et al. 2010), with more males being produced to younger parents and from larger and earlier clutches.

Sex ratio may also be affected by genetic factors. Inbreeding has been reported to distort offspring sex ratios by reducing the proportion of the homogametic sex (Worthington-Wilmer et al. 1993, Eldridge et al. 1999). A meta-analysis of published literature compiled by Wilcken (2001) documented a slight overall directional distortion in sex ratios due to inbreeding.

Ridgway's Hawk (*Buteo ridgwayi*) is a forest raptor endemic to Hispaniola in the Caribbean. The species was locally common in areas of Haiti and the Dominican Republic at the turn of the century (Cory 1885, Wetmore and Lincoln 1934), but is now listed as Critically Endangered (IUCN 2010). The current global population size is estimated at 91–109 pairs, limited to an area of 1600 km<sup>2</sup> of karst rainforest in Los Haitises National Park on the northeast coast of the Dominican Republic (IUCN 2010, Woolaver 2011). Deforestation due to slash-and-burn agriculture and human persecution of hawks have been major factors in the species' decline (Woolaver 2011). Nearly all of the original forest cover has disappeared from Haiti, and 90% of the Dominican Republic's original forests have been destroyed by human activity (Harcourt and Sayer 1996). We here report the degree of reversed sexual size dimorphism in Ridgway's Hawk from morphometric measurements of live birds, and examine the secondary (nestling) sex ratio to determine if sex ratio distortion could be placing this small population at increased risk of extinction.

#### METHODS

**Study Area.** The island of Hispaniola (19°0'N, 71°0'W) is located in the center of the Greater Antilles archipelago and consists of the nations of Haiti and the Dominican Republic. Less than 1.5% of Haiti's original forest is left, most of which is in the inaccessible uplands of the island and is highly degraded (Rimmer et al. 2005). The Dominican Republic has not fared much better, with only 10% of its original forest cover remaining intact but under threat of further loss from unregulated logging, slash-and-burn agriculture, and charcoal production (Latta et al. 2006). We conducted our study in Los Haitises National Park (19°N, 70°W) which ranges from 0–380 masl in elevation and is located on the northeast coast of the Dominican Republic

