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EFFECT OF SEX AND AGE AT RELEASE ON THE INDEPENDENCE OF HACKED HARPY EAGLES

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ABSTRACT.—Release methods used in species restoration can affect the success of establishment and survival of released animals. We evaluated the effect of age at release and sex on the length of the dependence period of hacked captive-bred juvenile Harpy Eagles (*Harpia harpyja*). Between 2002 and 2007, we released 34 (19 males and 15 females) young eagles in Panama and Belize. To test the effect of age, these eagles were divided into two age classes: younger age class 1 (5–7 mo old) and older age class 2 (18–22 mo old). Survival (hacking success) was lower for the younger release age (70%) compared to the older release age (100%; $Z = -2.05$, $P = 0.040$). This difference in hacking success was attributed to the extended period of dependence on provisioned food by the younger (18.9 ± 1.3 mo [SE]) compared to older eagles (1.5 ± 0.8 mo). Between-sex comparisons showed that the average length of the dependence period was longer for males of age class 1 (males = 21.8 mo vs. females = 14.3 mo) and for females of age class 2 (females = 2.7 mo vs. males = 0 mo). Cox regression models indicated that the interaction of age at release and sex had a significant effect on the dependence period, and that age at release was the most influential variable. Eagles released at 18 mo or older showed increased survival and shorter dependence periods. Hacking can be used to successfully release captive-bred Harpy Eagles into the wild, but this technique was more efficient when delayed from fledging age (when falconers traditionally hack falcons) to nearer the Harpy Eagle's age of independence.

KEY WORDS: *Harpy Eagle*; Harpia harpyja; *Belize*; *neotropical raptor*; *Panama*; *post-fledging dependence period*; *survival.*

EFECTOS DEL SEXO Y DE LA EDAD DE LIBERACIÓN EN LA INDEPENDENCIA DE INDIVIDUOS CRIADOS A CAMPO DE *HARPIA HARPYIA*

RESUMEN.—Los métodos de liberación utilizados en la restauración de especies pueden afectar el éxito de establecimiento y la supervivencia de los animales liberados. Evaluamos los efectos de la edad al momento de la liberación y del sexo sobre la duración del periodo de dependencia de juveniles criados en cautiverio de *Harpia harpyia*. Entre 2002 y 2007, liberamos 34 (19 machos y 15 hembras) águilas jóvenes en Panamá y Belice. Para evaluar el efecto de la edad, se dividió a las águilas en dos clases: clase de edad 1 (menores entre 5–7 meses de edad) y clase de edad 2 (mayores entre 18–22 meses de edad). La supervivencia (éxito de *hacking*) fue menor para la edad de liberación joven (70%) que para la edad de liberación mayor (100%, $Z = -2.05$, $P = 0.040$). Esta diferencia en el éxito de *hacking* se atribuyó al prolongado periodo de dependencia de provisión de alimento que presentaron los jóvenes (18.9 ± 1.3 meses [EE]) comparado con el de las águilas mayores (1.5 ± 0.8 meses). La comparación entre sexos evidenció que la duración promedio del periodo de dependencia fue mayor para los machos de la clase de edad 1 (machos = 21.8 meses vs. hembras =14.3 meses) y para las hembras de la clase de edad 2 (hembras = 2.7 meses vs. machos = 0 meses). Los modelos de regresión de Cox indicaron que la interacción de la edad de liberación con el sexo tuvo un efecto significativo en el periodo de dependencia y que la edad de liberación fue la variable de mayor influencia. Las águilas liberadas a los 18 meses de edad o mayores mostraron una mayor supervivencia y un periodo de

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dependencia menor. El método de *hacking* puede ser utilizado para liberar exitosamente a individuos de *H. harpyia*, pero esta técnica fue más eficiente cuando se la atrasó desde la edad de volantones (cuando los cetreros tradicionalmente crían a campo a los halcones) hasta cerca de la edad de independencia de *H. harpyia*.

