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TRIAL RESTORATION OF THE HARPY EAGLE, A LARGE, LONG-LIVED, TROPICAL FOREST RAPTOR, IN PANAMA AND BELIZE

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ABSTRACT.—We tested whether captive breeding and release is a feasible restoration strategy for the Harpy Eagle (*Harpia harpyja*) where suitable unoccupied habitat remains within its former range. From 1987 through 2006, 18 Harpy Eagles participated in a captive breeding program started in Boise, Idaho, and continued in Panama from 2001. From 131 eggs laid, 44 eagles were fledged. Most young were produced by just three females in the program, and at a higher annual rate after the birds were moved from Boise to Panama. Re-laying induced by collecting eggs for artificial incubation increased the number of viable eggs laid per female each breeding season up to six, but may have reduced female reproductive lifetime. Including rehabilitated eagles hatched in the wild, we released 49 eagles from 1998 through 2009. When the last released eagle with a functioning radio transmitter died in 2011, 63% were known or presumed to be dead, 31% were missing and possibly alive, and 6% were back in captivity. Shooting (44%) was the primary cause of death. Behavior interpreted as aggression toward humans was sufficiently frequent (23% of released eagles) in captive-raised and wild-rehabilitated eagles after release to be a concern for public safety and a potential cause of shooting deaths. This study demonstrated that it is feasible to breed Harpy Eagles in captivity at high rates needed for species restoration. It is possible to release captive-reared and rehabilitated Harpy Eagles to the wild, and is most cost effective (i.e., resulting in the highest survival to hunting-independence) when eagles are released close to the age of independence. Preventing shooting and other kinds of human persecution, and protecting remaining forest habitat, are the most urgent conservation needs for the Harpy Eagle.

KEY WORDS: *Harpy Eagle*; Harpia harpyja; *captive propagation*; *Central America*; *conservation*; *hacking*; *K-selected*; *Neotropical*; *persecution*; *raptor*.

RESTAURACIÓN EXPERIMENTAL DE *HARPIA HARPYJA*, UNA RAPAZ TROPICAL DE BOSQUE, GRANDE Y LONGEVA, EN PANAMÁ Y BELICE

RESUMEN.—Evaluamos si la cría en cautividad y la liberación en sitios donde aún existe hábitat adecuado dentro de su área de distribución pasada es una estrategia de restauración factible para *Harpia harpyja*. Desde 1987 hasta 2006, 18 individuos de *H. harpyja* participaron en un programa de cría en cautiverio iniciado en Boise, Idaho y, desde el 2001, continuado en Panamá. De 131 huevos puestos, 44 volantones fueron criados con éxito. La mayoría de los volantones fueron producidos solamente por tres hembras adultas del programa. La tasa anual de postura aumentó luego de que las aves fueron trasladadas de Boise a Panamá. La puesta repetida, inducida mediante la recolección de huevos para incubación artificial, aumentó hasta seis el número de huevos viables puestos por cada hembra en cada temporada de reproducción, si bien esta técnica de manejo podría haber reducido la vida reproductiva de las hembras. Entre 1998 y 2009 liberamos 49 águilas, incluyendo individuos rehabilitados y nacidos en la naturaleza. Cuando en 2011 murió la última águila liberada que aún contaba con un radiotransmisor en funcionamiento, se sabía o se sospechaba que había muerto el 63% de los individuos liberados, el 31% estaba desaparecido y posiblemente con vida, y el 6% se hallaba nuevamente en cautiverio. Disparos con armas de fuego (44%) fue la principal causa de mortalidad. El comportamiento de posible agresión hacia los seres humanos fue relativamente frecuente (23% de las águilas liberadas) en águilas criadas en cautiverio y silvestres rehabilitadas después de la liberación, al punto de constituirse en una preocupación para la seguridad pública y fue la causa potencial de muerte por disparos. Este estudio demostró que es posible criar individuos de *H. harpyja* en cautividad a tasas suficientemente altas para lograr la restauración de la especie. Es posible liberar al medio natural águilas criadas en cautiverio o silvestres rehabilitadas y es más eficiente en términos de costo/beneficio (i.e., mayor supervivencia de águilas llegando a la

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independencia de caza), si las águilas son liberadas cerca de la edad de independencia. La prevención de la cacería por disparos y otros tipos de persecución, y la protección del hábitat remanente son las necesidades de conservación más urgentes para esta especie.

[Traducción de los autores editada]

Harpy Eagles (*Harpia harpyja*) inhabit moist tropical lowland forests of Central and South America (Ferguson-Lees and Christie 2001). They are globally listed as Near Threatened (BirdLife International 2015) and considered endangered or extirpated in parts of their range, especially in Central America (Vargas-González et al. 2006). They breed slowly in the wild, normally producing only one fledgling every 2–3 yr because of their extended incubation (up to 56 d) and nestling (5–6 mo) periods (Rettig 1978) and post-fledging dependence period (estimated 27 mo, Álvarez-Cordero 1996). Like other K-selected raptors, adults must breed for decades to compensate for the slow annual rate of reproduction to produce at least two breeding adults to replace themselves at death, and even a small decline in annual survival of adults can have a large negative effect on population size (Watson 1990, Sæther and Bakke 2000, Clark and Martin 2007). Species with these life history traits may be lost from areas of otherwise suitable habitat when human persecution or other anthropogenic factors reduce average annual survival of adults to cause population decline (Owens and Bennett 2000). Loss of top predators, such as Harpy Eagles, may result in loss of ecological structure and function (Sergio et al. 2005, 2008). Therefore, to retain ecological integrity and biodiversity, species restoration (IUCN/SSC 2013) may be needed to return wild populations to viable numbers (Cade and Temple 1994, Armstrong and Seddon 2007, Seddon et al. 2014).

Several raptor species worldwide have been restored using either captive-bred or wild sources of fledgling juveniles that were translocated into areas where the species had been extirpated (Cade 2000). Of 28 attempts to translocate 25 species of diurnal raptors, 21 (75%) attempts resulted in the establishment of viable breeding populations (Cade 2000). For example, the Peregrine Falcon (*Falco peregrinus*) was restored using captive breeding and release after populations were decimated by reproductive failure caused by DDT in one of the largest and most successful raptor restoration efforts in North America (Cade and Burnham 2003, Dzialak et al. 2006). Bald Eagles (*Haliaeetus leucocephalus*) were successfully released in several locations in North America from both captive breeding and wild sources to help reinforce depleted populations (Cade 2000). The tactics used in these examples were adapted to fit the demographic and behavioral characteristics of each species (Cade 2000). We hypothesized that methods used in captive breeding and release of a large, long-lived raptor like the Harpy Eagle with an extended post-fledging dependence period and slow reproductive rate may be quite different and potentially more challenging than species like Peregrine Falcons, with shorter reproductive phases, that produce large clutches of eggs and return quickly to the wild when released (Sherrod et al. 1987) or Bald Eagles, which annually lay clutches of 2–3 eggs (Ferguson-Lees and Christie 2001).

Our objectives, therefore, were to test whether Harpy Eagles (1) could be bred in captivity at elevated rates using artificial incubation to stimulate the laying of additional eggs, (2) could be successfully released into the wild, and (3) would survive to breeding age in sufficient numbers to use this technique to restore populations of this top predator in the wild. To inform future restoration efforts, we documented breeding methods, rates, and senescence, measured rates and causes of mortality after release, and documented behavior that may influence survival.