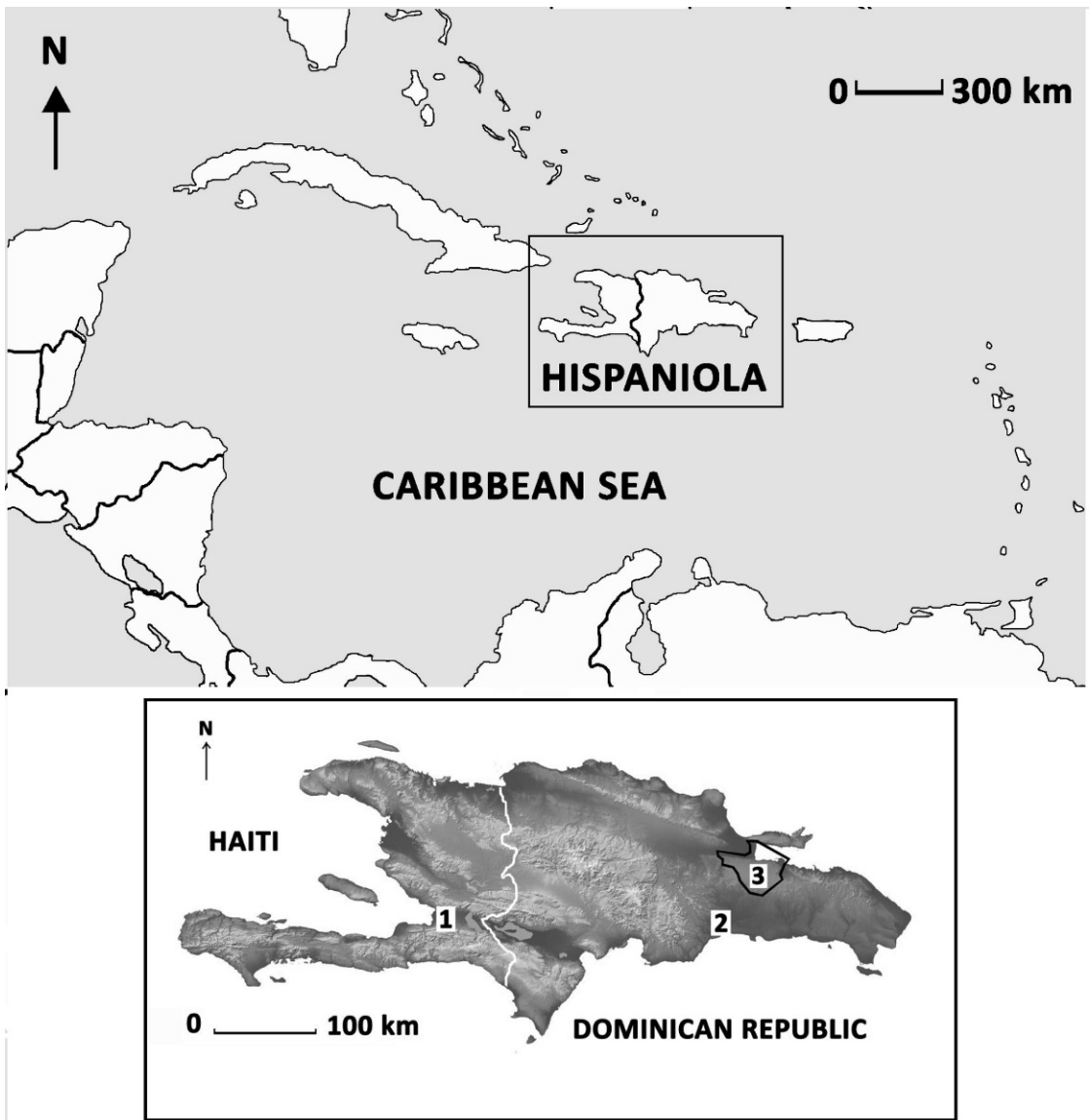


Figure 1. Maps showing relative location of Hispaniola in the Caribbean; and the island of Hispaniola with nations of Haiti and Dominican Republic and their respective capital cities: Port-au-Prince (1) and Santo Domingo (2). The study area of Los Haitises National Park boundaries are delineated in black (3).

(Fig. 1). It is a platform karst (eroded limestone) formation, with dense clusters of steep conical hills, or *mogotes*, of nearly uniform height (200–300 m) separated by sinkhole or *doline* valleys. The Los Haitises region consists of thousands of such *mogotes* within an area of ca. 1600 km<sup>2</sup>.

**Nest Monitoring.** Breeding pairs of *B. ridgwayi* were studied over four breeding seasons (January

to July 2005–2008). Early-season searches for breeding pairs were made from vantage points on hill-sides overlooking valleys to identify nest locations. Once a nest was found, it was visited every 1–3 d (for easily accessible nests), or every 1–2 wk (for sites that were more difficult to access) to determine which pairs laid a clutch (termed the “active” nests), and how many reared young to fledging.

Nest observations were carried out with binoculars and a spotting scope from a covered vantage point (25–75 m away). Due to the topography of the nesting valleys, it was generally possible to find a vantage point on a hillside above the level of the nest that allowed complete viewing into the nest cup. A nest was classified as successful if at least one young fledged. A nest was considered failed if it had been active but subsequently did not produce at least one fledgling. Indications of nest failure were the absence of both adults or the absence of one adult and inattendance of the remaining adult during a 2- to 4-hr observation on successive visits, or the death or disappearance of all eggs or nestlings. Nest contents were identified (when possible) by viewing through a spotting scope or climbing to nests. Nests were accessed during the late-nestling stage due to the risks of handling young nestlings and of abandonment/failure during the incubation period. Therefore it was only possible to assess secondary (nestling) sex ratio.