[Traducción del equipo editorial]

Reintroduction is an attempt to restore viable populations of species within their former ranges. It has become a powerful tool in conservation biology (Griffith et al. 1989, Fischer and Lindenmayer 2000, Seddon et al. 2007), effectively used to restore rare and threatened raptor populations such as the Peregrine Falcon (*Falco peregrinus*; Cade 2000), which was subsequently removed from the U.S. Endangered Species Act list (Cade and Burnham 2003).

Hacking, one method of releasing captive-bred raptors into the wild, has been used to help restore many raptor species (Cade 2000). The method consists of placing fledgling raptors in a hack box, a large free-standing cage, for a predetermined confinement period prior to release. The cage is then opened and the young raptors are allowed to fly. Attendents continue to provide food at the hack box until the young can hunt successfully on their own (Sherrod et al. 1987). Because this reintroduction procedure is more complex than other methods, attempts have been made to improve success via the evaluation of technical variations (Dzialak et al. 2006). Although hacking has been used successfully in the restoration of raptors from temperate zones (Cade 2000), its applicability to tropical regions needs further study. Tropical raptors have relatively small populations, low reproductive rates, long post-fledging dependence periods, and are long-lived (Newton 1979, Thiollay 1989). These life-history traits must be considered when adapting hacking techniques to a tropical environment. For instance, the long post-fledging dependence period, during which young raptors develop essential foraging skills, may be especially problematic in a tropical release program. Therefore, identifying and testing the variations on techniques that increase survival and reduce the post-fledging dependence period is essential to reintroduction success.

The Harpy Eagle (*Harpia harpyja*) is a long-lived, tropical forest raptor that reproduces slowly, with a post-fledging dependence period estimated at 27 mo (Alvarez-Cordero 1996). Throughout its range from Mexico to Argentina, it is sparsely distributed and several populations are declining or extirpated due to persecution by humans and deforestation (Stotz et al. 1996, Vargas et al. 2006). The species is classified as Near Threatened (BirdLife International 2011).

In 2000, The Peregrine Fund established the Neotropical Raptor Center (NRC) in Panama City, Panama to: (1) develop techniques for captive breeding of tropical raptors using the Harpy Eagle as a model species; (2) test methods for releasing and monitoring captive-bred eagles, and (3) experimentally restore a population of Harpy Eagles in their former range within Central America. In this report, we focus on objective (2), and our specific goal was to evaluate how the age at release and sex affect the length of the dependence period and survival of hacked young Harpy Eagles.

Methods

Study Areas and Hack Sites. The Peregrine Fund released captive-bred Harpy Eagles in Panama and Belize between 1998 and 2007. For this study, we used data collected from 2002 to 2007 on 30 eagles released in Panama (17 males and 13 females) and four in Belize (2 males and 2 females). In Panama, the hack sites were located in Soberania National Park (SNP), and in Belize in Chiquibul Forest Reserve (CFR). We selected these areas for several reasons: (1) eagles were protected from human persecution; (2) large forest tracts likely provided sufficient habitat and prey sources; (3) historical records confirmed the former presence and subsequent extirpation of local Harpy Eagle populations; and (4) road access and existing facilities supported fieldwork.

Soberania National Park. Soberania National Park (SNP) is a lowland, 22 000-ha moist tropical forest (Holdridge 1967) in central Panama (9°N, 79°W), bordering the Panama Canal (Leigh et al. 1982). Annual rainfall averages 250 cm, with 90% falling during the late-April to mid-December rainy season (Robinson et al. 2004).

Vegetation of SNP consists of a mixture of secondary and primary forest. Forest age ranges from 80 to 150 yr, though a few clearings and some small patches of old-growth forest, estimated to be >400 yr old, remain (Foster and Brokaw 1982, Heckadon-Moreno et al. 1999). Sloths (*Bradypus variegatus* and *Choloepus hoffmanni*), monkeys (*Alouatta palliata* and *Cebus capucinus*), iguanas (*Iguana iguana*), and coatis (*Nasua narica*) occurred regularly, which are known elsewhere (Wright et al. 2000) to be the main prey of Harpy Eagles (Alvarez-Cordero 1996, Touchton et al. 2002).

