



Individual and environmental effects on the extent of the post-fledging dependence period in an Endangered neotropical raptor

Diego Gallego-García^{1,2,*}, Bryan D. Watts^{3,4}, José Hernán Sarasola^{1,2}

¹Centro para el Estudio y Conservación de las Aves Rapaces en Argentina (CECARA), Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Avda. Uruguay 151, Santa Rosa, La Pampa 6300, Argentina

²Instituto de las Ciencias de la Tierra y Ambientales de La Pampa (INCITAP), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Calle Rivadavia 236, Santa Rosa, La Pampa 6300, Argentina

³Center for Conservation Biology, College of William & Mary, Williamsburg, VA 23187, USA

⁴Virginia Commonwealth University, Williamsburg, VA 23284, USA

ABSTRACT: In altricial birds, the post-fledging dependence period (PFDP) is a fundamental life-history stage with direct consequences for survival, dispersal, and future reproduction. Understanding the drivers of its variation is therefore crucial to developing effective management strategies. However, this information is lacking for most species of conservation concern and/or breeding in the Southern Hemisphere. We describe, for the first time, the PFDP of the Chaco eagle *Buteogallus coronatus*, an Endangered neotropical raptor. Using location data from 29 GPS-tagged fledglings, we analyzed the duration of the PFDP and the ranging areas occupied as a function of individual sex, body condition, and natal area ecoregion. We also calculated the overlap in space usage among juveniles born in the same territory but in different years. The PFDP lasted for more than 8 mo, as expected for a large, slow-developing raptor, during which juveniles covered more than 300 km². The PFDP was longer for larger females, probably due to slower development of flight skills; this could also explain why males had larger ranging areas. Juveniles born in the ecoregion with denser woodlands occupied larger areas, likely reflecting their preference for open habitats. Better body condition explained earlier dispersal and modulated the effects of sex and ecoregion. Spatial overlap among juveniles born in the same territory reached around 90%, indicating a high consistency in area use across years. Our results help understand the complex factors affecting juvenile space usage during this vulnerable life stage, increasing the capacity for addressing the conservation needs of this species.

KEY WORDS: Onset of dispersal · Post-fledging dependence period · Conservation · Independence · Satellite telemetry · Birds · *Buteogallus coronatus* · Chaco eagle

1. INTRODUCTION

In altricial birds, the post-fledging dependence period (PFDP), or the time between fledging and independence, is a key and vulnerable life-history stage that affects the survival probability of the individual, determines natal dispersal outcomes and distances,

and can impact future reproduction (Cox et al. 2014, Naef-Daenzer & Gruebler 2016). In species with slow life-history strategies, which usually involve investment in small clutches and delayed breeding, this extended parental care may enhance offspring survival (Russell et al. 2004, Gallego-García & Sarasola 2025). Thus, describing and examining the processes

*Corresponding author: diegothen@gmail.com

of animal movement is key to addressing conservation issues and designing effective management strategies (Nathan et al. 2008, Morales et al. 2010). However, knowledge on this subject is scarce for many species, especially for those of conservation concern and breeding in the Southern Hemisphere (Gallego-García & Sarasola 2025).

As with many other life-history traits, the extent of the PFDP in birds is highly variable at different scales, due to extrinsic drivers such as breeding latitude (Russell et al. 2004, Gallego-García & Sarasola 2025), food availability (Fattebert et al. 2019, Scherler et al. 2023), conspecific density (Matthysen 2005), brood size (Walls & Kenward 1995), and climatic conditions (Delgado et al. 2010), or intrinsic characteristics, such as an individual's body condition at fledging (Ferrer 1992, Balbontín & Ferrer 2005, Delgado et al. 2010), species' body mass, and migratory strategies of the population (Gallego-García & Sarasola 2025), or sex (Awade et al. 2017). Concerning body condition at fledging, the ontogenic switch hypothesis (OSH; Holekamp 1986) states that the start of natal dispersal is triggered by the achievement of a specific physical condition. Thus, if food is abundant and the young reach good condition earlier in life, the date of dispersal is advanced (Ferrer 1992, Walls & Kenward 1995, Delgado et al. 2010). For species with sexual size dimorphism, the PFDP is usually longer for the larger sex (Kenward et al. 1993), as those individuals require more time to reach full mobility (Weston et al. 2018). Furthermore, intra-specific variability in the PFDP involves not only differences in duration but also in spatial extent. Recent studies have shown that the areas occupied during the PFDP may show individual-specific variation. For instance, as happens with breeding home range sizes of adult raptors, the areas occupied by fledglings during the PFDP may be larger when prey abundance (Miller et al. 2017, Gallego et al. 2023) and/or the availability of suitable foraging sites are low (Moss et al. 2014). This could be mediated by an individual's body condition (Rémy et al. 2011), since better-provisioned young birds may be able to travel further during their early life (Ferrer 1993, Delgado et al. 2010). In addition, given that sex has a strong influence on the movement behavior of birds in other life cycle stages (e.g. sex-biased dispersal; Greenwood 1980), it is likely to affect the areas used during the PFDP. On one hand, females in many bird species disperse farther than males (Greenwood 1980, but see McCaslin et al. 2020). Thus, we could expect that during the PFDP, the longest-dispersing sex would show a similar behavior and occupy larger areas. However, since male raptors in sexually size-

