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Authors: Urios, Vicente, Muñiz-López, Ruth, and Vidal-Mateo, Javier

Source: Journal of Raptor Research, 51(4) : 439-445

Published By: Raptor Research Foundation

URL: <https://doi.org/10.3356/JRR-16-54.1>

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JUVENILE DISPERSAL OF HARPY EAGLES (*HARPIA HARPYJA*) IN ECUADOR

VICENTE URIOS¹

Vertebrates Zoology Research Group, University of Alicante, Apdo. 99, E-03080 Alicante, Spain
and

Estación Biológica Terra Natura, Foia del Verdader 03502, Benidorm, Alicante, Spain

RUTH MUÑIZ-LÓPEZ

Vertebrates Zoology Research Group, University of Alicante, Apdo. 99, E-03080 Alicante, Spain
and

Sociedad para la Investigación y Monitoreo de la Biodiversidad Ecuatoriana (SIMBIOE), C/Jorge Juan N31-120 y
Mariana de Jesús, Quito, Ecuador

JAVIER VIDAL-MATEO

Vertebrates Zoology Research Group, University of Alicante, Apdo. 99, E-03080 Alicante, Spain

ABSTRACT.—The movement ecology of Harpy Eagles (*Harpia harpyja*) is poorly known due to the difficulty observing this species. We studied the movements of two juvenile Harpy Eagles before and during dispersal using GPS satellite telemetry in the Reserva de Producción Faunística Cuyabeno, Ecuador. Both eagles were tagged at their respective nest tree. For each eagle, we calculated the daily distance moved and the distance from each recorded position to the nest. One eagle started dispersal during its 28th month, while at the same age the other eagle remained in its nest area, suffering repeated parental attacks that may have caused its death. The juvenile that dispersed moved a maximum of 35.1 km from the nest and occupied an area of 386 km². The long post-fledging and dispersal periods underscore the importance of directing conservation plans toward juveniles as well as adults. In addition, dispersal movements that are close to the natal nest facilitate the delimitation of areas for protection of Harpy Eagle nests.

KEY WORDS: *Harpy Eagle*; *Harpia harpyja*; Amazon; dispersal; movement ecology; parental aggression; satellite telemetry.

DISPERSIÓN JUVENIL DE *HARPIA HARPYJA* EN ECUADOR

RESUMEN.—La ecología del movimiento de *Harpia harpyja* es poco conocida debido a la dificultad de observación de esta especie. Los movimientos de dos individuos juveniles de *H. harpyja* antes y durante el periodo de dispersión fueron estudiados mediante telemetría satelital GPS, en la Reserva de Producción Faunística Cuyabeno, Ecuador. Ambas águilas fueron marcadas en su respectivo nido. Para cada águila se calculó la distancia diaria recorrida y la distancia al nido a partir de cada posición registrada. Un águila comenzó la dispersión a los 28 meses de edad, mientras que la otra a la misma edad permaneció en su área del nido, sufriendo repetidos ataques por parte de los padres, lo que posiblemente pudo haber causado su muerte. El juvenil que se dispersó se alejó un máximo de 35.1 km del nido y ocupó un área de 386 km². Los largos periodos post-emplumamiento y de dispersión subrayan la importancia de dirigir los planes de conservación hacia los juveniles y adultos. Además, los movimientos de dispersión cercanos a la zona del nido facilitan la delimitación de áreas para la protección de los nidos de *H. harpyja*.

[Traducción de los autores editada]

¹ Email address: vicenteurios@yahoo.es

The Harpy Eagle (*Harpia harpyja*) is one of the largest and heaviest raptors in the world (Brown and Amadon 1968). This species occupies lowland rainforests, with a discontinuous distribution from southern Mexico to northern Argentina (Ferguson-Lees and Christie 2001). Due to habitat loss and human persecution, populations of this eagle are declining (Álvarez-Cordero 1996, Vargas et al. 2006, BirdLife International 2016). Its long breeding interval, estimated at 2.5–3 yr (Rettig 1978, Álvarez-Cordero 1996), makes the species even more vulnerable. Currently, it is considered a Near Threatened species by the International Union for Conservation of Nature and Natural Resources (IUCN 2013), and in Ecuador it is included within the category Vulnerable (Granizo et al. 1997).