Harpy Eagles have been held in captivity in zoos and private collections around the world for decades, and some have laid fertile eggs and reared nestlings (Hamerton 1943, Hanif 1970, von Eberhand 1973, Todd and Meachan 1974, Laue 1982, Minnemann 1993, Nemesio et al. 2000, Anonymous 2002, Azeredo 2002, Benavides and Hilgert 2002, Blanco Márquez 2002, Rimlinger 2002, Oliveira et al. 2014). Despite this potentially valuable source of information, little data has been published on breeding parameters that could be valuable for understanding the species' population biology in the wild and informing conservation breeding projects. Likewise, results of animal reintroduction projects are rarely quantified and published, yet the information is invaluable for assessing this method as a conservation tool (Fischer and Lindenmayer 2000). Until this study, no attempt had been made to use captive breeding and release as a method to restore Harpy Eagles or any other large, long-lived tropical forest
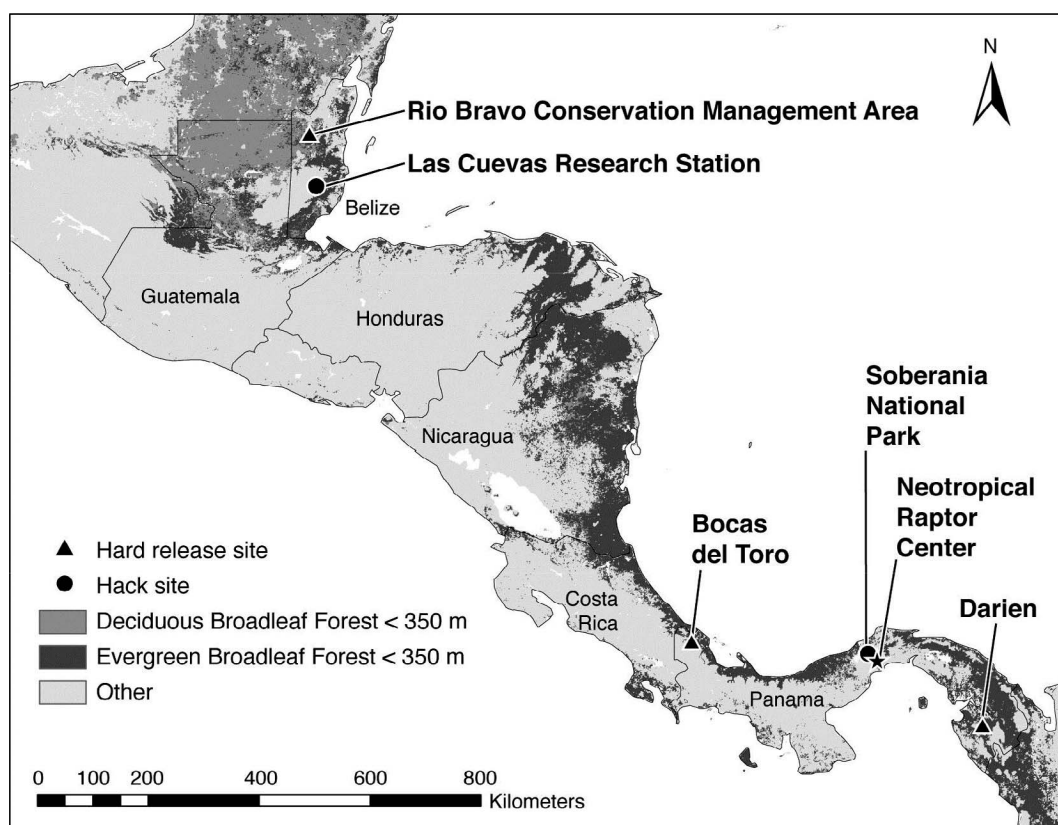
Figure 1. Map of potential Harpy Eagle habitat (evergreen and deciduous broadleaf forest below 350 m elevation) in the study area showing locations of hack sites, hard-release sites, and the Neotropical Raptor Center.

eagle species to areas from which they had been depleted or extirpated. This report is the first to quantify results of captive propagation of Harpy Eagles, and to examine captive breeding and release as a method for restoration of this species, a process that might be useful for other raptors with similar life-history traits that may be in need of conservation, such as the Philippine Eagle (*Pithecophaga jefferyi*; Salvador and Ibanez 2006).

METHODS

Breeding Facilities. The first breeding facility was completed in 1987 at The Peregrine Fund's World Center for Birds of Prey in Boise, Idaho, U.S.A. (43°31′N, 116°15.35′W). The facility, named the Tropical Raptor Building (TRB), consisted of six temperature-controlled indoor breeding chambers. The semiarid climate in Boise, with mean annual rainfall of 300 mm and temperatures that range from −18°C in winter to >40°C in summer, was considered too extreme for this tropical forest species to endure outdoors. Breeding chambers were equipped with closed-circuit TV cameras and small (100-mm diameter) one-way glass windows for observation by biologists. Chamber floor dimensions were 6.3 × 7 m. The interior wall was 9 m high and the roof sloped down to a 7-m exterior wall. Chambers were designed to admit sunlight through high windows while preventing visual disturbance from people outside.

The second facility, named the Neotropical Raptor Center (NRC, Fig. 1), was completed in 2001 in the Republic of Panama on a secluded hill in moist tropical lowland forest near the Panama Canal and the City of Knowledge (Ciudad del Saber, formerly U.S. Fort Clayton) located at 9°0.67′N, 79°35.17′W. This location was within the Harpy Eagle's natural range and has an annual mean rainfall of 2612 mm and annual mean temperatures that range from a

Table 1. Harpy Eagle breeding stock used for trial restoration from 1987–2006, in Boise, Idaho, U.S.A. and Panama City, Panama.

LENDER	ORIGIN	NAME	SEX	HATCH YEAR	AGE WHEN ACQUIRED (YR)	YEAR ACQUIRED
Los Angeles Zoo	Unknown	LA1M	Male	<1970	>20	1987
Los Angeles Zoo	Unknown	LA1F (Freedom)	Female	<1966	>21	1987
Oklahoma City Zoo	Unknown	OK City	Male	<1970	>23	1990
Panama	Panama	Ancon	Male	1984	7	1991
Ecuador	Ecuador	Olafa	Female	1989	2	1991
Ecuador	Ecuador	Military	Female	<1975	>16	1991
Ecuador	Ecuador	Coca	Male	1984	7	1991
Los Angeles Zoo	Unknown	LA2M	Male	<1967	>24	1991
Los Angeles Zoo	Unknown	LA2F	Female	<1963	>28	1991
Venezuela	Venezuela	Oliva	Female	1991	2	1993
Cheyenne Mountain Zoo	South America	Cheyenne	Male	<1967	>26	1993
Venezuela	Venezuela	Crawl	Male	1991	1	1992
San Diego Zoo	San Diego Zoo	San Diego F	Female	1994	1	1995
San Diego Zoo	San Diego Zoo	San Diego M	Male	1995	1	1996
Venezuela	Venezuela	GN	Female	1995	2	1997
Captive hatched in Boise	Ancon/Olafa	Zih	Male	1995	0	1995
Captive hatched in Boise	Ancon/Olafa	AC	Male	1998	0	1998
San Diego Zoo	San Diego Zoo	MV	Female	1998	0	1998

low of 19°C to a high of 35°C (Windsor 1990). It comprised seven separate outdoor breeding chambers built in the forest and an outdoor imprinting chamber that could accommodate eight nestling Harpy Eagles that were physically separated from, but in visual and aural contact with, an adult Harpy Eagle. About 40 ha of lowland forest surrounded the facility, which was adjacent to the Camino de Cruces National Park. Breeding chamber floor dimensions were 8 × 8 m. The chamber roof was horizontal but the topography sloped from a 4-m uphill wall to a 9-m downhill wall. The breeding chambers were constructed of steel beams hung with chain-link fencing. A sheet metal wall obscured the birds' view of people approaching with food, and another wall obscured the view of eagles in neighboring chambers. A 1.7 m × 1.7 m nest platform was built into one corner of the chamber about 6 m aboveground and a roof inside the chamber sheltered the nest platform from sun and rain. Elsewhere in the chamber, the birds were exposed to rain and sunlight partially filtered by overhanging trees and bamboo growing outside the chambers. The nest platform had log perches attached to the exposed front and side. A 4-m branch perch was attached diagonally in one corner about 5–6 m aboveground, a 3-m diagonal log perch was positioned in another corner about 2 m aboveground near the food door. A log perch was positioned vertically about 3 m inside the chamber and stood 2 m high. Food was dropped into the chamber through an obscured door. Access to the chamber was through a double-gated entrance.

Breeding Stock. The breeding stock of Harpy Eagles was formed between 1987 and 1998 with eagles on loan from zoos within the United States and from the governments of Ecuador, Panama, and Venezuela (Table 1). Male and female eagles were paired and re-paired from the first arrivals in 1987 through the last eggs laid in 2006. Pairs were formed based on similar ages when known and when possible, behavioral compatibility (e.g., no aggression between eagles and successful copulation; Arent 2007), and reproductive results; they were re-paired when birds were found to be incompatible, nonreproductive, or died. Pairing was timed to occur between breeding seasons when possible to minimize the potential effect of disturbance on breeding success. To facilitate identification, some breeding eagles were referred to by a previously conferred name, whereas others were identified by letter combinations on their leg band.