We built two hack boxes in the northern part of Soberania National Park at 9°12.151′N, 79°47.095′W (hack box 1) and at 9°11.845′N, 79°46.510′W (hack box 2). The distance between the boxes was 1.2 km. The hack boxes were 150 m (hack box 1) and 1100 m (hack box 2) away from the cabin where the hack-site attendants resided. Because of the behavior of released eagles approaching humans at the cabin, in 2006 we moved the first hack box 400 m farther away (9°307′N, 79°214′W).

Chiquibul Forest Reserve. The hack site in Chiquibul Forest Reserve (CFR) was located at the Las Cuevas Research Station in the 170 000-ha CFR (16°N, 88°W), Cayo District, southwestern Belize. The vegetation is a mosaic of deciduous semi-evergreen, deciduous seasonal forest, with stands of native pine (*Pinus caribaea*) in the northern sector (Wright et al. 1959). The forest is of relatively low stature because of periodic disruption by hurricanes (Morris et al. 2004). Rainfall ranges from 150 to 200 cm per year with a rainy season from June to December (Beletsky 1999). This reserve is located within the fully protected Chiquibul National Park. These protected areas, combined with areas of northern Guatemala and southern Mexico, make up the Maya Forest, the largest tropical rainforest in Central America (Rodstrom et al. 1998). As in Panama, this reserve is home to several species of mammals that form part of the Harpy Eagle's diet, excluding the two species of sloths whose distributions do not reach this part of Central America (Reid 1997, Caro et al. 2001).

Releases in the Chiquibul were cancelled after the first year as it was no longer safe for the eagles or the hack-site attendants in the CFR. The area had become inundated with *xaté* collectors (*xatéros*), who illegally crossed the border from Guatemala to harvest the *xaté* (palm *Chamaedorea*). Many *xatéros* lived in the forest for weeks at a time and survived, in part, by poaching the local wildlife (Perez et al. 2009).

Hacking. The hacking technique we implemented for releasing Harpy Eagles was adjusted to the particular needs of this large tropical raptor. Our hacking protocol consisted of placing one or two young Harpy Eagles in separate chambers within the hack box, where they remained for a period of 3–6 wk (see Table 1). This period varied according to equipment repair needs or the limited availability of hack-site attendants to track eagles after release.

The breeding stock included four pairs of Harpy Eagles formed with wild individuals from Ecuador, Venezuela, and Panama, and with captive-reared individuals from The World Center for Birds of Prey in Boise and San Diego Zoo. We inferred that this assemblage would provide sufficient genetic variation to counteract potential effects of inbreeding. Eaglets were captive-reared at the Neotropical Raptor Center in Panama City, Republic of Panama.

To conduct the experiment, we released twenty-three juvenile eagles at 5–7 mo old (age class 1) and eleven at 18–22 mo old (age class 2). We selected these age groups to test if releasing younger (class 1, approximately fledging age; see Rettig 1978) or older (class 2, approximately independence age in the wild; see Alvarez-Cordero 1996) affected the length of the dependence period.

Food Delivery and Feeding Regime. While in the hack box enclosure, eagles were fed at night to avoid their associating humans with food. We normally provided 250–300 g of food per eagle, per day (rats [*Rattus norvegicus*] and/or rabbits [*Oryctolagus cuniculus*]). After the hack box was opened and the birds were released, we continued to feed the eagles every day, just before sunrise to limit food losses to nocturnal animals, by securing their food on the hack-box perches. After the eagles had moved >50 m away from the hack box we delivered food to ''feeding trees'' to lure the Harpy Eagles away from the hack box. This avoided overcrowding at the hack box and allowed us to release more eagles at one site than otherwise would be possible. Feeding trees were also utilized early in the release period when some birds did not return to the hack box regularly. If a given bird had not eaten for seven days, we set up feeding trees close to its location to ensure availability of food. A feeding tree normally had at least one main horizontal branch, between 3 and 15 m above the ground, where food was easily seen and accessible to the birds. Food was hoisted to the branch and secured in place by ropes.