Different aspects of the biology of the Harpy Eagle have been studied, including trophic ecology (Fowler and Cope 1964, Piana 2007, Lenz and dos Reis 2011, Aguiar-Silva et al. 2014, 2015, Miranda 2016) and breeding behavior (Rettig 1978, Álvarez-Cordero 1996, Muñoz-López 2007, Rotenberg et al. 2012). Although there are some studies on its movement ecology (Álvarez-Cordero 1996, Campbell-Thompson et al. 2012, Muñoz-López et al. 2012, Aguiar-Silva and Sanaiotti 2013), due to the difficulty of observing this species, some aspects of its spatial ecology (e.g., juvenile dispersal) are still poorly known. Juvenile dispersal comprises the movements undertaken by juveniles in their search for a breeding area once they are independent from their parents (Greenwood and Harvey 1982, Clobert et al. 2001). In large raptors this process may take 3–4 yr (Urios et al. 2007, Cadahía et al. 2009, Whitfield et al. 2009), and it is preceded by a period of parental dependence called the post-fledging period. This post-fledging period occurs between the first flights of the bird and the onset of dispersal (Soutullo et al. 2006). The onset of dispersal is not easy to detect, and it can be influenced by a reduction in parental investment of their offspring (e.g., decreasing the food supply), or the presence of parent-offspring or between-sibling aggression (Holleback 1974, Alonso et al. 1987). We studied the movements of two female juvenile Harpy Eagles tracked by GPS satellite telemetry before and during the juvenile dispersal period.

METHODS

Capture and Tagging. We trapped two juvenile female Harpy Eagles, “Masakay” and “Tava,” at their respective nest trees in the Reserva de Producción Faunística Cuyabeno, Sucumbíos Province, north-

eastern Ecuador (0°7.00'S, 75°50.00'W). Located in the Amazon region of Ecuador, this is one of the most biodiverse places on the planet, dominated by primary lowland tropical moist forest between 250 and 300 masl and flooded tropical evergreen forests (Cañadas 1983, Stotz et al. 1996, Cerón et al. 1999, Palacios et al. 1999). For additional details on capture methods, see Muñoz-López et al. (2012).

We tagged eagles with 70-g Argos/GPS satellite transmitters (Microwave Telemetry Inc., Columbia, MD U.S.A.) affixed to their backs using a Teflon harness. This equipment did not exceed 1.5% of body mass, which is within the recommended limits (Kenward 2001). One GPS position (nominal accuracy of ± 18 m) was recorded every hour between 0900 and 0300 H (local time) for Masakay and between 1100 and 0300 H for Tava. Masakay was tagged on 15 July 2006 in its third month of age, and Tava on 28 March 2009 in its seventh month of age. In addition, in collaboration with the natives of nationality A'í/Cofan, a 30-m-high observation tower was built, which allowed us to observe Masakay. This tower was used from 0700 to 1630 H continuously every day until Masakay was 1 yr old. After that age, we monitored the juvenile for 5 hr in the morning (0700–1200 H), and used the tower sporadically to improve upon observations from the ground, because the juvenile did not stay in the nest and thus it was necessary to follow it on foot.

Statistical Analyses. We retrieved the data and managed it using the program Satellite Tracking and Analysis Tools (STAT; Coyne and Godley 2005). We calculated the distances covered every day for each eagle, selecting a location per day that was closest to midnight. These data failed a test for normality, so we used the nonparametric Mann-Whitney *U*-test to evaluate the differences in these daily distances between Masakay and Tava during the months that data were available for both birds. We also calculated the distance to the nest from every recorded position, and tested the differences between Masakay and Tava in the same way. In the case of Tava, we also analyzed the differences between the daily distances before the onset of dispersal when she was in the natal area, and the distances covered once the dispersal period began. Daily distances calculated between nonconsecutive days (due to lack of data) were excluded from the analysis. In addition, we estimated the hourly distances travelled as the straight-line distance between two locations corresponding to consecutive hours. These distances could be calculated between 0900 and 0300 H (local