Egg Laying and Incubation. At the start of the breeding season, we monitored birds on closed-circuit TV for 4–6 hr/d to record any breeding activity. Behaviors such as nest arranging, copulating, and carrying nesting material were used to predict when birds were preparing to lay eggs. After behavior

suggesting imminent egg-laying was detected, we made observations more often to record egg-laying time and date as accurately as possible. To maximize the number of eggs laid in captivity per breeding season, we left eggs under the female for a period of natural incubation of 12–18 d before removing them for artificial incubation. By removing the eggs we induced the female to recycle and lay a second and even a third clutch within the same breeding season. Eggs removed from the nest were incubated artificially at 37.0°C and at a humidity adjusted every two days to yield a linear rate of water loss through the shell that resulted in a total egg-weight loss of 14% prior to the onset of hatching, in a manner typical for most birds including raptors (Burnham 1983, Weaver and Cade 1991).

Rearing Nestlings. After hatching, nestlings were kept warm in a brooder for up to 30 d until they grew sufficient feathers to thermoregulate and were strong enough to tear food. They were hand-fed for the first few days in the brooder until strong enough to feed themselves ground meat offered on a small plate. At 30 d, nestlings were placed in a nest-sized chamber facing an adult Harpy Eagle in a separate large flight enclosure, to promote imprinting on their own species. At 4 mo of age, nestlings had grown enough feathers and were large enough to be placed in a flight enclosure where they could strengthen their wings and fledge at about 6 mo after hatching. Up to four fledglings were kept in these flight chambers until we were ready to transfer them to the release site.

Nutrition. *Tropical raptor building in Boise.* We fed Harpy Eagles a diet of freshly killed or freshly thawed frozen rats (*Rattus norvegicus*), rabbits (*Oryctolagus cuniculus*), chickens (*Gallus domesticus*), guinea pigs (*Cavia porcellus*) and mice (*Mus musculus*) raised in our food production facilities. A powdered vitamin and mineral supplement (Dynamite Zoo Formula®) was added to the food beginning in 1995 in an attempt to address a recurring problem of early embryo death. Beginning in 1996, vitamin and mineral supplementation was limited to the months between breeding seasons, as supplements were suspected in late embryonic death in both captive Aplomado Falcons (*Falco femoralis*) and Harpy Eagles. Although our study was not designed to test the effects of the nutritional supplement, once started, embryo development improved, and those nestlings that hatched appeared healthy. Supplemental vitamin E was injected into food (rats 0.1 ml, rabbits 0.5 ml, chickens 0.25 ml, guinea pigs 0.25 ml) early

in the breeding season beginning in 1998 after blood tests in the fall of 1997 suggested vitamin E deficiency in eagles fed domesticated prey, which tend to be deficient in vitamin E (Clum et al. 1997). The procedure improved serum vitamin E levels but did not reduce late embryonic death. Beginning in 1999, we began feeding eagles with more fresh than frozen food because freezing is also known to diminish vitamin levels (Clum et al. 1997).

Neotropical raptor center in Panama. Before the breeding pairs were relocated to Panama, a food production facility was built to raise mice and rats and keep live rabbits to produce quality food for adult eagles and their nestlings. We used strict bio-security measures to prevent the introduction of avian disease to our captive birds. During each breeding season we raised approximately 6000 mice and 400 rats to feed nestlings. Each year we also bought 800 live adult rabbits and 50 stillborn calves (*Bos indicus*) which we froze, and imported 7000 frozen rats used to feed eagles, including juveniles after release while they remained dependent. Breeding pairs were fed with previously frozen and thawed rats and beef, and freshly killed rabbits. Quail (*Coturnix coturnix japonica*) produced at our food production facilities, mainly for other raptor species, were also offered to Harpy Eagles once every two weeks. Eagles were provided unlimited food until satiated. Adjustments to the amount offered were made daily based on the observed amount of food left uneaten from the day before. This typically amounted to 1–3 rats per d, or roughly 350–500 g per d per eagle. As in Boise, we added vitamins to any previously frozen food.

Harpy Eagle nestlings were fed freshly killed food until they were at least 90 d old, starting with newborn mice fed to newly hatched eagles. Mouse production was started annually about 2 mo prior to expected egg hatch and continued until nestlings were 90 d old. As the nestlings grew, their diet was changed from newborn mice, to young mice, and adult mice until, at 4 mo of age, they were offered whole rat, rabbit, and chicken.

Releases. We adapted hacking, the falconry method of liberating falcons (Sherrod et al. 1987), to release captive-reared or wild-rehabilitated Harpy Eagles. Unlike falcons, which enter the wild within weeks (e.g., Peregrine Falcon hacking takes 4–5 wk, Sherrod et al. 1987), release of Harpy Eagles took up to 24 mo (Campbell-Thompson et al. 2012). The associated logistical complexity and expense therefore required a two-stage process. We first conducted a "soft release" from a fixed hack site that

was easily accessible to attendants but remote enough to avoid conflict with people. Soft-released eagles were followed and fed until they showed evidence of hunting independence by consistently capturing their own prey (i.e., when we observed them make two kills within 20 d, or when, due to difficulty in locating eagles, they survived for >30 d without receiving food from us). After the eagles reached hunting independence in the wild, we recaptured them, and conducted a "hard release" in their final destination, typically a remote site where we did not expect to track and feed the birds. Methods were described in detail in our Harpy Eagle hack-site manual (Muela et al. 2003) and by Campbell-Thompson et al. (2012).

Hack sites. We selected hack sites that met three criteria: (1) sites were surrounded by large forest tracts likely sufficient to provide habitat and prey, and a buffer from human persecution (at least 5 km); (2) historical records confirmed the former presence and subsequent extirpation of local Harpy Eagle populations; and (3) suitable road access and existing facilities were available to support fieldwork. Each hack site consisted of one or two hack boxes, with each box having a floor 2.5 m × 2 m and a height of 2 m, constructed on a platform at least 1 m wider than the box dimensions and 3 m above-ground. The first hack box was built of wood, but rotted quickly in the warm, moist forest environment; thereafter, hack boxes were constructed of steel. The back of the hack box was made of sheet-metal to prevent eagles from seeing the hack-site attendants approach with food. The remaining three sides of the hack box and the roof were made of chain-link fencing to allow the birds to observe and become accustomed to the surroundings into which they would be released. The platform was constructed of wood that could be replaced when it rotted, and the whole structure was mounted on six sturdy steel poles set in concrete. We erected a high voltage livestock fence around the hack box to deter predators and ensured there were no overhanging trees or other means for terrestrial predators to access the box.

Releases in Panama. The first hack site for soft releases in Panama was constructed in 1997 near the boundary between Soberania National Park (Fig. 1) and Camino de Cruces National Park at about 9°4′N, 79°37′W and was used for releases in 1998. The second was constructed in 2001 in Soberania National Park near the north end of Pipeline Road at about 9°12′N, 79°47′W. A third hack site

was constructed in 2003 in Soberania National Park 2 km south of the second at about 9°11′N, 79°46′ W. The latter two sites were used for releases from 2002 through 2008, when the last released birds reached independence.

Soberania National Park (SNP, Fig. 1) 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). Although surrounded by human habitation and regularly visited by local people and tourists, it provided the infrastructure needed to accomplish soft releases and the connection by biological corridor to additional protected areas that could support Harpy Eagles (J. Vargas pers. comm.). Annual rainfall averages 2500 mm, with 90% falling during the late-April to mid-December rainy season (Robinson et al. 2004). Vegetation consists of a mixture of secondary and primary forest ranging in age from 80–150 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*), all of which are known to be prey of Harpy Eagles (Touchton et al. 2002, Aguiar-Silva et al. 2014), occur regularly.

Hard-release sites in Panama were located in Parque Internacional La Amistad (PILA, 9°14′N, 82°50′W) and Rancho Quemado (RQ, 9°17′N, 82°44′W) both in Bocas del Toro Province of western Panama (Fig. 1). PILA is a transborder park of 401,000 ha split between Panama and Costa Rica and including ten life zones over an altitudinal gradient from lowland tropical humid forest to subalpine rain *páramo*. Harpy Eagles were released on the Caribbean watershed in lowland tropical to pre-montane forest up to 1500 m elevation where the climate is hot and wet throughout the year, with a short, poorly defined dry season. At low and middle elevations mean annual temperatures varied from 21°–26°C, and mean annual precipitation from 2800–6840 mm (Selles 1992, ANCON 1993). One eagle was hard-released in tropical lowland forest of Darien Province (DP, 8°07′N, 78°00′ W) located in eastern Panama adjacent to the border with Colombia (Fig. 1). Altitude ranges from 0–1800 m, annual rainfall from 1700–2000 mm, with distinct dry (January–April) and wet (May–December) seasons and temperatures from 17–35°C (PNUD-MEF 2003). Up to 18 eagles remained after soft release or were

hard-released in Soberania National Park, including two eagles on Barro Colorado Island in the Panama Canal (BCI, 9°9′N, 79°50′W).