Beginning 4 wk after release, we gradually reduced the frequency of food deliveries, providing 300–450 g of food every other day (wk 5–8) and then every third day (wk 9–12), and finally providing 750 g every fifth day from wk 13 onward. Once we confirmed an eagle had killed its first prey, we continued monitoring its movements, and delivered food every seventh day until there was a confirmed

Table 1. Captive-bred juvenile Harpy Eagles released in Soberania National Park (SNP—Panama) and Chiquibul Forest Reserve (CFR—Belize) between 2002 and 2007.

BAND	HACK-SITE	SEX	AGE AT RELEASE (mo)	DAYS IN HACK BOX	INDIVIDUALS IN HACK BOX	BODY MASS (kg)	SEASON	AGE AT INDEPENDENCE (mo)	STATUS AT INDEPENDENCE	INDEPENDENCE CRITERIA[a]
Age Class 1										
MY	SNP	Female	7	20	2	6.0	rainy	30	Alive	2
CZ	SNP	Male	7	20	2	5.0	rainy	26	Alive	2
MA	SNP	Female	7	31	2	5.4	rainy	14	Alive	1
EK	SNP	Male	6	31	2	4.1	rainy	21	Dead	4
DT	SNP	Male	7	38	1	4.1	dry	29	Alive	2
DD	SNP	Male	6	29	2	4.5	dry	6	Dead	4
DP	SNP	Male	6	29	2	4.3	dry	26	Alive	2
ET	SNP	Male	6	28	2	4.4	dry	28	Alive	2
MC	SNP	Female	6	28	2	6.2	dry	6	Dead	4
DX	CFR	Male	6	23	2	4.1	dry	21	Dead	4
MX	CFR	Female	6	23	2	6.0	dry	29	Alive	1
BZ	SNP	Male	6	32	1	4.3	rainy	29	Alive	2
LG	CFR	Female	6	22	2	6.0	rainy	29	Alive	2
CN	SNP	Male	6	30	2	4.3	rainy	31	Alive	1
HH	SNP	Female	7	30	2	6.3	rainy	15	Alive	1
DM	CFR	Male	5	22	2	4.4	rainy	30	Alive	2
AT	SNP	Male	6	24	2	4.4	dry	28	Alive	2
KK	SNP	Female	6	24	2	5.6	rainy	24	Alive	2
BY	SNP	Male	5	27	1	4.3	dry	28	Alive	2
EV	SNP	Male	6	36	2	5.0	rainy	17	Dead	4
LY	SNP	Female	6	36	2	5.7	rainy	16	Dead	4
MU	SNP	Female	7	37	2	5.8	rainy	17	Alive	1
BT	SNP	Male	6	37	2	3.9	rainy	15	Dead	4
Age Class 2										
HS	SNP	Female	22	40	1	6.7	dry	27	Alive	1
BC	SNP	Male	19	22	1	5	dry	19	Alive	3
KC	SNP	Female	18	21	1	6.3	rainy	24	Alive	1
DK	SNP	Male	18	25	2	4.7	rainy	18	Alive	3
KD	SNP	Female	18	25	2	6.8	rainy	18	Alive	3
CH	SNP	Male	19	29	2	4.9	dry	19	Alive	3
HC	SNP	Female	19	29	2	6.6	dry	19	Alive	3
LA	SNP	Female	20	21	2	6.4	rainy	20	Alive	3
LB	SNP	Female	20	21	2	6.3	rainy	27	Alive	2
BM	SNP	Male	20	21	2	5.4	rainy	20	Alive	3
BN	SNP	Male	20	21	2	5.1	rainy	20	Alive	3

[a] 1. Two kills <20 d apart; 2. Went >30 d without receiving food; 3. Never accepted the food provided; 4. Dead before independence.

second kill. After we found a bird's second kill, we only delivered food every tenth day. Food deliveries ended after the eagles became independent (see below).

