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Dispersal and Space Use of Captive-Reared and Wild-Rehabilitated Harpy Eagles Released in Central American Landscapes: Implications for Reintroduction and Reinforcement Management

Adrián Naveda-Rodríguez [1,2,*,†], Edwin Campbell-Thompson [1], Richard T. Watson [1], Jennifer McCabe [1] and Félix Hernán Vargas [1]

[1] The Peregrine Fund, 5668 West Flying Hawk Lane, Boise, ID 83709, USA
[2] Wildlife Conservation Society, Ecuador Program, Quito 170507, Ecuador
* Correspondence: adrian.naveda@gmail.com
† Current address: Adrián Naveda-Rodríguez, Department of Wildlife, Fisheries and Aquaculture, Mississippi State University, Starkville, MS 39762, USA.

Abstract: Understanding the spatial context of animal movements is fundamental for the establishment and management of protected areas. We tracked, by telemetry devices, 31 captive-reared and 5 wild-rehabilitated *Harpia harpyja* and estimated the dispersal and space use after release in Mesoamerica. We evaluated the effectiveness of protected areas in the protection of home ranges and examined how individual traits, release methods and landscape features influenced the dispersal and home range using mixed-effects models. The mean post-release dispersal was 29.4 km (95% CI: 22.5–38.5), and the annual home ranges averaged 1039.5 km^2 (95% CI: 627–1941). The home ranges were influenced by the release method, patch richness, patch and edge density and contagion. The currently protected areas in Mesoamerica may not be effective conservation units for this species. The Harpy Eagle average home range greatly exceeded the average size of 1115 terrestrial protected areas (52.7 ± 6.1 km^2) in Mesoamerica. Due to their wide use of space, including transboundary space, Harpy Eagle conservation efforts may fail if they are not carefully coordinated between the countries involved. Future restoration efforts of umbrella forest-dwelling raptors should select release sites with highly aggregated and poorly interspersed forests. The release sites should have a buffer of approximately 30 km and should be located completely within protected areas.

Keywords: animal movement; contagion; headstarting; landscape detective; landscape heterogeneity; Mesoamerican Biological Corridor; neotropical bird of prey

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1. Introduction

Birds of prey have key functional roles in terrestrial ecosystems and are often used as umbrella species (species with large habitat needs whose protection could lead to the conservation of many other co-occurring species) to achieve conservation goals [1]. Furthermore, their long-term conservation is contingent on the reliable knowledge of their natural history. Understanding the ecological consequences of movement strategies such as dispersal and space use and their drivers is fundamental in ecology and also for choosing the spatial scale of intervention that aids the creation and management of protected areas [2,3]. However, these data are usually not available for large raptors, particularly tropical species.

Raptor dispersal (intentional individual displacement to colonize new areas and/or find and establish breeding sites) and space use are key to colonizing new areas and connecting fragmented populations [4–6]. Dispersal and space use are related to body size, age, gender, habitat conditions, prey availability and breeding season [6–8]. Studies on the movements of large tropical raptors are often characterized by small sample sizes, limiting the ability to clearly identify ecological patterns. For example, Abaño et al. [9] found a large variability in the dispersal of six Philippine Eagles (*Pithecophaga jefferyi*), and van Eeden et al. [10] reported no major differences in space use between the males and females of six Martial Eagles (*Polemaetus bellicosus*) studied in South Africa.

The Harpy Eagle (*Harpia harpyja*) is the largest forest-dwelling eagle found in lowland forests from south Mexico to north-east Argentina [11]. It is threatened by habitat loss and human persecution and is thus globally classified as vulnerable and considered endangered or locally extinct in some countries of Central America [12]. This situation generated the proposal of conservation actions such as the creation of protected areas and the strengthening of populations by captive breeding programs. Between 1987 and 2006, The Peregrine Fund's Harpy Eagle restoration program bred eagles in captivity, rehabilitated confiscated eagles and successfully released 49 captive-born and wild-rehabilitated Harpy Eagles in Mesoamerica [13]. Since forest-dependent raptors are inconspicuous and difficult to study because of their naturally low population density, the Harpy Eagle restoration program has facilitated the development of applied research focused on the captive breeding and ecological monitoring of released individuals [14–16], with little attention to the spatial ecology.