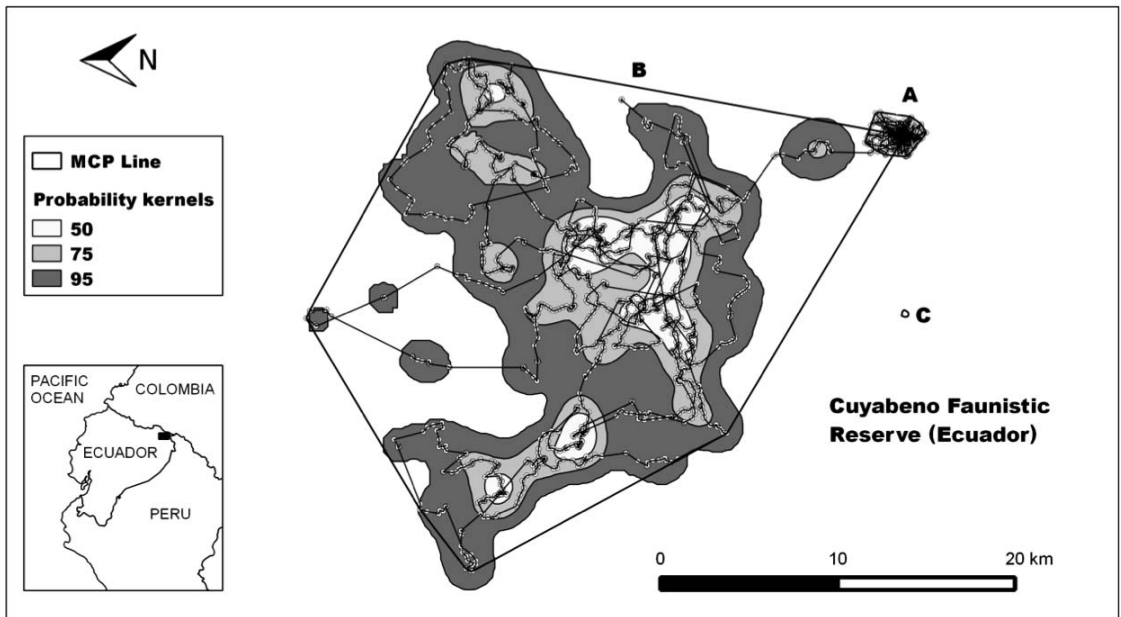


Figure 1. Dispersal and home range of two juvenile female Harpy Eagles in Ecuador, 2006 and 2009. GPS locations for one female eagle (Tava) are indicated by open dots connected by track lines. Polygons represent fixed kernels and Minimum Convex Polygon (MCP, solid line) for: (A) Tava's post-fledging area; (B) Tava's dispersal area; and, (C) Masakay's post-fledging area (MCP).

time), the time period during which the locations were obtained. We used the Kruskal-Wallis test (data were non-normal) to examine whether there were differences in the hourly distances according to the time of day, and the multiple comparison Games-Howell test (Zar 1999) to check whether there was any peak of activity. All statistical analyses were performed with IBM SPSS Statistics ver. 22.0. Significance level was established at $P < 0.05$ and we present data as mean \pm SD.

Home-range Estimation. We estimated the home range of both Harpy Eagles during the period in which the eagles were using the natal area and during the dispersal period, using all GPS locations. We calculated the 95%, 75%, and 50% fixed kernels (Worton 1989) using the Animal Movement extension for ArcView 3.2 (Hooge and Eichenlaub 1997). We used the least squares cross-validation procedure to calculate the smoothing parameter H (Silverman 1986). To estimate the real size of home ranges, we transformed the kernel polygons in geographic coordinates to an equal-area cylindrical projection using the Projector! Extension for ArcView 3.2. We also calculated the minimum convex polygon (MCP) encompassing all the locations obtained for the

different periods (post-fledging and dispersal period), performing the same transformation as for the kernel analyses.

RESULTS

Muñiz-López et al. (2012) described the movements of these two Harpy Eagles from hatching until they reached the age of 2 yr. In this study, we documented their movements after the age of 2 yr. Using the transmitters, we monitored Tava for 15 mo, until she was 39 mo old, and monitored Masakay for 4 mo, until she was 27 mo old.

The two young Harpy Eagles exhibited different behaviors. Tava remained in the natal area until the beginning of her 28th mo: on 6 December 2010 she began her juvenile dispersal by moving away from the nest toward the north (Fig. 1). Masakay remained within her natal area throughout the period that GPS data were available. Coinciding with the second month of dispersal of Tava, Masakay, in the middle of her 29th mo, began to suffer attacks by one of the parents, presumably the male. We were able to observe these attacks from the observation tower. The attacks consisted of quick flights by the adult, showing its talons and approaching the