Length of the Dependence Period. Although our eagles fledged at 4–5 mo in the flight chambers located at the NRC, we considered the initiation of the dependence period to be the moment eagles were released from the hack box. Therefore, dependence period is defined as the length of time that released eagles remained dependent on food at the hack box (see Amar et al. 2000) and/or feeding tree, up to the day of independence. We considered that released Harpy Eagles became independent: (1) when we recorded their making two kills <20 d apart, or (2) when, due to difficulties in locating them, they survived for >30 d without receiving food from us.

Radio-tracking. To check the health of eagles, to deliver food, and to determine independence, we tried to locate eagles at least once per week using VHF telemetry. We attached, as a backpack-mount, Biotrack® 70-g 2-yr (Biotrack Ltd., Wareham, Dorset, U.K.) or Merlin System® 60-g 4-yr (Merlin System Inc., Boise, Idaho, U.S.A.) transmitters on eagles (Kenward 2001). The devices did not exceed the 3% of eagles' total body mass recommended for such devices (Withey et al. 2001). We used three different models of receivers: Wildlife Materials Inc. TRX-1000S (Murphysboro, Illinois, U.S.A.), and Telonics® TR-2 and TR-4 in waterproof cases (Telonics Inc., Mesa, Arizona, U.S.A.), with three-element Yagi antennas. In addition to the transmitters, all birds were banded with a single color, alpha-numeric coded, rivet band (Acraft Sign and Nameplate Co., Edmonton, Alberta, Canada). A Passive Integrated Transponder (PIT) tag (AVID™) was also injected in the breast of each bird.

Statistical Analyses. Hacking success was defined as the percentage of released eagles surviving to independence (Barclay and Cade 1983). We used the binomial test of two proportions to test for a difference in hacking success between age classes.

Using the Kaplan-Meier method, we evaluated (1) if the length of the dependence period varied by age class and sex, considering the independence of eagles as the studied event and, (2) if survival to independence varied by sex, comparing the survival curves with a log-rank test (Kleinbaum and Klein 2005). We used this method because it allowed us to include those eagles that had died. We could not compare survival between age classes because all eagles of age class 2 survived to independence.

To evaluate the effect of age at release (continuous variable) and sex (categorical variable) on the dependence period, we used the Cox proportional hazard regression (Kleinbaum and Klein 2005), including covariates for: (1) enclosure time (days in hack box; continuous variable); (2) number of individuals simultaneously in the hack box (one or two individuals; categorical variable), (3) body mass (kg; continuous variable), and (4) season of release (dry or rainy; categorical variable). The first two covariates can influence the behavior of released eagles via stress and interaction among fledglings and can consequently affect the length of the dependence period (Teixeira et al. 2007). Body mass can reflect the physical condition of birds and their ability to reach independence (Pinter-Wollman et al. 2009); season can influence prey availability, and hunting success can affect the length of the dependence period. In survival analysis, the studied event typically has a negative outcome (e.g., death), however in our case, the event is positive. In the Cox model, covariate effects are interpreted in terms of hazard ratios. Hazard ratios >1.0 indicate an increasing risk of independence with increasing values for the covariate. Hazard ratios <1.0 indicate a decreasing risk of independence with increasing values for the covariate. In a second step, we reduced the model by using the forward stepwise regression method to identify which factors influenced the dependence period (Kleinbaum and Klein 2005). To verify the significance of the various predictive models, we examined the likelihood ratio (LR, $P < 0.05$), and to determine the significance of variables in each model we used the P value of each estimated coefficient. We used SPSS Statistic 17.0 (SPSS 2008) for both survival analyses.