dimorphic species take less time to develop their flying skills (Weston et al. 2018), they could potentially explore larger areas than females. Finally, environmental factors such as habitat heterogeneity and vegetation cover are also known to influence range size at a macroscale level (Mirski et al. 2021) and may contribute to variability in spatial use during the PFDP.

Many raptor species worldwide are of conservation concern due to declining population trends (McClure et al. 2018), thus requiring protection of breeding and foraging habitats (Tanferna et al. 2013, Rivers et al. 2014). Detailed knowledge of the PFDP may provide valuable information about the risks that juveniles face, and this is particularly important in the case of endangered species, which may face stochastic events during their exploratory PFDP (Martens et al. 2018). Moreover, the analysis of space use during the PFDP of juvenile individuals from the same breeding territories in different years is relevant to account for potential issues related to the scarcity of adequate territories for both breeding and foraging in territorial raptors, which is a well-known threat to their populations (Negro et al. 2007, Steenhof et al. 2017).

This study aims to describe and analyze the PFDP of an Endangered neotropical raptor, the Chaco eagle *Buteogallus coronatus*, using accurate location data and novel, unbiased, statistical methodologies. Specifically, we (1) determine the duration of the PFDP, (2) calculate the size of the total ranging areas during this period, (3) estimate the ranging area overlap between juveniles of successive years born in the same breeding territory, and (4) document variation in the duration and ranging areas of the PFDP as a function of sex, ecoregion, and body condition. We hypothesized that sex, habitat features, and body condition would affect the duration and ranging areas of the PFDP. First, the extent of the PFDP in males would be shorter, possibly due to a faster development of flight skills, which would allow them to occupy larger ranging areas than females (Weston et al. 2018). Second, since the Chaco eagle prefers open habitats for hunting (Sarasola et al. 2022), variation in the availability of clear-cuts would induce ecoregional differences in the area occupied during the PFDP. Third, individuals with better body condition would disperse earlier, in accordance with the OSH (Holekamp 1986), and occupy larger areas due to their enhanced physical abilities (Weston et al. 2018), but we expected such responses to vary according to sex and ecoregion. Additionally, we predicted that juveniles born at the same breeding site but in different years would show a high overlap in their ranging

areas due to a scarcity of preferred breeding and foraging sites (Negro et al. 2007, Fandiño & Pautasso 2013, Sarasola et al. 2022).

2. MATERIALS AND METHODS

2.1. Study species

The Chaco eagle is a large neotropical raptor that is listed as Endangered by the International Union for the Conservation of Nature (IUCN) (Sarasola et al. 2018, BirdLife International 2024). This bird of prey ranges from southern Brazil, Paraguay, and Bolivia to northern Patagonia in Argentina, with a global population estimated at less than 2000 reproductive individuals (Birdlife International 2024). The species is considered to be extirpated from Uruguay, with no recorded sightings since the 1930s (Azpiroz & Cortés 2014), and has suffered population declines and range contractions in other regions, primarily due to anthropogenic pressures. In addition to habitat loss, which has caused a significant reduction and degradation of forested habitats and a shortage of potential breeding and foraging sites (Bellocq et al. 1998, Fandiño & Pautasso 2013), the main sources of mortality for Chaco eagles include direct persecution (Sarasola et al. 2010, Barbar et al. 2016), electrocution on power lines (Galmes et al. 2018, Sarasola et al. 2020, 2022), and drowning in water reservoirs devoted to cattle ranching (Sarasola et al. 2022).