Releases in Belize. One hack site for soft releases was established in March 2003 near Las Cuevas Research Station (Fig. 1, 16°43′N, 88°59′ W) in the Chiquibul Forest Reserve of Belize and used to soft-release four eagles in 2003. 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). Rainfall ranges from 1500–2000 mm per year, with a rainy season from June to December (Beletsky 1999). The reserve is located within the Chiquibul National Park, which, 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, Whitacre and Schulze 2012). As in Panama, this reserve was home to several species of mammals that form the Harpy Eagle's diet (see Rotenberg et al. 2012 for diet in Belize), excluding the two species of sloth whose distributions do not reach this part of Central America (Reid 1997, Caro et al. 2001).

The hard-release site in Belize was located in Rio Bravo Conservation Management Area (Fig. 1, RBCMA) near La Milpa Field Station (17°50′N, 89°01′ W), the largest (102,000 ha) private conservation area in Belize managed by Programme for Belize and located in the Orange Walk District of northwest Belize. Vegetation consists of subtropical moist broadleaf and marsh forest disconnected by lowland savanna and agricultural areas (Brokaw and Sabido 1998). Altitude ranges from 40–160 m, rainfall averages from 1550–1600 mm per year, and temperature varies from 21 to 32°C (Brokaw and Sabido 1998).

Release process. All soft-released eagles were banded with a color and alphanumeric coded leg band for individual identification. They were also fitted with a ground-tracked VHF transmitter (Biotrack® 70-g 2-yr or Merlin Systems® 60-g 4-yr). Transmitters weighed <3% of body mass and were attached using Teflon ribbon in a backpack configuration. After release, eagles were followed for as long as possible to obtain information on survival, causes of mortality, dispersal distances, and behavior, and to maximize our ability to feed and rescue sick or injured eagles. Soft releases were conducted with two age groups, fledgling (6–8 mo) and juvenile (>18 mo). From two to four eagles were housed and fed in hack boxes to acclimate to their forest surroundings for up to 40 d prior to release. We provided thawed, previously-frozen white rats for food. After release, eagles were provided unlimited food at the hack box to attract them to the area while allowing them freedom to roam, build strength and flight skills, and learn to hunt. Unlimited feeding continued until they began dispersing. After dispersal commenced, eagles were tracked by following their VHF transmitters and fed every 3–7 d by hoisting food on a thin line to a perch in a tree near their evening roost. Feeding was always done under the cover of night to minimize association of food with humans. Dispersed eagles often settled for weeks at a time in one locality, allowing for habitual use of just two or three feeding trees for each eagle.

We observed dispersing eagles to look for evidence of successful hunting in the wild. Evidence included reduced interest in provisioned food, observation of eagles killing, carrying, or feeding on wild prey, and a richer yellow coloration of their feet caused by the antioxidant beta-carotene indicating feeding on wild rather than domestically raised animals. Once such evidence had been recorded at least twice, eagles were no longer offered food, and were only tracked until we were ready to capture them for relocation and hard release.

Recapture after release was most often accomplished using a noose-carpet trap hoisted on a line into a tree with a dead white rat for bait. Independent eagles too wary to be captured by this method were captured under veterinary supervision using a dart gun and ketamine shot into the breast (Redig 1993). Sedated eagles flew to the ground where they were captured by hand. Captured eagles were transported to their hard-release site in a large dog kennel modified for visual seclusion while maintaining ventilation.

Hard release of eagles occurred in the forest at their final destination by opening the transport kennel door and flushing the birds out with no period of acclimation. Hard-released birds were fitted with both a satellite-reporting platform transmitter terminal (PTT, Microwave Telemetry®) and a VHF transmitter for ground location. Transmitters were glued together, fitted using Teflon ribbon in a backpack configuration, and weighed <3% body mass. Birds were tracked from the ground or air by VHF radio for as long as possible after hard release but offered no food. We gathered data on survival and other parameters, and that information, including prey selection, hunting frequency, dispersal, and habitat use is reported elsewhere (Touchton et al. 2002,

Vargas-González 2010). Once VHF radio contact was lost, eagles were tracked remotely via satellite-reporting PTT radios for as long as the device functioned (up to 4 yr) to provide data on dispersal and habitat use. Prolonged reporting from the same location suggested either breeding behavior or mortality and was confirmed on the ground when feasible.

Post-release behavior. We opportunistically documented undesirable eagle behavior after release, which may affect the success of restoration by influencing humans' response to eagles. We recorded whenever eagles swooped toward observers, including our field personnel, tourists, and others. We examined patterns of occurrence of this behavior in age class, sex, and breeding origin of released eagles to reveal a cause and, therefore, a potential solution to this undesirable behavior.

Rehabilitation. During the course of the study, eight Harpy Eagles (six females, two males) were confiscated by government authorities, often with life-threatening injuries inflicted by humans, such as gunshot wounds. These birds were given to us for rehabilitation and release, which increased our sample size of released birds.

Statistical Analyses. We analyzed post-release behavior, mortality, and causes of death after release using Fisher's exact tests. For fertility, hatchability, and breeding phenology we ranked and compared mixed models (see below) using Akaike's Information Criterion (AIC, Akaike 1974) and considered models within $\Delta AIC < 2$ to be competitive for inference (Burnham and Anderson 2002). We considered covariates within competitive models to be useful if their 95% confidence intervals excluded zero. All analyses were conducted in R (R Development Core Team 2013). Mixed models were fitted using the package lme4 (Bates et al. 2013).

Fertility and hatchability. We examined the fertility and hatchability of eggs using generalized linear mixed models with binomial distributions (i.e., mixed logistic regression, Zuur et al. 2009). We considered an egg containing a fertilized embryo as fertile; hatchability was defined as the probability of a fertile egg producing a nestling. For each analysis we only included eggs for which either fertility or hatching success was known. We built models representing *a priori* hypotheses of the drivers of each process (Table 4, 5). These models included covariates indicating the linear and quadratic effects of the age of either parent, the location the egg was produced (Boise or Panama), clutch number of the season, and the position of the egg in the laying

sequence. All models contained random effects for the mother and father to control for the relatedness of the eggs.

We performed further exploratory analyses to examine possible reasons underlying the difference in hatchability between eggs laid in Boise and those laid in Panama. We noted anecdotally that failure to hatch in Boise was characterized by rapid egg-weight loss during natural incubation despite eggshell quality appearing sufficient. We therefore tested the *a posteriori* hypothesis that weight loss during incubation was the cause of hatching failure by fitting models that included the rates of weight loss during natural and artificial incubation as well as overall. Models were built including each rate separately and were fitted to a subset of the data including only fertile eggs for which all rates were known ($n = 38$ eggs).

Breeding phenology. To examine the phenology of production, we used generalized linear mixed models with Poisson distributions (i.e., mixed Poisson regression, Zuur et al. 2009). Each model used the number of eggs laid by each pair during a given month as the response variable. We built models representing *a priori* hypotheses of the drivers of laying phenology (Table 6). These models included covariates indicating the linear and quadratic effects of the age of either parent, the location the egg was produced, linear and quadratic effects of month as well as interactions between location and month, representing the hypothesis that phenology differed by site (Table 6). All models contained random effects for the parental pair to control for the repeated sampling of each pair.

RESULTS

Breeding Stock. The captive breeding was initiated with five eagles loaned to us by the Los Angeles, Oklahoma City, and Cheyenne Mountain Zoos (Table 1). All the birds had been imported as adults prior to 1970 and were of advanced, but unknown, age. Although the female eagles had laid eggs in the zoos, few hatched, and no young were ever raised. To develop viable breeding pairs, we borrowed young known-age eagles from Venezuela, Ecuador, and Panama. Many were rescued from bad situations, such as one that was chained to a tree, and another that was crippled after its nest tree was cut down. Some of our rescue attempts

Table 2.   Pairs of Harpy Eagles that laid eggs in Boise from 1988 to 2000, and numbers of eggs laid, fertile, and hatched, and young fledged in successive breeding seasons (separated by commas).