The movement ecology of this species remains largely unstudied. Efforts to understand Harpy Eagle dispersal and space use were initiated in 1996 in Venezuela [17]. However, data collected on more than 30 individuals have not been analyzed or published, and the published information is based on limited studies along its geographic range [18–21]. These published results illustrate the need for a more formal and quantitatively rigorous approach to elucidating the underlying mechanisms influencing the movement ecology of this major predator of neotropical forests.

We used data from 31 captive-reared and 5 wild-rehabilitated Harpy Eagles released in Belize and Panama between 2002 and 2009 to estimate the post-release dispersal and annual home range size. Further, we examined how these parameters were influenced by individual traits, landscape composition and configuration and human intervention. We analyzed whether the post-release dispersal and home range differed between sex or age, as observed in other large raptors [6,7]. Acknowledging that human intervention (e.g., captivity and translocation) can affect the behavior and personality of captive-reared and rehabilitated animals [22], we also analyzed the relationships of release methods (hard and soft-release) and the age at release regarding movement strategies of the eagles. Moreover, we examined the effect of landscape composition and configuration on dispersal and space use and assessed the effectiveness of natural protected areas in the conservation of this species.

Based on previous research on the movements of Harpy Eagles [18–21], we did not expect to see differences between sexes or ages. We predicted that hard-released eagles (no pre-conditioning or food provisioning after release) would exhibit greater dispersal rates and home ranges than soft-released eagles (food provisioning after release). Finally, considering that the Harpy Eagle is a forest specialist, we forecasted that the dispersal and space use would increase with increasing landscape heterogeneity, which is assumed to be a poor-quality habitat for Harpy Eagles since they rely on extensive areas of pristine forests with abundant arboreal mammals [23].

2. Methods

2.1. Study Area

Harpy Eagles were released in the Chiquibul Forest Reserve in Belize, Soberania National Park, La Amistad International Park and Darien National Park in Panama (Figure 1). Campbell-Thompson et al. [15] and Watson et al. [13] provided detailed information on the release sites. The release sites were selected considering: (i) the previous occurrence of Harpy Eagles in these areas prior to extirpation, (ii) protection from human persecution and (iii) the presence of large forest tracts of suitable habitat with suitable prey sources.