However, despite its critical conservation status and the spatial predictability of the types of human infrastructures that threaten its populations, it is a little-known species with no data on adult home range size or the areas occupied by juveniles during the PFDP (Sarasola et al. 2022, but see Gallego-García et al. 2025). The Chaco eagle lays only one egg per reproductive attempt (Galmes et al. 2018, Sarasola et al. 2022), so there is no between-sibling variability in the extent of the PFDP typical of species with larger broods (Ramos et al. 2019), simplifying the assessment of environmental factors affecting its behavior during the PFDP (Gallego-García &

Sarasola 2025). The occurrence of pair substitutions and breeding territory changes across years in this species is not uncommon (Canal et al. 2025).

2.2. Study area

The study was carried out in central Argentina, along the temperate-arid ecoregions of Espinal and Monte Desert and the ecotone landscapes between them (Busso & Fernández 2018) (Fig. 1). Within the Espinal ecoregion, vegetation types include deciduous xerophytic forests dominated by caldén *Neltuma caldenia*, grassy savannahs, and bushy steppes. These vegetation types often coexist in heterogeneous patches, typically comprising a mixture of arboreal, shrub, and grassy strata. Typical vegetation in the Monte Desert ecoregion is represented by communities of high shrub-steppe (characterized mainly by *Larrea* spp.), where grassy and arboreal strata are vestigial, with some isolated trees of algarrobo *Ceratonia*

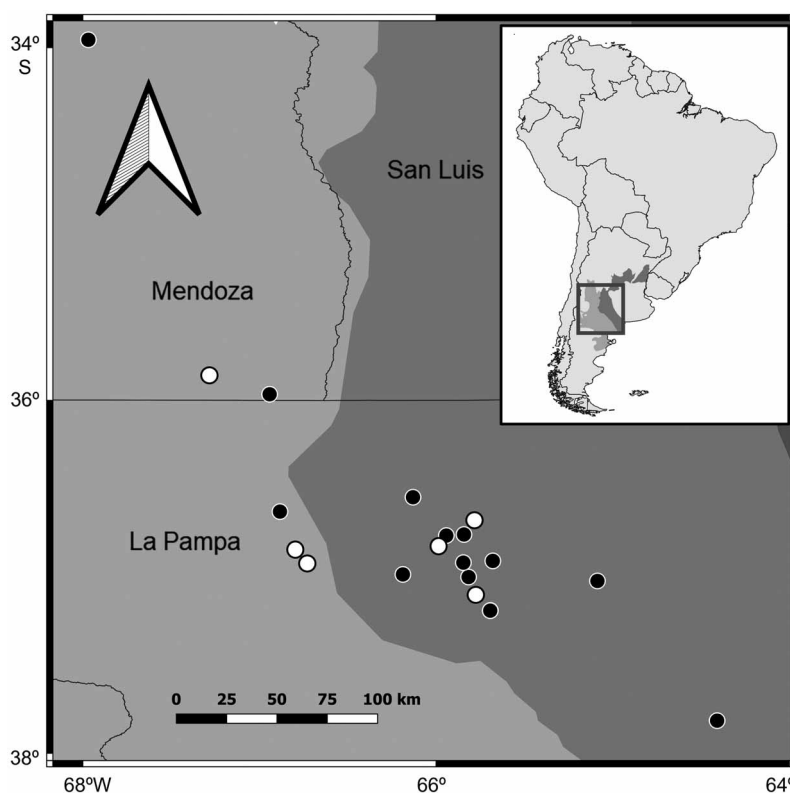


Fig. 1. Chaco eagle *Buteogallus coronatus* study area. Regional (provincial) limits are marked with continuous black lines, with the names of the provinces provided. Shaded areas mark the ecoregions (darker grey: Espinal; lighter grey: Monte Desert). Points (both black and white) indicate the location of the breeding territories where the juvenile eagles were born (Espinal, n = 13; Monte Desert = 6). White points indicate the breeding territories where more than one Chaco eagle juvenile was born and tagged in different years (n = 6)

siliqua and chañar *Geoffroea decorticans*. In both ecoregions, the climate is temperate arid, with mean annual temperatures of 15°C and high temperatures in summer (up to 45°C), when most of the scarce rainfall occurs. Annual rainfall ranges between 80 and 300 mm in the Monte Desert and 300–550 mm in the Espinal (Busso & Fernández 2018).

2.3. Individual sex determination and body condition assessment

As part of a long-term research and conservation program of the Chaco eagle in the area, we searched for, identified, and monitored active nests of this species by interviewing landowners and rural workers, traversing and exploring off-road sites, and surveying candidate trees using drones (Sarasola et al. 2010, Gallego & Sarasola 2021). Before young eagles fledged from the nest, we extracted a 1 ml blood sample from the brachial vein for sex determination using molecular procedures (Ellegren & Sheldon 1997). We also measured body weight (g) and wing chord (cm) using a digital scale and a steel ruler (Labocha & Hayes 2012). The residuals of the reduced major axis (RMA) regression between body weight and the wing chord were used as a body condition index (BCI) at fledging (Green 2001, Sarasola et al. 2004). Finally, we standardized raw residuals for representation and analysis by subtracting the average of the residuals from each residual and dividing the difference by the standard deviation of the residuals.