PAIR NUMBER	FIRST YEAR PAIR LAID EGGS	NAMES	SEX	NO. EGGS LAID	NO. EGGS FERTILE	NO. EGGS HATCHED	NO. YOUNG FLEDGED
1	1988	LA1M	Male				
		LA1F	Female	2,2	?,?	0,0	0,0
2	1992	LA2M	Male				
		Military	Female	3,3	?,0	0,0	0,0
3	1992	Coca	Male				
		LA2F	Female	2	1	0	0
4	1994	Coca	Male				
		Military	Female	1	0	0	0
5	1994	Ancon	Male				
		Olafa	Female	3,4,4,4,5,3,3	2,4,4,4,4,3,2,3	0,1,1,2,1,0,1,3	0,1,1,2,1,0,1,3
6	1995	Cheyenne	Male				
		Military	Female	1	0	0	0
7	1996	Crawl	Male				
		Oliva	Female	1	0	0	0
8	1997	Cheyenne	Male				
		Oliva	Female	2,3,4,4,4	0,0,3,2,2	0,0,0,1,1	0,0,0,1,0
9	1999	Zih	Male				
		San Diego F	Female	1,2	0,2	0,1	0,1
		Total		65	36	12	11

failed when birds died before permits could be issued to import them into the United States.

Breeding Parameters. Harpy Eagles laid 52 clutches of two eggs and 27 clutches of one egg. Of 57 eggs measured, mean length was 75.0 (SD = 4.1) mm and width 57.0 (SD = 2.3) mm. The median interval between eggs laid in 2-egg clutches was 6.0 d (mean = 6.2 d, SD = 2.2 d, n = 35). The mean incubation period was 53 d (SD = 1.9, n = 36) but ranged from 51–58 d, depending on whether eggs were the first or second laid. Fledging occurred at 5–6 mo after hatching.

Breeding Performance. The first eggs were laid by Harpy Eagles in Boise (Table 2) in 1988, but it was not until 1995 that we had the first hatching of one of four eggs laid that year by a 6-yr old female. From 1995 until the 2005–2006 breeding season, 131 eggs were laid, of which 72 (55%) were known to be fertile, 47 hatched (65% of fertile eggs) and 45 (96% of hatched) young fledged. Most fertile eggs (96%) and young (98%) were produced by three females (Table 2, 3).

Females laid their first eggs at 4 yr of age, with first fertile eggs laid at age 5 yr. Eggs continued to be laid by females up to 29 yr old, but among our sample of birds there was a unimodal distribution of fertile eggs that peaked from age 8–11 yr and diminished by age 15 yr. Males fertilized eggs for the first time at age

Table 3.   Pairs of Harpy Eagles that laid eggs in Panama and numbers of eggs laid, fertile and hatched, and young fledged in successive breeding seasons (separated by commas) from 2001–2002 through 2005–2006 breeding seasons.

PAIR NUMBER	FIRST YEAR PAIR LAID EGGS	NAME	SEX	NO. EGGS LAID	NO. EGGS FERTILE	NO. EGGS HATCHED	NO. YOUNG FLEDGED
5	1994	Ancon	Male				
		Olafa	Female	6,5,4,0	6,2,2,0	6,2,1,0	6,2,1,0
8	1997	Cheyenne	Male				
		Oliva	Female	2,4,3,2,2	2,2,0,0,0	2,1,0,0,0	2,1,0,0,0
10	2001	Zih	Male				
		GN	Female	6,6,6,6,6	2,6,5,3,6	2,6,5,3,6	2,6,5,3,6
11	2002	AC	Male				
		MV	Female	1,3,4	0,0,0	0,0,0	0,0,0
		Total		66	36	35	34

Table 4. AIC table of mixed-logistic regression models representing *a priori* hypotheses of the drivers of fertility of eggs of Harpy Eagles. k = number of parameters estimated by model, AIC = Akaike's Information Criterion, ΔAIC = the difference in AIC between the best model and a given model, w_i = Akaike weight.

MODEL	k	AIC	ΔAIC	w_i
Father age + Father age^2	3	121.57	0.00	0.64
Null	1	125.42	3.85	0.09
Site	2	125.52	3.96	0.09
Father age	2	126.61	5.04	0.05
Lay sequence	2	127.31	5.74	0.04
Clutch #	2	127.41	5.85	0.03
Mother age	2	127.41	5.85	0.03
Mother age + Mother age^2	3	128.90	7.33	0.02
Clutch # $\times$ Egg sequence	4	131.12	9.55	0.01

Table 5. AIC table of mixed-logistic regression models representing *a priori* hypotheses of the drivers of hatchability of eggs of Harpy Eagles. k = number of parameters estimated by model, AIC = Akaike's Information Criterion, ΔAIC = the difference in AIC between the best model and a given model, w_i = Akaike weight.

MODEL	k	AIC	ΔAIC	w_i
Site	2	62.87	0.00	1.00
Mother age + Mother age^2	3	82.57	19.70	0.00
Father age	2	84.61	21.74	0.00
Father age + Father age^2	3	85.96	23.10	0.00
Mother age	2	87.19	24.32	0.00
Null	1	90.68	27.81	0.00
Clutch #	2	92.42	29.55	0.00
Lay sequence	2	92.67	29.80	0.00
Clutch # $\times$ Egg sequence	4	95.49	32.62	0.00

5 yr and continued to fertilize eggs up to age 35 yr. Adults of all ages produced some infertile eggs. The only model ΔAIC < 2 for fertility contained the quadratic effect of Father Age (Table 4), demonstrating that the probability of fertility peaked at 0.89 (CI = 0.86–0.92) when males were 21.9 yr old (Fig. 2). Mother Age was a poor model for fertility (Table 4) which bears further consideration.

The only model ΔAIC < 2 for hatchability contained the factor for country (Table 5), indicating that hatchability was substantially greater in Panama

(0.97, CI = 0.83–0.99) than Boise (0.29, CI = 0.17–0.45). Breeding success increased dramatically when birds were moved from Boise to Panama beginning with the 2001–2002 breeding season with three females contributing most eggs (Table 3). From 2001–2002 through the 2005–2006 breeding season (the last egg of the season was laid in January 2006) 66 eggs were laid, 36 (55%) were fertile, 35 (97% of fertile eggs) hatched, and 34 (97%) of the nestlings survived to fledge (Table 3).

Further exploratory analyses to examine possible reasons underlying the difference in hatchability between eggs laid in Boise and those laid in Panama found the best model was again the model including the factor for country. The next-best model (ΔAIC = 2.5) included the covariate for overall rate of change in weight from laying to hatching (or failure) and indicated that eggs with the lowest observed rate of weight loss (0.04 g/d) were 188 times (CI = 6.83–5156.61) more likely to hatch than eggs with the highest rate (0.53 g/d) of weight loss. The rate of weight loss was higher in Boise (mean = 0.40 g/d) than in Panama (mean = 0.13 g/d, $t = -21.13$, $P < 0.01$). However, the model including the factor for country was higher-ranked than any weight loss model. Therefore, factors other than, or in addition to, weight loss likely contributed to the differences in hatchability between the two countries.

Breeding Phenology. The only model ΔAIC < 2 for egg-laying phenology was the model that represented the hypothesis that phenology varied by site, containing an interaction between site and the quadratic effect of month. The best model for breeding phenology indicated that during January breeding reached its peak in Boise with 0.65 (CI = 0.42–
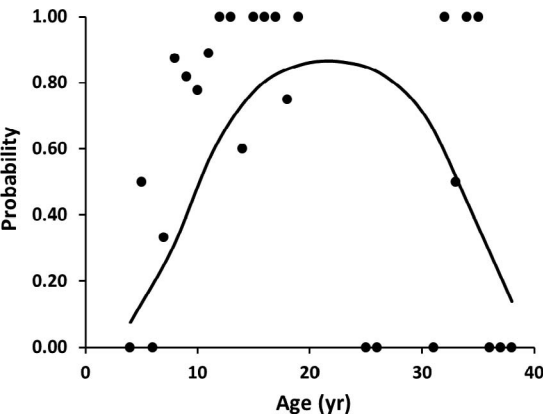

Figure 2. The probability of a Harpy Eagle egg being fertile in relation to the age of the father. The solid line is the predicted probability and the circles are the proportion of fertile eggs laid by adults at a given age.
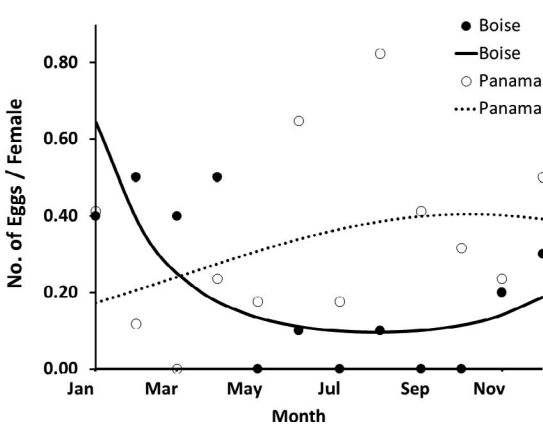
Figure 3.   The relationship between the number of Harpy Eagle eggs laid per female per month in Boise, Idaho, and Panama. Lines represent the predicted number per month at a given site and circles represent the observed number per month at a given site.