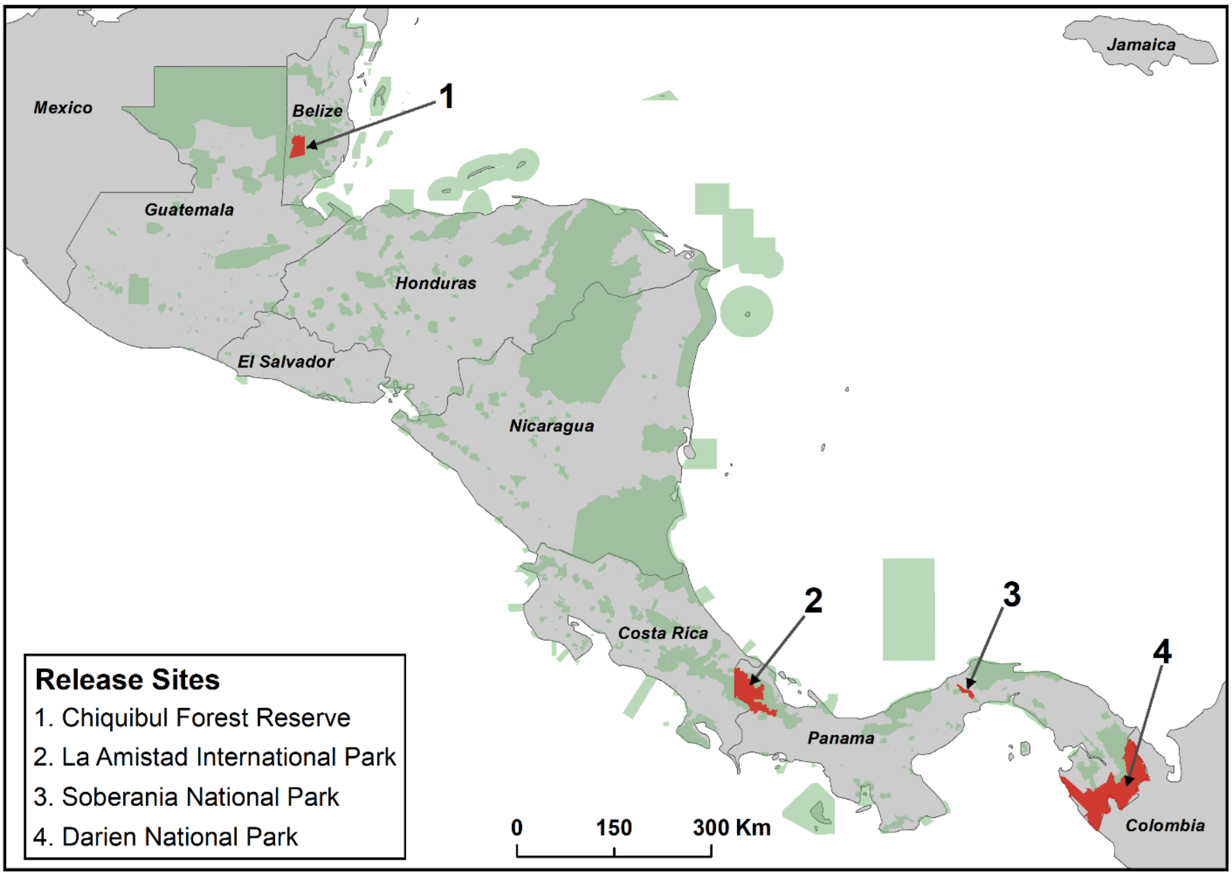

Figure 1. Location of release sites of captive-reared and wild-rehabilitated Harpy Eagles (*Harpia harpyja*) in Central American landscapes. Protected areas are indicated in green. Protected areas where eagles were released are highlighted in red.

2.2. Harpy Eagle Data

Harpy Eagles were bred or rehabilitated at the Peregrine Fund's World Center of Birds of Prey in Idaho, USA and the Neotropical Raptor Center located in Ciudad del Saber, Republic of Panama. Muela et al. [24] and Watson et al. [13] outlined details on the breeding facilities, the rehabilitation of wild eagles and the management of breeding pairs and nestlings. We analyzed data from 31 captive-bred and 5 wild-rehabilitated eagles (20 females and 16 males, determined by the marked reversed sexual dimorphism in this species [11]). The eagles were classified into four age classes at release. Class one included 10 individuals aged 6–7-months, class two included 11 individuals aged 18–23-months, class three included 10 individuals older than 30 months and class four included 5 adult wild-rehabilitated eagles. Eagles older than four years were classified as adults; the age of wild-rehabilitated individuals was determined based on plumage [11]. Thirteen eagles were released in Belize and twenty-three eagles were released in Panama.

2.3. Movement Data

The eagles were fitted with radio telemetry (VHF Biotrack 70 g, Merlin System 60 g) and satellite telemetry (Doppler PTT-100 95 g, Argos/GPS LC4T PTT-100s 105 g, Solar Argos/GPS PTT-100s 70 g) units attached in a backpack configuration. The mean of the weights of the tagged birds was 5947 g (range = 3720); the percentage weight of the tags in relation to the mean weight of the involved birds was between 1 and 1.8%. Locations were obtained from November 2002 to December 2011. Eagles with VHF transmitters were located by two observers three times per week by homing (animals are located by visual contact within a distance < 100 m, and their positions are recorded with a handheld GPS). Satellite units were programmed to record data for 11 consecutive hours (1 GPS-fix per hour) every four days. The fixes recorded by each PTT were processed by the Argos System. For analysis, we used positions with an estimated accuracy $\leq$ 500 m (Argos location classes 2 and 3).

2.4. Release Methods

Harpy Eagles were released using two basic approaches. Soft-releases were conducted using the adapted hacking technique developed for this species [15], by which 19 captive-bred eagles were placed in hacking boxes for a period of 3–6 weeks until release, and food was provisioned after release until independence. See [15] for details on the release protocol.

Hard-releases included 12 captive-bred and 5 wild-rehabilitated eagles. Hard-released eagles were transported in kennels to the release site; the cage door was open, and the eagle flushed without pre-conditioning or food provisioning after release.