Independently from the forward step method, we applied the Cox regression in order to evaluate the effect of combining covariates in pairs on the length of dependence period. In addition, to evaluate the possible interaction effects of variables we also considered the association of the two variables in the model. To select the best-fitting model, we used Akaike's Information Criterion (AIC). We ran this analysis in the Survival package available in the R program (R Development Core Team 2011) and calculated the AIC value with the extract AIC function in the same program.

The age at independence (mo) between age classes was evaluated using the Student's t-test after excluding dead eagles and checking for normality and homoscedasticity.

RESULTS

Twenty-four eagles in Panama and three in Belize survived to independence (79.4% hacking success). We found a significant difference in the hacking success between age classes (binominal test, $Z = -2.1$, $P = 0.040$): the hacking success for age class 1 and 2 were 70% and 100%, respectively.

The overall mean survival time during the dependence period was 19.3 mo (SE = 1.5). Seven eagles died before independence, all of them in the younger age class 1. Survival by sex within the younger age class 1 was not significantly different ($\chi^2 = 0.6$, df = 1, $P = 0.903$). The main cause of mortality was predation. Three eagles were killed by wild cats (*Panthera onca* and *Leopardus pardalis*): two of these

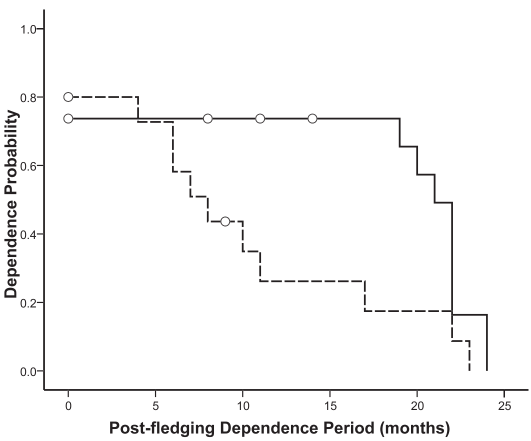

Figure 1. Dependence probability (Kaplan-Meier survival function) of captive-bred and released Harpy Eagles by sex. Males represented by solid line, females by dashed lines, and dead individuals by circles.

fatalities occurred in the first days after release, when these 6-mo-old birds (one of each sex) were either resting on the hack-box perches or perching in a nearby tree. The third case (a female 16 mo old) took place 9 mo after release, while the eagle was on the ground with its first prey (a sloth). Two male eagles died at 17 and 21 mo old (11 and 14 mo after release, respectively) by entangling themselves in the rope placed on feeding trees, and the cause of death of the other two individuals (males aged 15 and 21 mo, 8 and 14 mo after release, respectively) could not be determined.

Mean length of the dependence period varied significantly between age classes ($\chi^2 = 40.1$, df = 1, $P < 0.001$), averaging 18.9 ± 1.3 mo (SE; 95% CI = 16.5 to 21.4) for younger age class 1, and 1.5 ± 0.8 mo (SE; 95% CI = 0.0 to 3.0) for older age class 2. Similarly, the mean length of the dependence period varied significantly between sexes ($\chi^2 = 4.4$, df = 1, $P = 0.035$, Fig. 1). Comparison of the length of the dependence period by sex within each age group showed significant differences ($\chi^2 = 5.0$, df = 1, $P = 0.025$) for eagles of age class 1, but not for those of age class 2 ($\chi^2 = 3.1$, df = 1, $P = 0.077$): the average length of the dependence period for females of age class 1 was 14.3 mo (95% CI = 4.8 mo) and for age class 2 was 2.7 (95% CI = 2.4 mo). However, the dependence period for young males from class 1 was 21.8 mo (95% CI = 1.1 mo) and for older males was 0 mo, indicating that, at this older age class, males achieved independence immediately after release from the hack box.

In the general model fitted by the Cox proportional hazard regression (LR = 32.7, df = 6, $P < 0.001$), only the age at release was significantly related to the length of dependence period; this was confirmed in the reduced model (LR = 31.8, df = 1, $P < 0.001$, Table 2). This variable showed a highly significant effect ($P = 0.001$) on the length of the dependence period, suggesting that each year of age at release increases by a factor of 1.4 (hazard ratio) the likelihood of reaching independence (Table 2).