**Capture, Measurement, and Banding.** Nestlings were accessed at the nest when 15–40 d old. Nestlings were placed in cotton bags and lowered to the ground below the nest, where they were measured and banded, and a blood sample was collected for molecular sexing. Handling time of nestlings did not exceed 20 min per individual. Adults were captured using bal chatri noose traps baited with white domestic mice (*Mus musculus*; Thorstrom 1996). Adults were not trapped during incubation.

Morphometric measurements were carried out prior to banding or collection of blood for DNA. Twelve measurements were taken on all birds: body mass (g), unflattened wing chord, tail length (measured on the central rectrice), skull length (posterior of cranium to base of mandible), skull width, culmen (anterior edge of cere to tip of bill), bill depth and width (both measured at anterior edge of cere), tarsus length (length between the intertarsal joint and the last leg scale before the toes emerge), tarsus width (width of widest part of tarsus, measured at mid-point between the foot and tibiotarsal articulation), middle toe length, middle toe talon. All characteristics were measured to the nearest 0.1 mm using callipers, except for wing chord and tail length which were measured to the nearest 1.0 mm using a meterstick, and mass which was measured to the nearest 0.1 gram. Ridgway's Hawks were banded with individually numbered, colored, anodized Acraft<sup>®</sup> aluminium rivet bands. No more than one band was ever placed on a leg.

**DNA Collection and Extraction.** Approximately 0.2 ml of blood was drawn via capillary tube from a patagial vein puncture, half of which was stored in 1.6 ml of Queen's lysis buffer (Seutin et al. 1991). The other 0.1 ml of blood was stored in 1.8 ml of 95% ethanol. All samples were stored at ambient temperature until delivered to laboratory facilities where they were preserved at  $-20^{\circ}\text{C}$ .

Total cell DNA was isolated by blood cell lysis, followed by DNA precipitation using ammonium acetate and isopropanol (L. de Sousa, B. Woolfenden, and S. Tarof unpubl. protocol for York University Molecular Ecology Lab). This involved the addition of 50  $\mu\text{l}$  of blood/Queen's lysis buffer to 600  $\mu\text{l}$  of cell lysis buffer and 5  $\mu\text{l}$  of ice-cold Proteinase K (40 ng/ $\mu\text{l}$ ). This solution was then incubated at  $55\text{--}60^{\circ}\text{C}$  for 5 hr and then at  $37^{\circ}\text{C}$  overnight. Ice-cold ammonium acetate (200  $\mu\text{l}$ ) was then added, mixed gently, and centrifuged to precipitate protein. The aqueous phase, including the dissolved genomic DNA, was removed and placed in a fresh tube. Ice-cold isopropanol (600  $\mu\text{l}$ ) was added and the solution inverted until DNA was visible as a white floating string or flake. This solution was then centrifuged to collect genomic DNA as a pellet at the bottom of the tube. The supernatant was removed and the DNA pellet washed with ice-cold 70% ethanol. This solution was then centrifuged again and the ethanol then removed. This ethanol wash was repeated a second time. The tube was then left open and inverted overnight to allow the DNA pellet to dry completely. The DNA pellet was then suspended in 100–200  $\mu\text{l}$  of TE buffer (10 mM Tris-HCl, 1 mM EDTA) at  $37^{\circ}\text{C}$  for 24 hr. DNA was stored at  $4^{\circ}\text{C}$  while in use, and at  $-20^{\circ}\text{C}$  for longer-term storage.

DNA was visualized under ultraviolet radiation on a 1% agarose test gel, pre-stained with ethidium bromide. Samples were visualized next to a Mass-Ruler high range DNA ladder mix (Fermentas O'GeneRuler<sup>™</sup>). Samples were run along with positive (DNA sample of known size) and negative (distilled water) controls.