2.5. Dispersal

Dispersal was considered to have occurred once eagles flew beyond the average inter-nest of the neighboring pairs distance [25] and remained for 30 continuous nights outside the radii created by the inter-nest distance. The inter-nest of the neighboring pairs distance for Harpy Eagles in Central America has been estimated to be 4.1 km [26]. We measured the post-release dispersal with a net-squared displacement analysis using the *amt* R package [27,28]. Maximum distances from the release point were used as a measure of the maximum post-release dispersed distance.

2.6. Home Range

We estimated the space use following the workflow proposed by Calabrese et al. [29]. We used the autocorrelated kernel density estimation (AKDE) [30] with the default parameters in the *ctmm* R package [31] to calculate the error-informed home range sizes and to implement the small sample size bias correction proposed by [32]. We estimated the home range for each bird in each calendar year. We applied Argos location classes to account for telemetry error. Since eagles with VHF telemetry were located by homing, we assigned these positions to Argos location class 3 (estimated error < 250 m).

Because eagle relocations followed different sampling schedules, we used the optimal weighting method implemented in *ctmm* to account for sampling bias and to correct for irregular and missing data [33]. Eagles with at least 180 days of continuous tracking data and which exhibited home ranging behavior were selected for space use calculation. Home ranging behavior was determined by analyzing the empirical semi-variogram of each individual [30]. We calculated the annual core areas and home ranges as the 50% and 95% isopleths of utilization distribution using AKDE, respectively, along with 95% confidence intervals on the areas estimated.

2.7. Landscape Metrics

We used land cover information for 2003–2011 at a 500 m grain size from Terra MODIS MCD12Q1 [34] to calculate the landscape composition, configuration and connectivity metrics (hereafter, landscape metrics) within the annual home range of each eagle. We calculated the most common landscape metrics used in landscape ecology [35,36]. The composition metrics comprised patch richness (the number of landcover types) and Shannon's diversity index (a measure of landscape heterogeneity). The configuration metrics included patch density (the number of landcover patched per area unit), largest patch index (the percentage of the landscape occupied by the largest patch), edge density (edge length in the landscape in relation to the total landscape area), landscape shape index (a measure of change in the shape of a landscape patch), contagion index (a measure of aggregation and interspersion) and landscape division index (a measure of single landcover type aggregation). Landscape metrics were calculated in Fragstat 4.2 using the eight-neighbor rule [37].

We set the spatial scale of our analysis to one kilometer. We clipped the annual land cover raster using the upper limit confidence interval of the individual annual home ranges as the clipping feature. The grain size of the input raster and the clipping features allowed us to have grain and extent sizes 2 times smaller and >2 times larger, respectively, than the scale of analysis recommended by O'Neill et al. [38] to avoid the sensitivity of the landscape metrics to grain size and calculation scales.

2.8. Data Analysis

We calculated and reported the average, standard errors or 95% nonparametric bootstrap confidence intervals (95% CI) of tracking time, maximum post-release dispersed distance, annual core area, annual home range, landscape metrics and protected areas sizes. Nonparametric bootstrap confidence intervals correspond to the adjusted bootstrap percentile interval and were calculated in the *boot* R package [39].

We performed a GAP analysis (gaps in the representation of eagle's home ranges within protected areas [40]) to assess the efficacy of the protected areas in the Harpy Eagles' habitat conservation. Using ArcGIS 10.4 [41], we intersected the network of protected areas of Central America [42] with the annual home ranges to calculate the proportion of home ranges inside of the protected areas. Since Pearce et al. [43] proposed 40% of habitat protection for avian species with little identified suitable habitat; we assumed that the protected areas are effectively protecting the Harpy Eagles in Central America if >40% of the annual home range is included within them.

Since post-release dispersal was positively correlated with annual home range (r_s = 0.93), a similar response is expected; therefore, we only determined the relationships of home range (response variable) with selected independent variables and their interactions. We fitted 11 linear mixed-effects models for our response variable (Table 1) using the *lme4* R package [44]. We acknowledge that the effect of age at release and the release method may not be the same after the first year. Captive-reared, wild-rehabilitated or translocated wildlife may not display long-term shifts in movement parameters after being exposed to captivity [45,46]. Thus, we are assuming that the artificial selection placed by the captive-breeding and rehabilitation of Harpy Eagles in this study can impose a radical and permanent shift in temperament, as suggested by McDougall et al. [47] and Shier [48], so we expect the effect of age at release and the release method to be the same in the long term.