1.00) eggs laid per female, whereas in Panama breeding was lowest (0.17 eggs/female, CI = 0.15–0.20) during January (Fig. 3).

Rehabilitation. Of eight confiscated eagles submitted to us for rehabilitation, four eagles were released. In addition, six eagles that participated in the breeding program were released as breeding adults in the final stages of the project for a total of 10 rehabilitated and released eagles.

Releases. The first soft releases into the wild of Harpy Eagles that had been bred in captivity in Boise ($n = 3$) and San Diego Zoo ($n = 2$) occurred in Panama in 1998. Two of these birds were shot within 10 and 27 mo of release, respectively. As a result, we halted releases while we conducted an intensive public education campaign in the communities adjacent to the release site in Soberania National Park (Valdez 2002, Curti and Valdez 2009). We also recaptured two of the eagles and placed them in the breeding program in the NRC, Panama. The remaining eagle from this cohort died from predation. Releases resumed in 2002 in Panama and 2003 in Belize.

From 1998 to 2006, we released 49 eagles, including 39 soft-released captive-bred birds and ten rehabilitated eagles, 24 females and 25 males. Of the females, two were hatched in Boise in the TRB, one in San Diego Zoo, 15 in Panama at the NRC, and six were hatched in the wild and rehabilitated. Of the males, four were hatched in Boise in the TRB, one in San Diego Zoo, 19 in Panama at the NRC, and one was hatched in the wild and rehabilitated.

Table 6.   AIC table of mixed-Poisson regression models representing *a priori* hypotheses of the drivers of egg-laying phenology of Harpy Eagles. k = number of parameters estimated by model, AIC = Akaike's Information Criterion, ΔAIC = the difference in AIC between the best model and a given model, w_i = Akaike weight.

MODEL	k	AIC	ΔAIC	w_i
Site × (month + month²)	6	457.56	0	0.94
Site	2	465.19	7.63	0.02
Null	1	466.48	8.93	0.01
Mother age	2	467.01	9.45	0.01
Mother age + Mother age²	3	467.91	10.36	0.01
Father age	2	468.37	10.82	0.00
Month	2	468.39	10.83	0.00
Month + Month²	3	469.74	12.18	0.00
Father age + Father age²	3	470.09	12.53	0.00

Of the seven eagles hatched in the wild and rehabilitated, three were adult when released, and four were estimated to be 24 ($n = 2$), 36, and 48 mo of age. Of the captive-bred eagles, three were released as adults after participating in the breeding program and were therefore considered rehabilitated eagles.

Survival and Causes of Death After Release. All the juvenile captive-bred eagles ($n = 39$) were soft-released first in either Soberania National Park (SNP, $n = 35$) or Chiquibul Forest, Belize ($n = 4$). Of these, 12 (31%) died before reaching hunting independence and the remaining 27 (69%) reached hunting independence and were either left in SNP ($n = 8$) or relocated and hard-released ($n = 19$) in one of four locations (Rio Bravo Management Area, Belize, RBMA, $n = 14$; Parque Internacional La Amistad, Panama, PILA, $n = 3$; Rancho Quemado, Panama, RQ, $n = 1$; Darien Province, Panama, DP, $n = 1$). All 10 rehabilitated birds were hard-released in SNP.

The last hard-released bird with a functioning transmitter died in 2011. At that time, 31 (63%) of 49 released birds were known or presumed (they went missing soon after they were released and while the transmitter still functioned) to be dead, three (6%) had been returned to captivity, and 15 (31%) birds were missing and possibly alive because they went missing at about the predicted lifespan of the transmitter. There was no significant effect of sex on survival of birds (Table 7, Fisher's exact test $P > 0.05$) and no significant difference in survival of captive- and wild-hatched birds (Table 8, Fisher's exact test $P > 0.05$). Birds survived in the wild until they were either found dead or went missing (possibly still alive) from less than a month up to 55 mo, with a mean of 16.6 mo (SD = 12.5 mo, $n = 49$) and

Table 7.   Comparison between sexes of numbers of Harpy Eagles released from 1998–2006 that were alive, dead, or missing and possibly alive in 2011.

STATUS	MALE	FEMALE	TOTAL
Alive	1	2	3
Dead	17	14	31
Missing and possibly alive	6	9	15
Total	24	25	49

median of 14.0 mo. Birds found dead had survived a mean 12.0 mo (SD = 9.5, n = 26) in the wild while those that went missing (possibly still alive) were last detected at a mean of 21.8 mo (SD = 13.6 mo, n = 23) in the wild. None of the released birds were recorded breeding, having either died or gone missing prior to the onset of breeding. One bird was seen breaking branches from a tree in what might be interpreted as nest-building behavior. Another bird was observed once on 24 September 2014 in Soberania National Park and identified by leg band as being 7 yr old and therefore of breeding age; however, no breeding behavior was seen at the time.

Among the 29 birds that were known to have died, 18 died of causes that were identified. Among identified causes, gunshot wounds were the largest cause, accounting for 44% (Table 9). Predation by jaguar (*Panthera onca*), ocelot (*Leopardus pardalis*), or other predator accounted for 22%, accidental death by entanglement in the feeding line made up 11%, and septicemia, snake bite, suspected electrocution, and internal parasites accounted for 5.6% each. There was no detectable effect of sex on death by shooting compared with all other causes combined (Table 9, Fisher's exact test $P > 0.05$). We had insufficient numbers of wild-hatched birds that died of known causes to make a comparison between cause of death in wild- (n = 1) versus captive-hatched eagles (n = 17).

Post-release Behavior. Diving (swooping) at humans was observed in 23% of eagles we released.

Table 8.   Comparison between captive-reared and wild-reared Harpy Eagles released from 1998–2006 that were alive, dead, or missing and possibly alive in 2011.

STATUS	CAPTIVE	WILD	TOTAL
Alive	3		3
Dead	26	5	31
Missing and possibly alive	13	2	15
Total	42	7	49

Because similar behavior may have different functions in juvenile and adult age classes, we examined swooping behavior in each age-class separately. Swooping was observed in both juvenile (14% of 35) and adult (22% of 27) age classes. Among juvenile eagles, males (5 of 18) were significantly more likely to swoop than females (none of 17, Fisher's exact test $P < 0.05$). Of the five swooping juveniles, three were not known to swoop as adults and two died before reaching adult age. All the swooping juveniles were raised at the NRC, released in the young cohort between 5–7 mo of age, and tracked and fed in the wild up to age 19–25 mo. Although all the swooping juveniles were male and all raised in the NRC, many more eagles (n = 30) did not swoop and of these 13 were male and 17 were female; 26 were raised in the NRC, one in Boise, and three in the wild and rehabilitated. There was no significant effect of rearing location (Boise or Panama) on swooping behavior in juveniles (Fisher's exact test $P > 0.05$). There was no significant difference in swooping between male (3 of 13) and female (3 of 14) Harpy Eagles in the adult age class (Fisher's exact test $P > 0.05$). None of the swooping adults were known to swoop as juveniles. Their release age varied from young cohort at 7 mo (two birds), older cohort (one bird at 18 mo), to adult cohort at age over 60 mo (three birds). Three of the swooping adults were raised at the NRC, and one each in Boise, San Diego Zoo, and the wild. There was no significant effect of rearing location on swooping behavior in adults (Fisher's exact test $P > 0.05$). Among all 11 birds that swooped in either juvenile or adult age classes, three were returned to captivity (one juvenile, two adults), four died (two shot, one electrocuted, one bitten by a snake), and four went missing with fate unknown.