**Sex Determination.** Molecular sexing of the Ridgway's Hawk samples (adults and nestlings) was carried out by PCR amplification of the CHD1 gene. The methods of Fridolfsson and Ellegren (1999) with primers 2550F/2718R were modified as follows. DNA samples were removed from  $-20^{\circ}\text{C}$  storage and incubated in a  $37^{\circ}\text{C}$  water bath for 30 min. Polymerase Chain Reactions (PCR) were run on all adult and nestling samples collected in 2005–2007. Genomic DNA was amplified in 10  $\mu\text{l}$  reactions

Table 1. Mean  $\pm$  SD (range) for twelve measurements from 20 adult female and 15 adult male Ridgway's Hawks. All variables are reported in mm except for body mass (g).

MEASUREMENT	MALE	FEMALE	<i>P</i> <sup>a</sup>
Body mass	310.5 $\pm$ 11.0 (286–323)	402.6 $\pm$ 24.6 (352–450)	<b>0.00</b>
Wing chord	228.3 $\pm$ 13.8 (200–244)	250.9 $\pm$ 7.6 (226–260)	<b>0.00</b>
Skull length	44.3 $\pm$ 2.0 (40.3–47.6)	45.6 $\pm$ 1.9 (40.9–49.7)	<b>0.04</b>
Skull width	36.9 $\pm$ 2.6 (34.4–40.6)	37.8 $\pm$ 3.3 (35.2–40.9)	0.07
Culmen	17.0 $\pm$ 1.4 (14.9–19.1)	18.5 $\pm$ 1.2 (16.4–21.0)	<b>0.01</b>
Bill width	13.3 $\pm$ 3.4 (8.6–16.3)	13.5 $\pm$ 3.4 (9.1–16.7)	0.35
Bill depth	13.4 $\pm$ 1.0 (12.1–15.6)	13.9 $\pm$ 0.8 (12.5–15.2)	<b>0.04</b>
Tail length	147.7 $\pm$ 9.0 (125–161)	153.8 $\pm$ 6.8 (139–164)	<b>0.03</b>
Tarsus length	73.4 $\pm$ 3.3 (68.3–78.0)	75.2 $\pm$ 3.8 (69.7–80.9)	0.12
Tarsus width	6.2 $\pm$ 0.8 (5.4–7.4)	7.0 $\pm$ 0.8 (5.8–8.1)	<b>0.00</b>
Middle toe	29.9 $\pm$ 2.3 (26.1–34.0)	31.0 $\pm$ 2.4 (27.2–35.5)	0.17
Middle toe talon	16.7 $\pm$ 1.2 (14.5–17.7)	17.4 $\pm$ 1.1 (15.5–18.9)	0.11

<sup>a</sup> Mann-Whitney *U*-test.

containing 3.7  $\mu$ l of distilled water, 1.25  $\mu$ l of PCR reaction buffer (10X TSG), 3.25  $\mu$ l of 2.0 mM MgSO<sub>4</sub>, 0.25  $\mu$ l of 10 mM dNTPs, 0.25  $\mu$ l of fluorescently dyed 10 uM forward (2550F) and reverse (2718R) primers, 0.05  $\mu$ l of Taq DNA polymerase (TSG), and 1  $\mu$ l of DNA template (ca. 15 ng DNA in TE buffer). PCR reactions were carried out in an Eppendorf MasterCycler™ thermal cycler. An initial 2-min denaturing step at 94°C was followed by 30 cycles of 30 sec at 94°C, 30 sec at an annealing temperature of 50°C, and a 30-sec extension step at 72°C. The PCR reaction finished with a final 5-min extension step at 72°C, and samples were then held at 4°C until taken from the thermal cycler. Samples were run on a 2% agarose (1.0 g agarose powder to 50 mL of 1X TBE) gel post-stained with ethidium bromide (10  $\mu$ l ETBR per gel). Gels were run at 70 V for 75 min in order to achieve sufficient band separation to discern males (one band) from females (two bands). Male Ridgway's Hawks showed a clear single band for the CHD1-Z gene at 600 bp, while females showed bands at the CHD1-Z gene (600 bp) and at the CHD1-W gene (350 bp). Sexes of the adult birds were known through both plumage differences observed during handling (sexes are distinguishable by plumage when in the hand; Wiley and Wiley 1981) and also further support from field observations of nesting behavior. Sex assignment using the CHD1 gene agreed with sex assignment by plumage and behavior for all 20 adult female and 15 adult male Ridgway's Hawks, so we were confident the molecular method worked successfully.