The selection of covariate pairs also highlighted the influence of age at release on the length of the depen-

Table 2. General and reduced models predicting the length of the dependence period of hacked juvenile Harpy Eagles in Soberania National Park (Panama) and Chiquibul Forest Reserve (Belize) between 2002 and 2007. General model: Likelihood ratio = 32.69, df = 6, $P < 0.001$. Reduced model: Likelihood ratio = 31.79, df = 1, $P < 0.001$.

VARIABLES	COEF.	SE	z	$P\|z\|$	HAZARD RATIO	95% CI	
General model							
Age at release[a]	0.36	0.13	2.70	0.007	1.44	1.10	1.87
Sex	−0.34	1.70	0.20	0.840	0.71	0.25	19.78
Enclosure time[b]	0.01	0.04	0.12	0.905	1.01	0.92	1.09
Body mass (kg)	0.34	1.09	0.32	0.750	1.41	0.17	11.89
Season[c]	0.01	0.48	−0.02	0.988	0.99	0.39	2.58
Individuals in hack box[d]	−0.37	0.63	0.60	0.551	0.69	0.20	2.36
Reduced model							
Age at release[a]	0.38	0.12	3.20	0.001	1.46	1.16	1.84

[a] Age in months.
[b] Days in hack box.
[c] Dry or rainy season.
[d] One or two eagles released in hack box at the same time.

Table 3. Selection of Cox proportional hazard models of covariate pairs of the length of dependence period of hacked juvenile captive-bred Harpy Eagles in Panama and Belize. Only models which were significant at $P < 0.05$ and AIC weight greater than zero are listed.

MODELS	LR	P	AIC	ΔAIC	AIC WEIGHT
Age at release + sex + interaction	35.9	<0.001	113.21	0.00	0.19
Age at release + body mass + interaction	35.8	<0.001	113.33	0.12	0.18
Age at release + individual in hack box	32.4	<0.001	114.71	1.49	0.09
Age at release + body mass	32.1	<0.001	114.99	1.78	0.08
Age at release + sex	32.0	<0.001	115.10	1.89	0.07
Age at release + enclosure time	32.4	<0.001	115.15	1.94	0.07
Age at release + season	31.9	<0.001	115.29	2.07	0.07
Age at release + individual in hack box + interaction	32.6	<0.001	116.55	3.33	0.04
Age at release + enclosure time + interaction	32.3	<0.001	116.85	3.64	0.03
Age at release + season + interaction	31.9	<0.001	117.27	4.06	0.02

[a] Likelihood ratio.
[b] Akaike's Information Criterion.

dence period. This variable was included in all models with low AIC values (Table 3). The model that best fit our data was the one with the age at release, sex, and their interaction, indicating that sex also influenced the length of the dependence period (LR = 35.9, df = 3, $P < 0.001$; Table 4). We found marginal differences in the age at independence between the two age classes (t-test = 2.1, df = 25, $P = 0.048$). For younger eagles, the average was 25.1 mo (SD = 5.8, range 14–31, $n = 16$); for older eagles, the average was 21.0 mo old (SD = 3.4, range 18–27, $n = 11$).

DISCUSSION

Although the hacking technique has been used to release more than 20 species of Nearctic raptors (Cade 2000), this is the first documented hacking of a tropical forest raptor species. Our hacking success (survival) with Harpy Eagles was greater than 70%, and was maximized (100%) when delayed to near independence age (18–22 mo old), indicating that the age at release was an important factor in the hacking success of Harpy Eagles.