2.4. Duration and ranging areas of the PFDP

Young Chaco eagles were tagged with solar-powered GPS-satellite transmitters or platform transmitter terminals (PTTs) (Microwave Telemetry) at the time of sampling. These transmitters were set to record one location per hour during the daylight period (i.e. from 08:00 to 21:00 h), allowing for the continuous monitoring of their locations and movements through the ARGOS satellite system. The weight of the transmitters (70 g) accounted for less than 5% of the average body weight of the eagles (3000–3500 g; Sarasola et al. 2022). The GPS data were stored on the movebank.org online platform and then extracted and edited using R (R Core Team 2024). We first assigned the individual date of fledging (i.e. day 0 of the PFDP) by looking at the locations of the GPS fixes (we discarded less-accurate ARGOS–Doppler locations) relative to the nest site

during the first days after tagging; when this distance exceeded 50 m, we determined that the juvenile had started its PFDP (Krüger & Amar 2017, Gallego-García et al. 2025).

Next, we followed the method proposed by Gallego-García et al. (2025) of sequential comparison of weekly ranging areas to determine the end of the PFDP and, thus, the onset of dispersal. Specifically, we calculated weekly ranging areas (95% estimator) from fledging for each individual using autocorrelated kernel density estimation (AKDE; Fleming et al. 2015) in the 'ctmm' package (Calabrese et al. 2016). This package models the autocorrelation structure of tracking data by using Ornstein-Uhlenbeck foraging (OUF) or Ornstein-Uhlenbeck (OU) models, and therefore performs more accurate predictions of the home range than traditional kernel density estimation (KDE) methods (Calabrese et al. 2016, 2021), which usually underestimate the home range areas (Fleming et al. 2015). Outliers were visually detected using 'ctmmweb' (Calabrese et al. 2021), and we removed those that had unusual speeds (i.e. over 80 km h⁻¹, since similar resident eagles do not exceed this speed; Sur et al. 2020). Whenever the ratio between the ranging area of one week over that of the previous week reached 20 times, we considered that the juvenile had ended its PFDP (Gallego-García et al. 2025) (Fig. 2). This method provides more accurate and standardized estimations on the onset of dispersal than previously suggested techniques, and it is very useful for little-known species for which adult movement patterns are unknown.

For the whole PFDP and for each juvenile, we calculated the total ranging areas occupied (95% estimator) (Börger et al. 2008). Then, since some of them were born in the same territory but in different years, and to assess the consistency of utilization of ranging areas by juveniles of different years, we used the function 'overlap' in the 'ctmm' package to analyze the proportion of area used by a sibling that matched that of the others born in the same territory.

2.5. Statistical analysis

We modeled the extent of the PFDP (in days) and the size of the ranging areas (in km²) separately as a function of sex (male, female), individual BCI, and biome (ecoregion) of the natal territory (Monte Desert, Espinal), including the interactions of BCI with sex and biome. All response variables followed a normal distribution of residuals (Shapiro-Wilk normality test, $p > 0.30$ in both cases). Some juveniles