DISCUSSION

Breeding Stock. Beginning this study with Harpy Eagles of unknown age and origin on loan from zoos within the United States was not successful. The females laid poor quality eggs that appeared symptomatic of senescence and resulted in breeding failure, as found in other raptors both in captivity and the wild (Clum 1995, Newton and Rothery 1997, Penteriani et al. 2009). Successful breeding was first accomplished with young eagles of known age loaned from Panama, Ecuador, and Venezuela. However, the uncertain and potentially troubled histories of some of these birds may have influenced their breeding success in captivity in ways that could

Table 9. Comparison between sexes of cause of death of Harpy Eagles released from 1998–2006.

CAUSE OF DEATH	MALE	FEMALE	TOTAL
Unknown	3	8	11
Shot by poacher	5	3	8
Predation	2	2	4
Accident	2		2
Septicemia		1	1
Snake bite	1		1
Electrocution	1		1
Internal parasites	1		1
Total	15	14	29

not be understood. Ideally, a future breeding program would consist of birds of known age from the wild or reared in captivity from parents of known origin. Starting a breeding program with female birds aged 4–5 yr, when they normally lay their first fertile eggs, would maximize production of nestlings in captivity. Furthermore, recent advances in analyses of mitochondrial DNA (mtDNA) control region sequence (Lerner et al. 2009) and development of nuclear DNA microsatellite loci (Banhos et al. 2008) from Harpy Eagles make it possible to consider the genetic consequences of mixing Harpy Eagles of different geographic origin and intended destination in future restoration programs. To preserve maximal level of genetic diversity, for example, Lerner et al. (2009) concluded that evidence for geographic differentiation of Harpy Eagles between Central and South America supports a conservation strategy that maintains diverse local populations rather than any single extant population.

Breeding Performance. A quadratic function of male age was the best model for egg fertility, with fertility increasing at young ages up to about 15 yr, followed by decreasing fertility after about 30 yr. Increasing productivity at young ages in captive Peregrine Falcons (ca. 3–5 yr) was believed to result from experience, while physiological changes resulting in declining quality of gametes, either eggs or sperm, likely caused reproductive senescence in peregrines >7 yr (Clum 1995). A similar pattern of reproductive success was also observed in Eurasian Sparrowhawks (*Accipiter nisus*; Newton 1988) and other birds in the wild (Newton 1989) and was attributed in part to changes in resource acquisition over the lifetime of the individual (Newton 1989). Intrinsic experiential and physiological effects are not mutually exclusive of extrinsic ecological effects, which may be additive. Evolution of a seemingly maladaptive

character like senescence is thought to occur under a pleiotropic theory of aging in which mutations that encourage senescence are selected for because of a linked increase in reproduction earlier in life (Partridge 1989). Senescence has emerged as a significant factor in avian life histories, affecting both reproduction and survival (Newton 1989) and was apparent in our captive Harpy Eagles.

Female age was a poor model of fertility among Harpy Eagles in this study, possibly because of the large range of ages in the sample (up to 29 yr old), with only a small sample of three younger females (aged from 5–15 yr) producing the most fertile eggs. The attempt to breed Harpy Eagles in Boise was plagued initially by poor egg fertility and embryo death that we attributed to senescent birds past their prime breeding age that also produced eggs with visibly poor shell quality, as found in other raptors both in captivity and the wild (Clum 1995, Newton and Rothery 1997, Penteriani et al. 2009). The rate of water loss from eggs was higher than the ideal 14% through the incubation period (Burnham 1983, Weaver and Cade 1991), and although it could be controlled in artificial incubators, rapid water loss during the period of natural incubation immediately post egg-laying remained problematic. Atmospheric humidity in Boise was generally low year-round, and was not controlled in the indoor breeding chambers. After younger birds were introduced to the breeding stock, egg fertility improved, but hatchability remained low due to a high rate of late-term embryo death attributed to metabolic bone disease. Among underlying causes, we believed that feeding previously frozen food was important, as the switch to freshly killed food improved the nutritional status of eagles. We also believed that calcium deficiency might have been linked to low vitamin D production resulting from life indoors with only glass-filtered sunlight.

Moving the breeding pairs of Harpy Eagles from Boise to Panama had a positive effect on their productivity. We believe that the combined effect of unfiltered sunlight, warm temperature, and high humidity, as well as quiet seclusion in a tropical forest landscape, contributed significantly to this improvement. Through egg removal for artificial incubation and the resulting relaying, three breeding pairs laid 18 fertile eggs and hatched 17 nestlings in 2002, their first breeding season in Panama. This was a marked improvement over the nine eggs and three nestlings hatched in Boise in the previous breeding season. This high rate of production made it possible to

consider a full species restoration effort as potentially feasible.

One young female, GN, bred for the first time in Panama at age 6 yr. Beginning with the 2001–2002 breeding season, GN laid six eggs each season with high fertility and hatchability rates for all five consecutive seasons until the breeding program was ended after the 2005–2006 season. GN's rates of fertility and hatchability suggested there was no short-term negative effect of removing clutches to increase numbers of eggs laid per year by this female and implied that if all breeding stock were young, sexually mature females, potentially large numbers of young Harpy Eagles could be produced from captive breeding. However, egg-laying by the other female eagles in the breeding program, Oliva aged 10 yr and Olafa aged 12 yr in 2001, was greatest in their first year in Panama, but declined thereafter. Declining overall egg fertility by female Oliva and male Cheyenne may have been the result of the male's age (>35 yr). Female Olafa laid declining numbers of fertile eggs after her first year in Panama, ending with no eggs laid in the final season at age 16 yr, much earlier than expected, which may indicate early reproductive senescence. Early reproductive senescence would be consistent with Peregrine Falcons that bred in captivity for fewer years when clutch removal was used to boost annual productivity than peregrines bred without such recycling, yet produced similar numbers of fledglings over their reproductive lifetimes (Clum 1995). Early reproductive senescence suggests there is a cost to future reproductive potential that results from clutch removal and relaying to boost annual productivity. Although the reproductive lifetime of female Harpy Eagles in the wild is assumed to be similar to males', three to four decades, it appears that manipulation of annual reproductive output by recycling may have reduced this period by at least half in our study birds.

The onset of egg-laying by a young female, MV, who laid only infertile eggs, also contributed to reduce the fertility rate in Panama. Female MV and male AC were of breeding age when paired, but their eggs were infertile because the pair did not copulate for unknown reasons. MV and AC were originally released in 1998 and recaptured in 2000 for their own safety before being placed in the breeding program. Achieving mate synchrony remains a process of trial and error until a larger sample of pairings can be examined for patterns.

Breeding Phenology. Normally in the wild, one clutch is laid in a breeding season. Successful incubation, nestling, and post-fledging dependence periods can delay the start of the next breeding period for up to 2 yr. In captivity, we extended breeding seasons by removing clutches, causing the birds to lay more eggs. This technique greatly increased productivity and was feasible because of the extended breeding season. Breeding phenology in Boise suggested a relationship with winter months, with the breeding season starting in November and continuing through April (Table 2). Temperature and humidity varied little year-round in the indoor breeding chambers; only day length varied from 15 hr 26 min to 8 hr 56 min from the longest to shortest day of the year, a markedly different regime from that in Panama (latitude 9°N) where day length varied only from 12 hr 39 min to 11 hr 36 min from longest to shortest day of the year. In Panama, captive Harpy Eagles also experienced daily and seasonal variation in temperature and humidity in their outdoor breeding chambers. Egg-laying occurred in 10 mo of the year, and the phenology suggested a relationship between the start of the breeding season of Harpy Eagles and the start of the wet season in mid-April. Generally the wet season extended from mid-April to mid-December, and the last eggs of the season were laid around January or February, so breeding seasons were considered to begin in April and end by February of the next calendar year (Table 3).

The breeding phenology data of the captive Harpy Eagles in Panama makes up the largest known sample of such information for the species within their normal geographic range. In Panama, Harpy Eagles laid eggs from the onset of the wet season in April through the onset of the dry season in the following January/February, with highest frequencies in June and August. Breeding phenology of Harpy Eagles in the wild is poorly documented. In Ecuador, egg-laying and incubation dates showed no seasonality in a small sample of six breeding attempts in the wild in 2003 and 2004 (Muñiz-López 2007). In a single nest in Guyana (Rettig 1978), two eggs were laid in mid-June, one hatched in early August, and one nestling fledged by early January. In Brazil, a single nest at Costanhal, near the Rio Apehu, about 85 km east of Belém, contained a fresh egg on 27 April, and another slightly incubated egg was collected from the nest on 9 May on a second visit (Norris 1927). Eggs were laid between September and November in Goiás, Brazil (Sick 1993). A pair of Harpy Eagles in Belize was observed copulating in April 2008 and a nest was found in the same area with a 4–5 wk old

nestling on 27 November 2010 (Rotenberg et al. 2012).