**Data Analysis.** Mann-Whitney *U*-tests were used to compare morphometric measurements between

adult males and females. Binomial tests were used to test whether nestling sex ratios (number of males/number of females) deviated significantly from a 1:1 ratio for each year 2005–2008, and for all years combined. Data were analysed using the SPSS statistical package (SPSS 2003). *P* values  $\leq 0.05$  indicated a significant result; *P* values  $> 0.05$  and  $< 0.10$  indicated a trend.

# RESULTS

**Reversed Sexual Size Dimorphism.** Adult female Ridgway's Hawks were significantly greater in size for 7 of the 12 morphometric variables measured (Table 1). Females were ca. 25% heavier than males on average. There was no overlap in mass, with all females weighing  $\geq 352$  g and all males weighing  $\leq 323$  g. Wing chord, tarsus width, and culmen were all highly significantly different, with very little overlap between females and males (Table 1). Skull width showed a trend toward differentiation between the sexes (*P* = 0.07, Table 1). There was no significant difference in size between males and females for bill width, tarsus length, middle toe length, and middle toe talon (Table 1).

**Nestling (Secondary) Sex Ratio.** Sixty-three broods were sampled at the nestling stage: one brood contained three nestlings, 37 contained two nestlings, and 25 contained one nestling. Sex was determined for 103 nestlings (42 male, 61 female) between 2005 and 2008 (Table 2). Nestling sex ratios (M:F) ranged from 1:1.25 in 2005 to 1:1.90 in 2007 (Table 2) and in each year were female-biased. None of the years exhibited statistically significant deviations from 1:1 (Table 2), but statistical testing



Table 2. Observed annual nestling (secondary) sex ratios of Ridgway’s Hawk from 2005–2008.

YEAR	MALES	FEMALES	NO. BROODS	SEX RATIO (M:F)	% MALES	P-VALUE <sup>a</sup>
2005	8	10	12	1:1.25	44.4	0.82
2006	10	15	14	1:1.50	40.0	0.42
2007	10	19	19	1:1.90	34.5	0.12
2008	14	17	18	1:1.21	45.2	0.72
All years	42	61	63	1:1.38	42.0	0.09

<sup>a</sup> Binomial test.

was limited due to the unavoidably small sample sizes inherent in dealing with critically endangered populations. However, an overall trend in favor of females was evident when all years were combined (Table 2).

The majority of broods with two or more nestlings contained mixed sexes (25/38, 65.7%; Fig. 2). For single-sex broods containing two or more nestlings, more than twice as many were all-female (9/13) compared to all-male (4/13) for all seasons combined (Fig. 2). In addition, there were almost twice as many nests with a single female nestling (16/25) compared to a single male nestling (9/25; Fig. 2). Of the 63 nests monitored, 13 showed a reduction in brood size compared to clutch size (Table 3). Six of these reductions were caused by a nestling succumbing to botfly (*Philornis pici*) parasitism, three were caused by one egg not hatching, and the remaining five causes were unknown but suspected to be related to predation and human persecution. During 1000+ hours of nest observation during the nestling stage, there were no incidents of direct aggression among nestlings (Woolaver 2011). Although this does not preclude nestling aggression from occurring within the species, it does suggest that aggressive bouts were relatively infrequent.

DISCUSSION

**Reversed Sexual Size Dimorphism.** Measurements of live birds during the current study verified reversed sexual size dimorphism in Ridgway’s Hawk, as initially reported from museum specimens by Wiley and Wiley (1981). Females were approximately 25% heavier than males on average, and had significantly larger skulls, wings, and tails. Sexual dimorphism is typical of the genus *Buteo* with many species showing varying levels of reversed sexual dimorphism (Ferguson-Lees and Christie 2001). There also appears to be a trend for insular species to exhibit higher rates of dimorphism than mainland *Buteos*. Two island *Buteos*, the Galapagos Hawk (*B.*

*galapagoensis*) and the Hawaiian Hawk (*B. solitarius*), exhibit the highest levels of reversed sexual dimorphism within the genus, with females being  $\geq 30\%$  larger in mass than males (Paton et al. 1994). In the Red-shouldered Hawk (*B. lineatus*), the closest taxonomic relative to Ridgway’s Hawk (Amaral et al. 2009), females are up to 25% heavier than males (Dykstra et al. 2008, 2012).