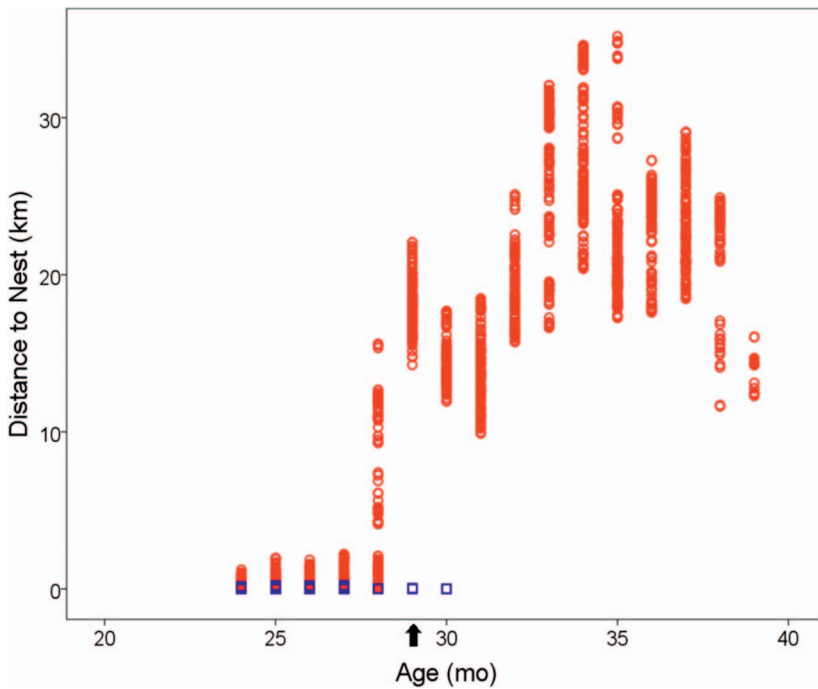


Figure 2. Distances to nest of two juvenile Harpy Eagles (blue squares for Masakay and red dots for Tava) for every month during the study period, Ecuador, 2006 and 2009. Distances were calculated from every recorded GPS location (and from visual records for Masakay during months 28–30). The black arrow indicates the month we observed the parental attacks suffered by Masakay, found dead in the 30th mo of life.

juvenile who was perched on a branch of a tree adjacent to the nest tree. Subsequently, Masakay was found dead the following month (at 30 mo old) a few meters from the nest tree.

The daily distances covered by Tava and Masakay during the months for which data are available for both birds (i.e., within their natal area) differed significantly ($Z = -10.72$, $P < 0.000$); Tava averaged $0.48 (\pm 0.46)$ km per day whereas Masakay made much shorter movements, averaging $0.03 (\pm 0.05)$ km per day. Similarly, the daily distances to the nest were significantly different ($Z = -34.29$, $P < 0.000$): Tava was $0.35 (\pm 0.38)$ km from the nest before the onset of the dispersal while Masakay moved away an average distance of only $0.03 (\pm 0.04)$ km (maximum distance = 2.2 km and 0.24 respectively; Fig. 2). The daily distances covered before and after the onset of the dispersal by Tava also differed significantly ($Z = -8.72$, $P < 0.000$), with an average of $0.48 (\pm 0.46)$ km before dispersal and $1.47 (\pm 0.90)$ km during dispersal. The maximum daily distance recorded was close to 4 km, although during the dispersal period it was > 2 km in most cases (69%). Only in 4% of

the daily segments did the distance exceed 3 km. During the study period (i.e., from age 24–39 mo old), Tava moved away from the nest a maximum of 35.1 km (during her 35th month; Fig. 2). Tava’s transmitter stopped functioning when she was 39 mo old.

Hourly distances were only calculated for Tava because Masakay remained static most of the time, making only short movements. The average hourly distances moved by Tava (0.11 ± 0.14 km/hr) changed significantly throughout the day ($\chi^2 = 65.61$, $df = 11$, $P < 0.001$), although there was no prominent peak of activity. The maximum distance recorded in one hour was 0.99 km, although in 95% of the hourly movements it was < 0.42 km. There was activity during all daylight hours.

During the time that Tava remained in the natal area (Fig. 1A), she occupied an area of 0.39 km^2 according to the 95% fixed kernel (0.07 and 0.03 km^2 for 75% and 50% kernels respectively, and 6.06 km^2 for MCP). The estimated area during the 11 mo of dispersal (Fig. 1B) that we studied was 386 km^2 according to the 95% fixed kernel (137 and 42 km^2

for 75% and 50% kernels, and 579 km² for MCP). The 95% kernel for Masakay encompassed only 2.78×10^{-3} km² (7.93×10^{-4} and 3.70×10^{-4} km² for 75% and 50% kernels, and 0.112 km² for MCP; Fig. 1C).

DISCUSSION

The Harpy Eagle and Philippine Eagle (*Pithecophaga jefferyi*) exhibit the longest post-fledging dependence period within raptors (del Hoyo et al. 1994, Álvarez-Cordero 1996, Muñiz-López et al. 2012). According to our data, based on only one female, Harpy Eagles in Ecuador begin their juvenile dispersal period around the 28th mo of life, which is older than in other eagles (Wood et al. 1998, Soutullo et al. 2006, Cadahía et al. 2008). Perhaps coincidentally, the onset of the dispersal of Tava and of the aggressive behavior by one of the parents of Masakay occurred at the same approximate age. At 28–29 mo old, Tava began to disperse, whereas Masakay remained near the nest, making shorter movements (Fig. 2) and perhaps inciting the parental attacks that might have caused her death. Although not common in all raptors (Bustamante and Hiraldo 1990, Bustamante 1994, Boileau and Bretagnolle 2014), parental aggression toward the juveniles has been observed in other species, such as the Spanish Imperial Eagle (*Aquila adalberti*; Alonso et al. 1987). This conflict between adults and offspring (Trivers 1974), promoted by parents that reduce the food supply or increase their aggressive behavior toward juveniles, favors independence and the onset of the dispersal (Hiraldo et al. 1989, Arroyo et al. 2002, Balbontín and Ferrer 2005).