Our 70% hacking success when releasing younger eagles (5–7 mo old) was comparable to the survival rates of hacked juvenile raptors such as the Mauritius Kestrel (*F. punctatus,* 73%), Peregrine Falcon (75%), Aplomado Falcon (*F. femoralis,* 67%) and White-tailed Eagle (*Haliaeetus albicilla,* 73%; Barclay and Cade 1983, Green et al. 1996, Jenny et al. 2004, Nicoll et al. 2004). Our 100% success rate for older (18–22 mo old) Harpy Eagles was likely a consequence of the shorter length of the dependence period and reduced risk of mortality that the dependence period entails. Older Harpy Eagles adapted more rapidly to the new environment than younger eagles and became independent faster. The strong effect of age at release on the length of the dependence period of Harpy Eagles suggested that this factor may be important for the successful reintroduction of other tropical raptors given the longer dependence periods predicted for other tropical birds of prey (Newton 1979, Russell et al. 2004). Age at release was also identified as an important factor in reintroduction models for the Griffon Vul-

Table 4. Cox hazard regression model of covariate pairs on length of the dependence period selected by AIC value (113.21). Likelihood ratio = 35.93, df = 3, $P < 0.001$.

VARIABLES	COEF.	SE	z	$P\|z\|$	HAZARD RATIO	95% CI	
Age at release	0.339	0.128	2.662	0.008	1.40	1.09	1.80
Sex	−1.658	0.845	−1.963	0.049	0.19	0.04	1.00
Age × sex[a]	0.130	0.067	1.953	0.051	1.14	1.00	1.30

[a] Interaction term.

ture (*Gyps fulvus*, Sarrazin and Legendre 2000) and in the reintroduction of the California Condor, in which released condors >1 yr old were significantly more likely to survive than individuals <1 yr old (Woods et al. 2007). Our findings were also consistent with those of Pomarol (1994), who found that older hacked Montagu's Harriers (*Circus pygargus*) had shorter dependence periods which were associated with migratory urge. However, the higher hacking success in older Harpy Eagles may be related to the maximum age for achieving independence. Because of this extended period of juvenile dependence, captive-bred Harpy Eagles released at an early age of 5–7 mo are probably not sufficiently mature to defend themselves, forage, and secure the needed prey in their new environment.

Sex had a moderate influence on the length of the dependence period. We found that females became independent faster than males when released at 5–7 mo old, and males achieved independence more rapidly than females when released at 18–22 mo old. The effect of the interaction of age at release and sex on the length of the dependence period was identified as very important in the hacking success of Peregrine Falcons (Dzialak et al. 2006). We do not know the influence of the length of the dependence period on differential foraging behavior of males and females. Female Harpy Eagles capture larger, slow-moving prey, whereas males appear to be adept hunters of smaller and quicker prey (Touchton et al. 2002). Perhaps learning to capture large, slow-moving prey, such as sloths, requires less time than learning to capture smaller, quicker prey; this might explain some of the sex differences we found in the dependence period.

Further studies on other tropical raptor species are needed to verify the influence of age at release and sex on survival of reintroduced raptors. Hacking has been used to release several species of raptor, but there has been no previous documentation for such practice focused on captive-bred tropical forest raptors. The development of improved methodologies for species recovery is important in the emerging field of reintroduction biology (Seddon et al. 2007, Armstrong and Seddon 2008). Our experimental approach provided important insights into the reintroduction biology of tropical raptors, especially factors for the successful establishment of new populations (Armstrong and Seddon 2008). As species restoration receives increasing attention worldwide, it is also important to assess the cost-benefit ratio of reintroduction methods. Releasing captive-bred Harpy Eagles at younger ages (5–7 mo) was costly in terms of personnel and time to track and feed birds in the wild for, sometimes, in excess of 24 mo, and also resulted in lower hacking success. In contrast, keeping Harpy Eagles in captivity until near independence incurred financial costs of maintaining the birds in captivity, but these costs were compensated by higher survival of individuals after release, and substantially reduced burden of tracking and feeding eagles in the wild. We stress the importance of new studies on neotropical raptors, based on solid theoretical and experimental approaches, in order to improve reintroduction techniques.

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