There were no significant differences between male and female Ridgway’s Hawks in tarsus length, middle toe length, middle toe talon, or bill width. Although males are approximately 25% lighter in mass than females, and smaller in other physical traits including skull, wing and tail length, they have similar-sized talons, tarsus length, and bill width. For raptors, these are morphological traits that are important for hunting. In terms of hunting capability, being smaller and lighter for easier maneuverability within forested areas, yet retaining ample-sized hunting morphology including long legs and talons for catching prey, and a wide bill for retaining, killing, or ripping larger prey may make males more efficient hunters.

**Nestling Sex Ratios.** Our results suggested there was a weak but consistent sex-ratio bias toward females. In terms of sex allocation, this trend toward females could suggest that food resources are more than adequate for the number of breeding pairs currently nesting in the area, that adults are in relatively good physical condition during the breeding episode, and/or that no other obvious environmental stresses are promoting sex allocation of the least costly sex by the parents. During a concurrent 4-yr study of Ridgway’s Hawk feeding ecology, food provisioning rates did not vary between successful and failed nests, there were no incidents of nest failure due to starvation, and excess food was observed at the majority of nests during observations. These findings suggest that food availability was not limited and may have been in ample supply (Woolaver et al. 2013a). There was also no indication that the

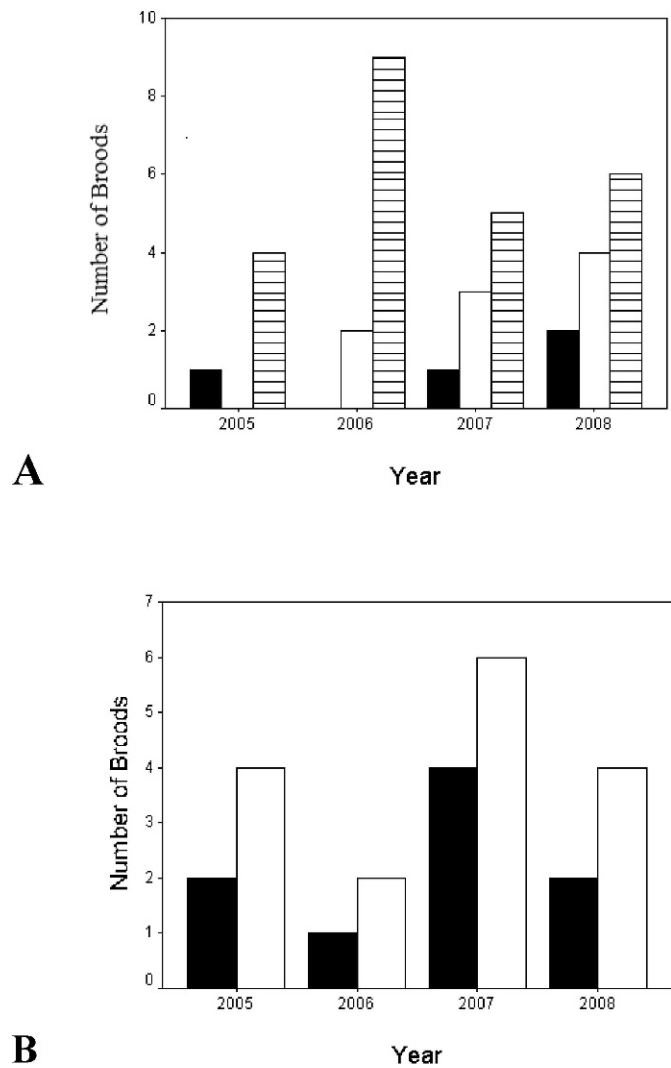


Figure 2. Number of Ridgway's Hawk broods per year with mixed-sex nestlings (striped bar), all female nestlings (white bar), and all male nestlings (black bar). (A) Broods with two or more nestlings and (B) Broods with only one nestling.