Once she initiated dispersal, Tava remained north of the natal area and explored the area without stopping permanently in any region until 39 mo of age, at which time her transmitter stopped functioning and we could no longer track her movements. Rotenberg et al. (2012) tracked the movements of a juvenile Harpy Eagle after fledging; it explored an area of approximately 3.2 km² during the first months of the post-fledging period. Based on her MCP, Tava occupied an area twice as large for the last 4 mo of the post-fledging period, a consistent result as the juvenile increases its distance from the nest during this post-fledging period (Muñiz-López et al. 2012). The area explored by Tava during dispersal comprised hundreds of square km, considerably larger than the size of a breeding territory occupied by a breeding pair (range = 16–79 km²; Álvarez-Cordero 1996, Muñiz-López 2008, Vargas and Vargas

2011). This suggests that juvenile Harpy Eagles cover a large area before settling in a breeding territory.

Although the studies on juvenile dispersal for large forest eagles are scarce, estimated dispersal area and the distances covered in the first months after the start of the dispersal by Harpy Eagles are lower than those for other species. For instance, Spanish Imperial Eagles (González et al. 1989, Muriel et al. 2015), Bonelli's Eagles (*Aquila fasciata*; Cadahía et al. 2005, 2010) and Crowned Solitary Eagles (*Buteogallus coronatus*; Urios et al. 2014) move hundreds of km away from the natal nest and explore large areas before occupying a territory. These differences may be due to the homogeneity of the forested habitat occupied by the Harpy Eagle, allowing for suitable conditions and prey availability in a smaller area (Muñiz-López 2008, Aguiar-Silva et al. 2015). In addition, the Harpy Eagle uses perch-hunting and does not soar like other eagles, so this species does not need to cover large distances when hunting. Abaño et al. (2015) also reported greater movements for the Philippine Eagle, a species similar to the Harpy Eagle in size and biology (del Hoyo et al. 1994). However, the results are not directly comparable because that study involved released individuals. The Papuan Eagle (*Harpyopsis novaeguineae*), which is smaller in size, inhabits tropical forests of similar homogeneity, in which it occupies relatively small territories of several tens of square kilometers (Watson and Asoyama 2001). There are no quantitative data on dispersal areas for other large forest eagles, such as the Crested Eagle (*Morphnus guianensis*) and the African Crowned Eagle (*Stephanoaetus coronatus*).

Despite the need to conduct more studies on juvenile Harpy Eagle dispersal and movement ecology, important implications for the conservation of this species can be discerned from our results. The small clutch size and long breeding period (Rettig 1978), together with the long post-fledging and dispersal period, underscore the importance of directing conservation plans at juveniles as well as adults. Therefore, understanding the movements of juveniles during dispersal, a period with relevant demographic consequences, may be of great importance for the conservation of the species (Clobert et al. 2001, Soutullo et al. 2008, Penteriani et al. 2011). The long time period spent in the nesting area and the relatively short-distance dispersal movements, facilitate the delimitation of buffers around Harpy Eagle nests that should be protected from harmful human

activities for ≥ 30 mo (i.e., 2 mo of incubation and the 28 mo that juveniles remain in the natal area).

ACKNOWLEDGMENTS

Special thanks are due to Terra Natura Foundation for funding the Project on tracking of Harpy Eagles in Ecuador. SIMBIOE, the Environment Ministry of Ecuador and EcoFondo funded the fieldwork. We are also thankful to Alexander Blanco and the team of participants and volunteers for their help in the captures, and to the indigenous communities for their constant support and for allowing us to work in their territories. Permissions for the study were granted from the Environment Ministry of Ecuador (18-2009-IC-FAU-DPS-MA-2009). J. Vidal-Mateo was supported by FPU grant of the Spanish Ministry of Education (reference FPU014/04671). This report is a portion of the Ph.D. dissertation of R. Muñoz-López at the University of Alicante.

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Received 20 June 2016; accepted 27 February 2017
Associate Editor: Stephen B. Lewis