Table 1. Models fitted to explain the home range size of captive-reared and wild-rehabilitated Harpy Eagles (*Harpia harpyja*) released in Central American landscapes. All models contain a random effect for the individual. *K* = number of model parameters, ΔAICc = difference between AICc values from the competitive and top model, AICc *wi* = model weight, ModelLik = relative likelihood of the model. RM = Release method, AR = Age at Release, PR = Patch richness, PD = Patch density, ED = Edge density, Con = Contagion.

Models	*K*	AICc	ΔAICc	AICc *wi*	ModelLik
RM*PR + RM*PD + RM*ED + RM*Con	12	139.9	0.0	0.999	1.0000
Age*PR + Age*PD + Age*ED + Age*Con	12	154.3	14.4	0.001	0.0008
Sex + Age + AR + RM + PR + PD + ED + Con	13	165.3	25.4	0.000	0.0000
PR + PD + ED + Con	7	165.7	25.8	0.000	0.0000
Sex*PR + Sex*PD + Sex*ED + Sex*Con	12	166.5	26.6	0.000	0.0000
AR*PR + AR*PD + AR*ED + AR*Con	22	183.3	43.4	0.000	0.0000
RM	4	231.1	91.2	0.000	0.0000
Age	4	232.1	92.2	0.000	0.0000
Sex	4	244.5	104.6	0.000	0.0000
Null	3	245.1	105.2	0.000	0.0000
Age at Release	6	245.3	105.4	0.000	0.0000

Response variables were log-transformed and landscape metric variables were standardized (x-μ/σ) prior to analysis. We checked for multicollinearity among these variables using the variance inflation factor (VIF) metrics and removed any variables where VIF > 2 [49]; the largest patch index, division, Shannon's diversity index and landscape shape index were omitted because of collinearity. Each individual eagle was included as a random effect, and the models were validated by checking the diagnostic plots.

We used the second-order Akaike's Information Criterion (AICc) and AICc weights to rank and select competitive models (ΔAICc < 2) for inference. We evaluated the goodness-of-fit of the selected top-ranked model using the marginal (R^2m) and conditional (R^2c) coefficient of determination, as suggested by Nakagawa and Schielzeth [50].

3. Ethical Statement

The Harpy Eagle releases were approved by the Belize Forest Department's Wildlife Conservation Division and the National Environmental Authority of the Ministry of Environment of Panama.

4. Results

We recorded 6873 telemetry fixes (559 VHF and 6314 Argos/GPS) from 31 captive-reared and 5 wild-rehabilitated Harpy Eagles released in Belize and Panama. During the course of this study, we did not find any of these individuals breeding. The average tracking period per individual was 551 ± 59 (range = 1263) days. Six out of thirty-six eagles did not establish a home range and/or did not have at least 180 continuous days of tracking data; therefore, they were not included in the analysis of space use.

Dispersal and home ranges were highly variable among sex, age, age at release and release method (Figure 2). In general, older eagles and hard-released individuals dispersed further and had greater core areas and home ranges. Females had larger average core areas and home ranges than males (details provided in the supporting information; Tables S1 and S2). The post-release dispersal averaged 29.4 km (95% CI: 22.5–38.5). All individuals performed exploratory movements, going back and forth from the release site (supporting information; Figure S1). Since we tracked eagles from one to four years, we estimated 55 individual eagle annual core areas and home ranges; these averaged 247.5 km^2 (95% CI: 144–483) and 1039.5 km^2 (95% CI: 627–1941), respectively. Nine individuals released in Belize dispersed to Guatemala and/or Mexico, and their home ranges were distributed among the three countries. The representation of the Harpy Eagle home ranges within the network of protected areas varied from 0 to 100%, with a mean value of 71.8 ± 5%. Twenty-four Harpy Eagles had >40% of their home ranges within the protected areas.