Release Methods. Release methods used in species restoration can affect the survival and successful establishment in the wild of released animals (Cade and Temple 1994). Other factors include habitat quality at release sites, numbers of animals released per site, and removal of the cause of decline (Cade and Temple 1994, Cade 2000, Fischer and Lindenmayer 2000). We demonstrated that hacking can be used successfully to release captive-bred Harpy Eagles into the wild, but this technique was more efficient when delayed from the fledging age, at which falconers traditionally hack falcons, to nearer the Harpy Eagle's age of hunting independence (Campbell-Thompson et al. 2012). Harpy Eagles released at 18–20 mo, near the age of hunting independence, had higher survival and shorter dependence periods than eagles released near fledging age around 5–7 mo (Campbell-Thompson et al. 2012). The two-stage release process of a soft release by hacking in a convenient location for tracking and feeding eagles, followed by translocation and hard release in the final destination after independence was a method we developed from necessity. This two-stage method, to our knowledge, has not been widely used in avian reintroduction projects, although both methods have been used independently (Cade 2000). The two-stage soft-hard release method and soft-release delayed to independence age method are two strategies that may be most appropriate for release of long-lived raptors with an extended post-fledging dependence period.

We evaluated habitat quality at release sites based on the presence of suitable prey (Touchton et al. 2002, Rotenberg et al. 2012, Aguiar-Silva et al. 2014), low elevation wet forest for foraging and nesting (Matola 2006, Vargas-González 2008, Vargas-González and Vargas 2011), and low human population density to reduce the probability of shooting or other kinds of anthropogenic interference (Valdez 2002). Survival to hunting independence of 69% of soft-released eagles indicated that suitable prey species and their abundance, as well as appropriate forest type, were present at the soft-release sites in Soberania National Park, Panama and Chiquibul Forest, Belize. However, young eagles were capable of dispersing over large areas after relocation and hard release (Campbell-Thompson 2011); one travelled about 270 km in 11 mo after release (A. Muela pers. comm.), traversing the extent of contiguous forest, with fatal results when it encountered humans at the forest edge. Our education program reduced shooting as a cause of mortality (Curti and Valdez 2009) around Soberania National Park where we concentrated effort around the soft-release site and where the largest number of eagles remained after reaching hunting independence. At hard-release sites, such as RBMA in Belize, the large and unpredictable dispersal distances of hard-released eagles precluded an effective education program on behalf of these individuals, though our partners in Belize worked diligently around the release area to change human attitudes toward eagles to prevent shooting (Matola 2004, 2006).

Survival. Mortality rates of raptors between fledging and breeding age can be high, up to 75% for larger eagles and up to 90–95% for smaller falcons (Newton 1979), although recent telemetry studies have revealed lower rates, such as 54% for Bald Eagles (Hunt et al. 2009) and 40% for Golden Eagles, 60–65% first-year mortality in Peregrine Falcons, and 66% in Aplomado Falcons (G. Hunt pers. comm.). In this study, mortality of Harpy Eagles after release was at least 63% and probably higher because a substantial number of eagles ($n = 15$; 31%) disappeared after their transmitters stopped working, so their fates were unknown. Only three (6%) released eagles were known to survive to breeding age because they were returned to captivity. Of identifiable causes of death ($n = 18$), shooting (44%) was by far the largest single cause. For species restoration to succeed, human persecution must be prevented. We established a community-based education program to reduce human persecution of Harpy Eagles by promoting positive attitudes toward them among the local community (Curti and Valdez 2009). The program demonstrated that when equipped with a set of clearly defined goals, an identifiable target audience, and a variety of well-developed presentations and activities, an effective education program can reduce persecution rates of Harpy Eagles (Curti and Valdez 2009).

None of the Harpy Eagles released in this project were known to breed in the wild, as most either died before reaching maturity or their telemetry failed and they could not be found. We observed one eagle breaking branches off a tree and carrying them to a nearby tree in what appeared to be nest-building activity. There was no other Harpy Eagle in the vicinity to form a breeding pair, so this eagle eventually moved to a more remote location where we could not track or see it. Had we released all the eagles in one location, the probability that a pair

would survive to breed in the vicinity might have been greater than observed in this project. By releasing eagles in two main locations, we may have produced an insufficient number that survived to breeding age in any one location, or produced other Allee effects with negative demographic results (Stephens et al. 1999, Stephens and Sutherland 1999, Gascoigne et al. 2009). Understanding the effect of number, age, and sex composition of the release group on the probability of establishing a breeding population may be important for ensuring the success of reintroductions (Armstrong and Seddon 2007, Lambertucci et al. 2013). Post-release mortality and dispersal described in this study are therefore important parameters needed to inform predictive models for successful reintroductions in the future.

Post-release Behavior. Behavior that may be interpreted as aggressive because it could result in human injury is an unacceptable outcome of reintroduction involving captive breeding or rehabilitation and release of large, powerful predators such as Harpy Eagles. A lack of fear or even curiosity of humans may have contributed to eagles being targeted for shooting. Although not usually seen in juvenile Harpy Eagles in the wild, aggressive behavior was recorded in a wild juvenile suspected of having been fed by people (J. Vargas pers. comm.). Post-release association of humans with food may account for this behavior. Alternatively, similar lack of fear of humans and attraction to human-built structures was problematic in reintroduced California Condors (*Gymnogyps californianus*; Cade 2000, Grantham 2007). Although it was proposed that rearing method might influence this behavior, parent-reared condors were no less likely to exhibit this behavior than puppet-reared condors (Grantham 2007). Likewise, we found no association between rearing location (Panama, Boise, or wild-reared) and aggressive behavior in Harpy Eagles that would suggest that the method used to rear eagles might account for their behavior toward humans. Given the similarity of this behavior between species, we suggest that curiosity or aggression may be innate behaviors characteristic of large, long-lived raptorial birds in which learning from parents normally plays a prominent role in the development of their behavior (Mee and Snyder 2007), including avoidance of humans. Future species restoration efforts for Harpy Eagles and raptors with similar life-history traits may need to address aggression or curiosity before restoration is likely to succeed.

Conclusions. It was feasible to breed Harpy Eagles in captivity at high rates using artificial incubation to induce relaying and maximize annual productivity, especially in Panama in the species' natural tropical moist forest environment with unobstructed sunlight, warmth, and moisture. Clutch recycling boosted annual production, which is desirable for reintroduction success, but might have reduced female reproductive lifespan. Breeding eagles appeared to produce viable eggs more often when fed with freshly killed food rather than food that had previously been frozen and thawed. It would be best to start a captive breeding program with known-age, young (4–5 yr old) breeding stock rather than stock of unknown age with unknown and potentially adverse histories. It was possible to release captive-reared Harpy Eagles to the wild using a two-stage soft release followed by hard-release method, and most cost effective and with highest survival to independence if the young were released close to their age of independence, around 20 mo old. Shooting was the single largest cause of death of released eagles but may be mitigated through public education. Curiosity or aggression toward humans is not known in wild Harpy Eagles, but was frequent enough after release in both captive-raised and wild-hatched and rehabilitated eagles to be a concern for the safety of the public and survival of eagles. Aggression in juvenile and adult eagle age-classes was not linked, nor was aggression linked to location and method of rearing, nor to sex, and therefore may be an unavoidable result of tameness in a proportion of eagles that are kept in captivity for a period or post-release association of humans with food. None of the released eagles were known to breed in the wild, though at least one showed signs of nest-building behavior. Although as many as 15 released eagles may have survived, because their radios failed we lost contact with them before they reached breeding age. Thus, we learned little about survival to breeding age, although we note that one sighted in 2014 had reached 7 yr of age. We released too few eagles in too many separate sites to compensate for mortality and allow sufficient numbers to reach breeding age in any one site. We recommend a strategy of releasing a large number of eagles over a short time period in the same location to maximize the probability that males and females will survive to form breeding pairs.

Harpy Eagles are now rare in much of their former range in Central America and in some parts of their South American range, such as the Atlantic forest of

Brazil (Vargas-González et al. 2006, Aguiar-Silva et al. 2012). Captive breeding and release might be used to reinforce or reintroduce Harpy Eagle populations in such locations, provided sufficient habitat remains and the problems revealed in this study can be overcome. Restoration is an expensive, long-term endeavor, so where breeding Harpy Eagles remain extant, it may be more cost effective to focus effort on preventing human persecution and habitat loss.

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