Table 3. Clutch and brood sizes of 63 sampled nests monitored from 2005–2009.

CLUTCH OR BROOD SIZE	NO. OF CLUTCHES	NO. OF BROODS
1	12	25 <sup>a</sup>
2	50	37
3	1	1

<sup>a</sup> All 12 one-egg clutches produced one nestling; the remaining 13/25 one-nestling broods were the result of reductions from 2-egg clutches.

adults' body conditions were compromised during the study (L. Woolaver unpubl. data). As a result of an adequate prey base, Ridgway's Hawk may have been investing in the more costly sex. Arroyo (2002) found that more female nestlings were produced in years with higher food availability in the dimorphic Montagu's Harrier (*Circus pygargus*). In a population of the critically endangered Kakapo (*Strigops habroptila*) that was provided supplementary food, production of young was biased toward males, which in Kakapo are the more costly sex (Clout and Merton 2002).



Nesting sex ratios can also become biased through the selective elimination of the smallest nestlings(s) either by starvation and/or competition and aggression from larger siblings (Viñuela 1999, Bortolotti 1986, Wiebe and Bortolotti 2000). This type of brood reduction is fairly common in many raptors and generally results in biased nestling sex ratios (Bortolotti 1986). However, there was no evidence of this type of brood reduction during the present study. To our knowledge, 80% of nests (50/63) did not exhibit any reduction in size between the clutch and brood stages, and in nine cases of reduction the causes identified were infertility ( $n = 3$ ) and botfly parasitism ( $n = 6$ ). Furthermore, there were no observations of aggression among nestlings over the 5-yr study period.

Several other factors have been found to affect sex ratio including age of parents, clutch size, egg mass, and laying order. Ferrer et al. (2009) documented a sex-ratio distortion for the endangered Spanish Imperial Eagle (*Aquila adalberti*) where younger breeding birds produced significantly more male-biased broods. Wu et al. (2010) found that clutch size and egg mass affected the secondary brood sex ratio of the Eurasian Kestrel (*Falco tinnunculus*) with larger clutches and heavier eggs producing more male nestlings. Laying date can also affect the secondary sex ratios, with eggs laid earlier producing a greater proportion of males (Griggio et al. 2002, Wu et al. 2010). It is recommended that breeding Ridgway's Hawk pairs continue to be monitored to determine if any age-related trends in breeding pairs, or laying patterns or characteristics (size, date, egg mass) are responsible for sex-ratio distortion of Ridgway's Hawk nestlings.

If the trend toward a female-biased sex ratio found in this study is related to environmental and breeding conditions, then this could be a positive sign for the population. However, molecular evidence has revealed that inbreeding is occurring in the population and that up to 18% of potential random pairings of Ridgway's Hawk could be inbred (Woolaver et al. 2013b). Although directional distortions in sex ratio do not appear to be a consistent signal of inbreeding depression, small random populations can exhibit severe distortions from autosomal sex-limited alleles that have drifted in isolated populations (Frankham and Wilcken 2006). Inbreeding can potentially distort sex ratios by reducing the proportion of the homogametic sex (Worthington-Wilmer et al. 1993, Eldridge et al. 1999). If this were occurring within the Ridgway's

Hawk population, we would expect distortions toward female-biased broods among breeding pairs. Since our result did reveal a trend toward the production of female nestlings, it would be important for future population research to continue monitoring the sex ratio of this small vulnerable population and incorporate this component into any future conservation strategy (Ferrer et al. 2009). At the moment, the current trend toward female-biased broods is not significant enough on its own to warrant brood-specific intensive management (i.e., brood manipulations) of this critically endangered species, but caution is warranted and monitoring of nestling sex-ratio should be a priority.

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