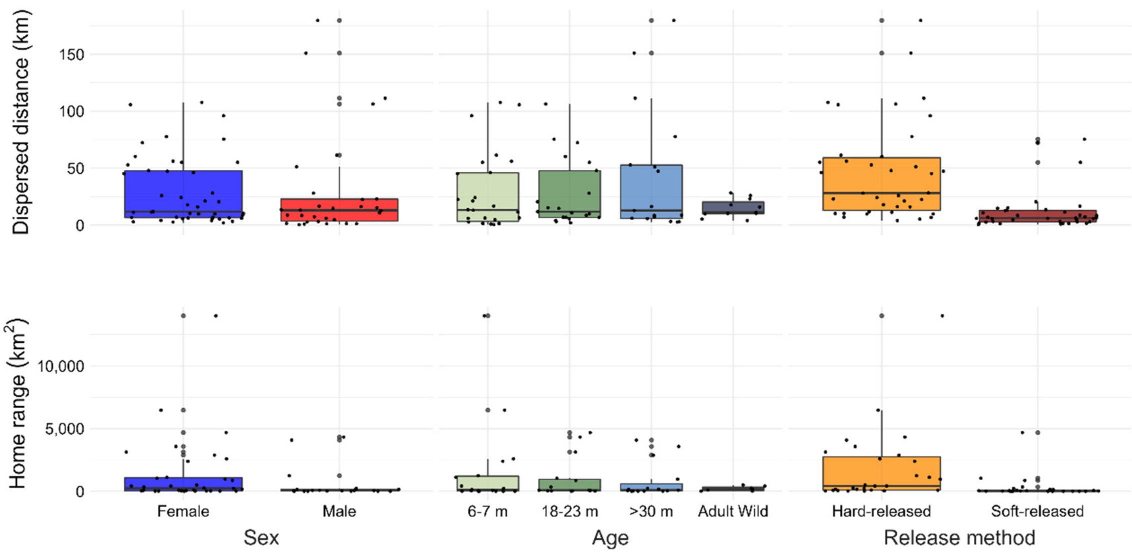

Figure 2. Dispersal and home ranges among sex, age at release and release method of captive-reared and wild-rehabilitated Harpy Eagles (*Harpia harpyja*) in Central American landscapes.

In general, the home ranges were characterized by having 7 ± 1 land cover types, 0.2 ± 0 patches/km^2, 392.1 ± 37 m of edge/km^2 and a high contagion (77 ± 2%). The top-ranked model had a good fit (R^2m = 0.93 R^2c = 0.95) and indicated that the home ranges were highly influenced by the release method, patch richness, patch density, edge density and contagion (Tables 1 and 2). The home range responded positively to patch richness (Figure 3A) and negatively to patch density (Figure 3B). The space use of hard- and soft-released individuals decreased in landscapes with a high edge density and contagion (Figure 3C,D).

Table 2. Parameter estimates and 95% confidence intervals (CI) from the top-ranked model explaining the relationship of landscape metrics with the space use of captive-reared and wild-rehabilitated Harpy Eagles (*Harpia harpyja*) released in Central American forests between 2002 and 2009.

Home Range~Release Method*Landscape Metrics	Estimate	CI
Hard-released	5.14	4.71, 5.57
Soft-released	−0.94	−1.49, −0.40
Hard-released:Patch richness	2.25	1.71, 2.80
Hard-released:Patch density	−0.97	−2.78, 0.84
Hard-released:Edge density	−1.48	−3.43, 0.47
Hard-released:Contagion	−0.21	−2.28, 1.85
Soft-released:Patch richness	−0.3	−0.98, 0.37
Soft-released:Patch density	0.44	−1.38, 2.26
Soft-released:Edge density	0.71	−1.36, 2.77
Soft-released:Contagion	−0.78	−3.00, 1.44