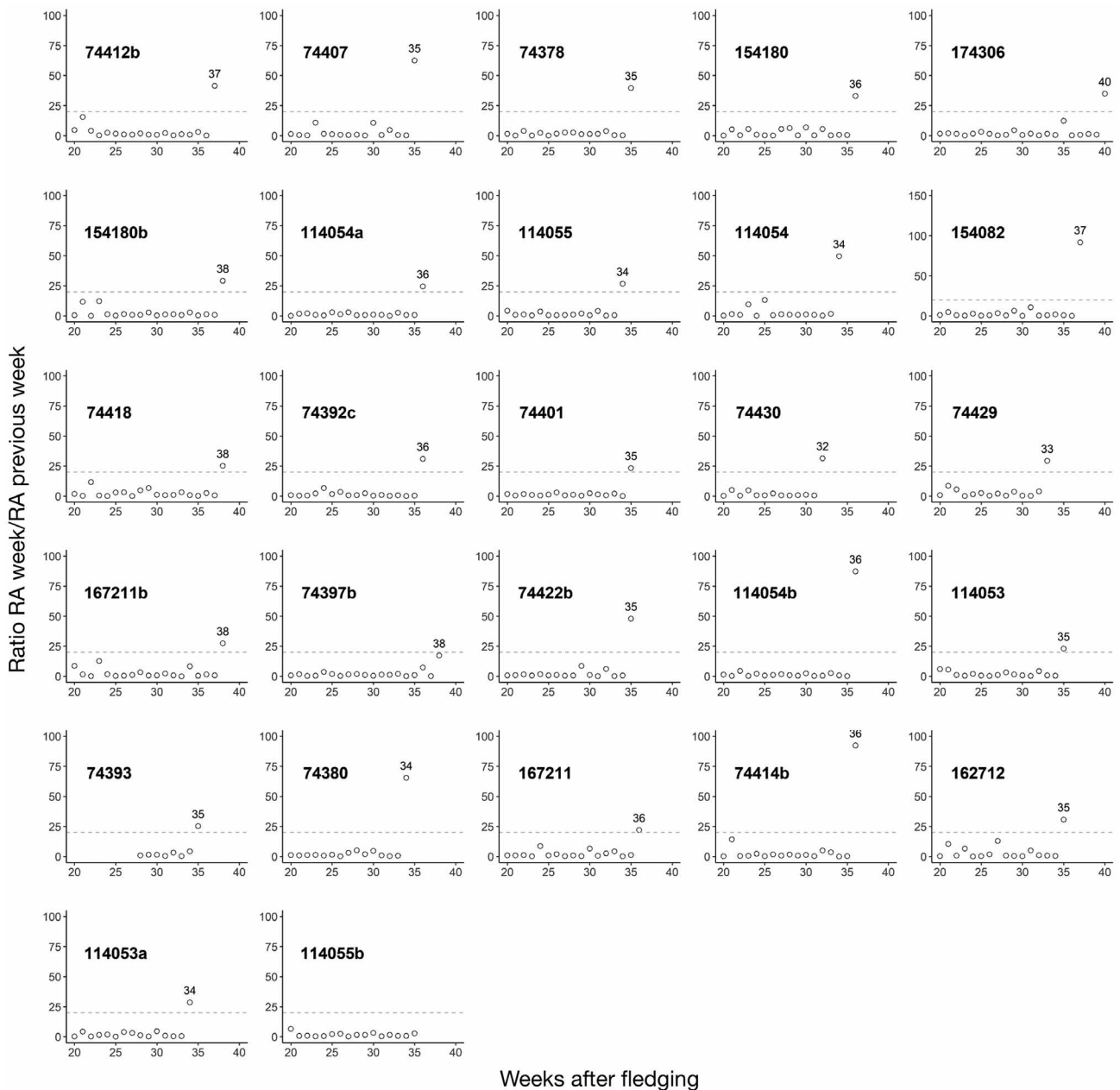


Fig. 2. Ratio of the ranging area of one week divided by that of the previous one of the 27 GPS-tagged Chaco eagle *Buteogallus coronatus* juveniles that completed their post-fledging dependence period (PFDP), over time (in weeks). Dotted grey horizontal line: threshold ratio used to determine the onset of dispersal (i.e. ratio ≥ 20) according to Gallego-García et al. (2025). The weeks fulfilling the conditions established in this method to detect the onset of dispersal (or the end of the PFDP) are labelled. Individual #114055b died before ending its PFDP, although it had surpassed the average duration of the PFDP of this population. Individual #74397b did not fulfill the condition 'ratio ≥ 20 ', although it was close (17.33), so we used visual analyses to confirm that the individual had dispersed

shared the same natal site or territory. However, since we have no genetic data for the years when this study was done to determine whether they were related (siblings or half-siblings in the case of an adult turnover) or unrelated, we included the natal territory as a random variable. For these analyses, we used general-

ized linear mixed models (logit link function) using the 'lme4' package (Bates et al. 2015). We used automated model selection with the MuMIn package (Bartoń 2009), and models were compared based on Akaike's information criterion adjusted for small sample size (AIC_C ; Burnham & Anderson 2004). If candi-

date models had $\Delta AIC_C \leq 2$, they were considered to be equally plausible given the data. Unless otherwise indicated, results are presented as mean \pm SD. All analyses were carried out using R (R Core Team 2024), and the maps were created using QGIS (QGIS.org 2023).

3. RESULTS

We GPS-tracked 29 juvenile Chaco eagles from 19 breeding sites (Fig. 1). The natal site (and surrounding area) of one of the juveniles was burnt soon after it started the PFDP, so its unusually extensive ranging area was not considered in the analysis. However, the duration of its PFDP was not an outlier and, thus, that information was used in the analysis. In addition, for the analyses of ranging areas, we used data from a juvenile individual that died very close to finishing its PFDP (with respect to the average of this population), but not for the analysis of the extent of the PFDP. Two other individuals provided sufficient information for an analysis of the area of overlap between eagles born in the same territories, but not for the total ranging areas or the extent of the whole PFDP. We used an average of 3339 ± 442 location points of 29 Chaco eagle fledglings.

3.1. Duration of the PFDP

The mean date of fledgling for Chaco eagles was 8 February (± 12 d, $n = 29$), and the mean date of the onset of dispersal was 15 October (± 15 d, $n = 26$). The mean duration of the PFDP of Chaco eagle juveniles was 247.81 ± 13.27 d ($n = 26$). The best model to explain the variation in the duration of the PFDP of the Chaco eagle juveniles included sex, biome, BCI, and the interactions of body condition with sex and biome (Table 1). The PFDP lasted for a longer time in females (250.63 ± 14.55 d; $n = 16$) than in males (243 ± 9.98 d, $n = 10$) (Table 2). The PFDP was longer for individuals born in the Espinal ecoregion (249.19 ± 15.68 d, $n = 16$) than in the Monte Desert ecoregion (245.60 ± 8.41 d, $n = 10$) (Table 2). In addition, earlier dispersal was associated with a higher BCI only for females (Fig. 3A) and for individuals in the Espinal ecoregion (Fig. 3B).

Table 1. Model selection results of generalized linear mixed models (GLMMs) explaining the variation in the duration (in months) and in the ranging areas (95% AKDE; autocorrelated kernel density estimation) of the post-fledgling dependence period (PFDP) of juvenile Chaco eagles *Buteogallus coronatus* in central Argentina ($n = 26$ individuals). The top 4 models for each response variable (PFDP duration and ranging area) are shown. Sex: male or female; biome of the natal site: Espinal or Monte Desert; BCI: body condition index

Model	df	AIC _C	ΔAIC	w
PFDP duration				
Biome \times BCI + Sex \times BCI	8	185.5	0.00	0.824
Biome \times BCI + Sex	7	190.6	5.08	0.065
Biome + Sex + BCI	7	190.7	5.20	0.061
Biome \times BCI	6	192.6	7.07	0.024
PFDP ranging area				
Biome \times BCI + Sex \times BCI	8	283.4	0.00	0.990
Sex \times BCI + Biome	7	293.2	9.81	0.006
Biome \times BCI + Sex	7	295.8	12.43	0.002
Sex \times BCI	6	300.9	17.49	0.001

3.2. Ranging areas and area overlap

The mean ranging area (95% AKDE) of Chaco eagle juveniles during the PFDP was 309.73 ± 166.69 km² ($n = 26$). The best model to explain the variation in the ranging areas of the Chaco eagle juveniles during the PFDP included sex, biome, BCI, and the interactions of body condition with sex and biome (Table 1). Ranging areas were larger for males (334.27 ± 168.67 km², $n = 10$) than for females (294.39 ± 169.09 km², $n = 16$) (Table 2). In addition, ranging areas during the PFDP were larger for those juveniles that were born in the Espinal ecoregion (354.28 ± 156.01 km², $n = 15$) than for those born in the Monte Desert ecoregion

Table 2. Coefficient estimates and SEs for each parameter from the top models explaining the variation in the duration (d) and in the ranging areas (AKDE: autocorrelated kernel density estimations, km²) of the post-fledgling dependence period (PFDP) as a function of sex (male or female), biome (Espinal or Monte Desert), body condition index (BCI), and the interactive effects of BCI with sex and biome, of GPS-tagged juvenile Chaco eagles *Buteogallus coronatus* in central Argentina ($n = 27$ individuals). Coefficient estimates for sex are relative to female; coefficient estimates for biome are relative to Espinal

Fixed effects	Duration of the PFDP		Ranging areas (AKDE 95)	
	Estimate	SE	Estimate	SE
Sex: male	−4.45	5.13	76.89	62.77
Biome: Monte Desert	−4.71	8.46	−74.46	82.74
BCI	−10.08	25.61	−160.44	345.70
(Sex: male) \times BCI	−24.08	33.38	706.66	409.17
(Biome: Monte Desert) \times BCI	24.76	35.59	−14.84	458.17