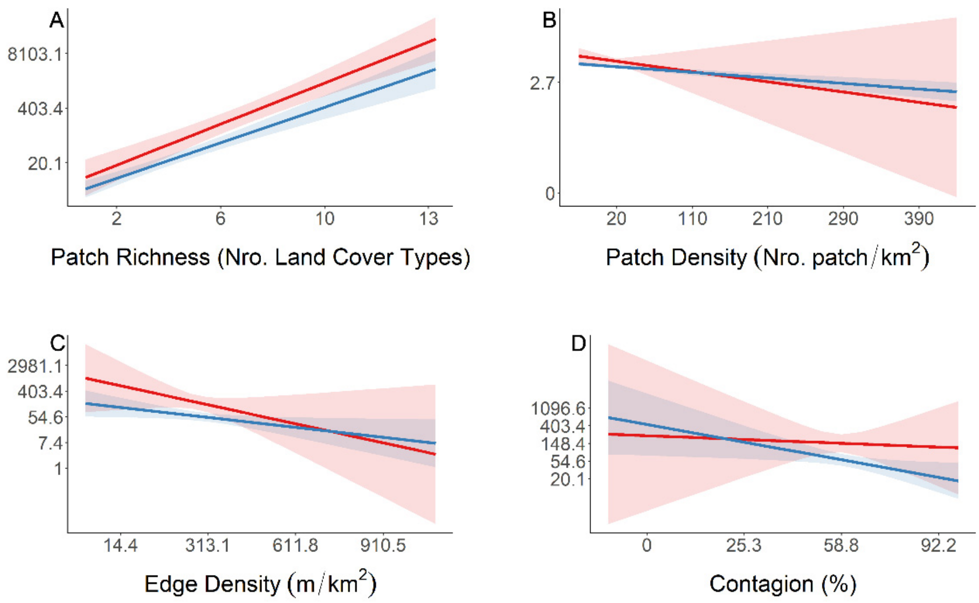

Figure 3. Marginal effects of the release methods and landscape metrics on the space use (home range size) of captive-reared and wild-rehabilitated Harpy Eagles (*Harpia harpyja*) in Central American landscapes. Red and blue lines correspond to hard- and soft-released individuals, respectively. The vertical axis is a natural logarithmic scale (back-transformed to km^2). The color shadows represent 95% confidence intervals.

5. Discussion

Our results on dispersal and space use were consistent with the observed variability in the dispersal and space use of individual eagles reported in previous studies [15,18–21,51]. The observed differences in movements by individuals of the same population may reflect individual behavioral or physiological traits [52]. Abaño et al. [9] attributed the large variability in the space use and dispersal distance of Philippine Eagles to the randomness of dispersal directions and habitat preferences. We have no information on whether wild Harpy Eagles similarly exhibit a great variability in movement strategies, as the captive-reared and wild-rehabilitated individuals did in our study and in Brazil [18]. However, we suggest that this variability in movement and space use may be a species-specific trait and not a pattern, as may occur with other neotropical forest raptors [53], and it is not necessarily connected to habitat quality and availability, since pristine habitats still existed in the release sites.

Our GAP analysis indicated that the protected areas in Central America may not be effective for the protection of Harpy Eagles. Although 80% of the individuals had >40% of their annual home ranges within 200 protected areas (mean $\pm$ SE size = 213.7 $\pm$ 53.7 km^2), the average size of these areas did not cover >40% of the average home range size ($\geq$415 km^2). The average core areas and home ranges were considerably greater than the average size (52.7 $\pm$ 6.1 km^2) of 1115 terrestrial protected areas in Central America, where 37 of these protected areas were $\geq$415 km^2 [41]. Conversely, the protected areas where we conducted the study averaged 2178.2 km^2, which is barely larger than mean home range. These 37 protected areas, including the 2 where we released the eagles, are largely disconnected. Thus, connectivity among protected areas in Central America must be prioritized.

The fact that 69% of the eagles released in Belize dispersed and established home ranges in more than one country suggests that population conservation efforts may fail if these are not rigorously articulated among the countries involved. For instance, a binational protected area will not suffice if the management plan for the same area differs between countries (e.g., La Amistad International Park) or if two protected areas with different management objectives and conservation goals share borders, as is the case with the Columbia River Forest Reserve and Chiquibul-Montañas Maya Biosphere Reserve.