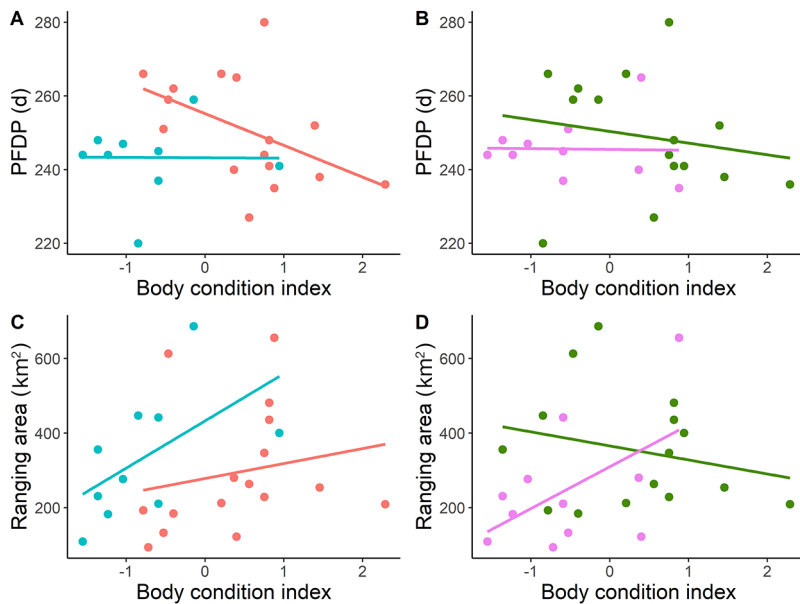


Fig. 3. Final linear mixed-effects models explaining the variation in (A,B) the duration and (C,D) the ranging areas (autocorrelated kernel density estimations) of the post-fledging dependence period (PFDP) compared to the body condition index of GPS-tagged juvenile Chaco eagles *Buteogallus coronatus*. Red and blue colors in (A) and (C) represent females and males, respectively, while dark green (Espinal) and violet (Monte Desert) colors in (B) and (D) represent natal biomes

($248.97 \pm 168.39 \text{ km}^2$; $n = 11$) (Table 2). The positive relationship between BCI and ranging areas was more marked in males than in females (Fig. 3C) and had an opposite effect on individuals living in the Espinal ecoregion (Fig. 3D). Lastly, the area covered by young eagles during the PDFP was not correlated with the time they spent until natal dispersal began (Pearson's coefficient = 0.176, $p = 0.40$).

For 6 breeding territories, we obtained information on the duration and ranging areas of PDFP for at least 2 individuals and years (range: 2–4 juveniles per breeding territory, $n = 19$; Fig. 4). For these individuals, the values of ranging area overlap were high, with some exceeding 95% (0.90 ± 0.08 , range: 0.69–1.00; Fig. 4).

4. DISCUSSION

This is the first study to assess the spatial and temporal dynamics of the PDFP in the Chaco eagle, including environmental and individual drivers of variation. Our findings reinforce the importance of intrinsic (sex and body condition) and extrinsic (ranging area ecoregion) factors in shaping the duration and areas used by juvenile Chaco eagles during this critical stage of their life cycle. Additionally, we dis-

covered a high similarity of areas used by juveniles that were born in the same breeding territory during their PDFP in different years, which highlights the strength of some environmental factors (e.g. habitat features) over others that would vary yearly (e.g. primary productivity, prey abundance).

4.1. Duration of the PDFP

Our results confirm that juveniles of this Endangered raptor depend on their parents for a prolonged time, spanning around 8 mo. As expected for a slow-developing species, this strategy may enhance juvenile survival (Martin 2015, Lloyd & Martin 2016) and compensate for its small clutch sizes and low reproductive outcomes (Martin 2014, Sarasola et al. 2022). The duration of the PDFP is key to achieving an appropriate body condition and learning the skills needed for dispersal and survival. Thus, the potential cost of

early dispersal can be high, particularly for long-lived species such as resident eagles. In this case, Chaco eagle juveniles have some years to prepare for their first reproductive attempt and therefore do not need to hastily leave their natal areas (Cramp & Simmons 1980, Gallego-García & Sarasola 2025). The PDFP in the Chaco eagle is longer than that of other raptors with similar body weights that breed at the same latitudes of the Northern Hemisphere (e.g. residents such as the Spanish imperial eagle *Aquila adalberti*, the wedge-tailed eagle *A. audax*, and migrants such as the eastern imperial eagle *A. heliaca*), but shorter than the African crowned-eagle *Stephanoaetus coronatus*, which breeds at lower latitudes (Gallego-García & Sarasola 2025). These findings highlight the influence of extrinsic and intrinsic drivers of variation in the extent of the PDFP at both species and individual levels and underscore the need for further research into this poorly understood life-history stage in birds (Russell et al. 2004, Gallego-García & Sarasola 2025). Additionally, we documented that the onset of juvenile dispersal occurred at the start of the breeding season, which is consistent with previous studies of large-bodied raptors (López-López et al. 2014, Krüger & Amar 2017). The Chaco eagle starts its breeding season before the beginning of austral spring (i.e. egg-laying occurs during October; Galmes et al. 2018,