Landscape heterogeneity affected the dispersal and space use of Harpy Eagles. The space use was smaller where the resources for this species (e.g., closed and continuous canopy of the same habitat) were probably more aggregated—that is, where patch richness and edge density were low and patch density and contagion were high. An increased edge density may entail resistance to eagle movements. Conversely, a high edge density could be related to habitat quality, where some species may find high-quality habitats. For instance, home range size and edge density are negatively correlated in Crested Serpent-Eagles (*Spilornis cheela*, [54]) and Eagle Owls (*Bubo bubo*, [55]). These studies explained that edge habitats acted as food magnets because they offered abundant resources for herbivores frequenting these areas and attracted predators. Therefore, since resources are spatially concentrated, there is no need for large home ranges.

The resources being spatially concentrated may explain the Harpy Eagles' dispersal and space use. First, some of the main prey species (sloths and monkeys) of Harpy Eagles have a strong preference for intact forests characterized by tall and continuous forest canopy, namely, a low patch richness, patch density and edge density and a high contagion [22,56–59], suggesting that these resources are spatially concentrated. This is consistent with the observed response of soft-released eagles that were food-provisioned in specific feeding trees (spatially concentrated resources).

Habitat aggregation and interspersion have been found to shape the movement strategies of birds of prey, as well as habitat management recommendations. For instance, Red-shouldered Hawks (*Buteo lineatus*) and Red-tailed Hawks (*Buteo jamaicensis*) selected foraging areas with more and less habitat interspersion, respectively [60]. The management plans for the Common Buzzard (*Buteo buteo*) and Northern Goshawk (*Accipiter gentilis*) recommend the establishment of an interspersed vegetation matrix to favor prey species [61,62]. Territories of forest-dwelling raptors are typically associated with large and undisturbed forest areas [63,64]. Our results on the relationship of dispersal and space use with contagion are consistent with these previous studies.

Harpy Eagles had the largest home ranges when the landscapes were poorly aggregated and highly interspersed. We suggest that Harpy Eagles track resources and limit their movements where resources are aggregated. Luz [65] found that Harpy Eagles prefer to nest in forests with a greater canopy height, which is reduced in fragmented forests [66,67]. Eagles explored different areas until they found suitable habitat conditions such as continuous canopy, which, besides offering more prey, can also provide suitable areas for shelter.

Implications for Conservation

Future Harpy Eagle restoration efforts should select release sites based on the landscape composition and the configuration and size of protected areas, not only considering the presence of large forest tracts. Beyond large forest tracts, Harpy Eagles may respond to a high contagion in the landscape. Thus, there could be areas with more than two forest types that are poorly aggregated and highly interspersed and should be avoided. On the other hand, since the average dispersed distance was approximately 30 km, we recommend that release sites include a buffer of at least this size, resulting in a polygon of 2826 km^2. Such polygons should be characterized by a high contagion and should be located within one or more protected areas to increase Harpy Eagle persistence. Areas fulfilling these requirements may be scarce and are probably located in remote areas where soft releases will be difficult to conduct. Thus, we suggest using the hard-release technique for future restoration efforts. To conclude, umbrella large tropical raptors, such as the Harpy Eagle, can be considered a landscape detective species [68], with wide-ranging movements that provide information from the landscape on how to design, manage and connect dynamic conservation concepts such as protected area networks. Further information regarding resource selection and survival are necessary to support this designation and the identification of potential release sites and suitable areas to be protected and/or connected.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14100886/s1, Figure S1: Average net-squared displacement of 36 captive-reared and wild-rehabilitated Harpy Eagles (*Harpia harpyja*) released in Central American forest between 2002 and 2009. Each point represents the average dispersal distance by month.; Table S1: Maximum post-release dispersal distance (km), core areas (50% AKDE, km^2) and home ranges (95% AKDE, km2) of captive-reared and wild-rehabilitated Harpy Eagles (*Harpia harpyja*) released in Central American forest between 2002 and 2009. Numbers in parentheses correspond to 95% nonparametric bootstrap confidence intervals. n is the number of individual in each group.; Table S2: List of the telemetry-tracked Harpy Eagles released in Central America with information on bird ID and year of study, tracking time in days (TTd), home ranging behavior (HRB), number of telemetry fixes (Fixes), sex, release site, release method, age at release, age when included in the analysis, dispersed distance in km, core are in km^2, home range in km^2, home range protected in km2 and proportion of home range protected in percentage.

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Conflicts of Interest: The authors declare no conflict of interest.

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