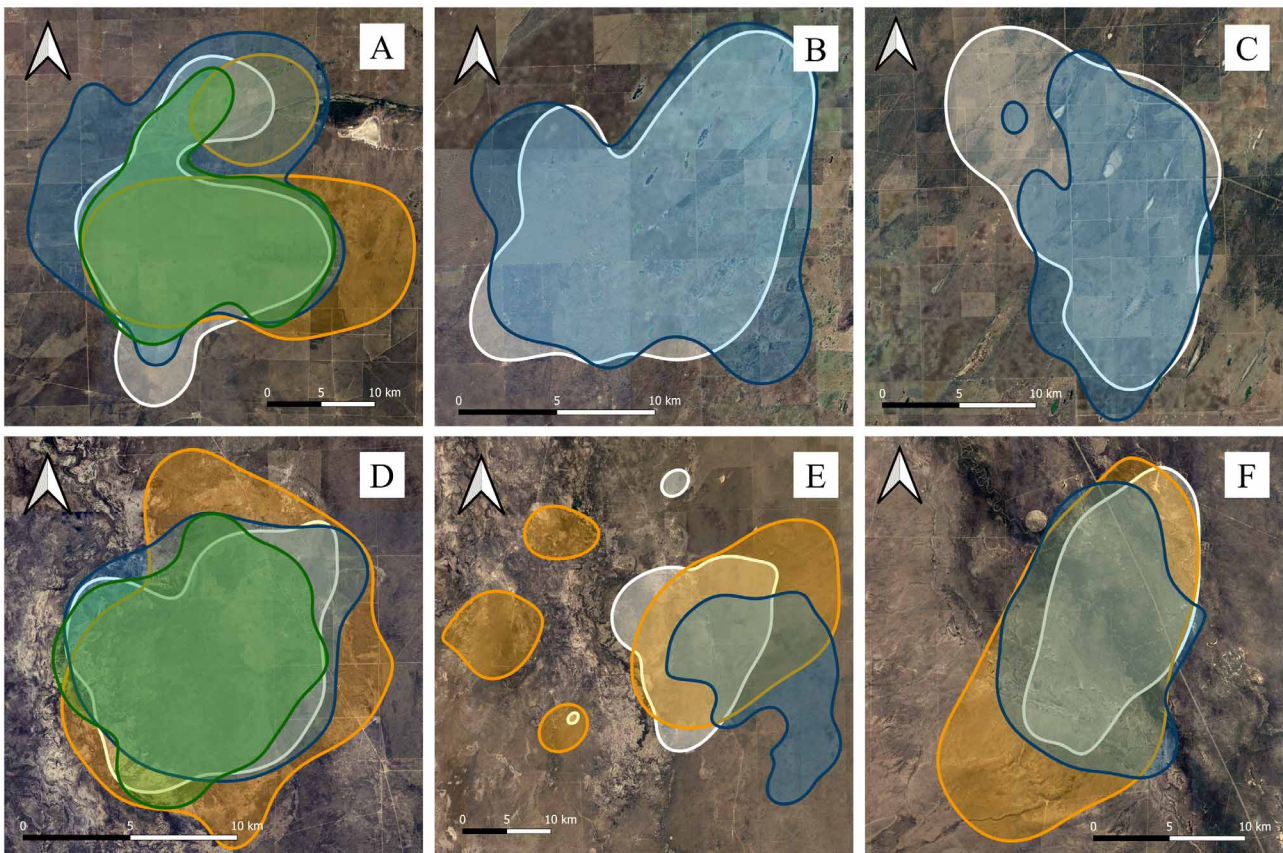


Fig. 4. Ranging areas (95% AKDE) of juvenile Chaco eagles *Buteogallus coronatus* during their post-fledging dependence period (PFDP) in (A–C) Espinal and (D–F) Monte Desert, the 6 breeding sites or territories where more than one Chaco eagle fledgling was born and tagged in different years (i.e. white points in Fig. 1)

Sarasola et al. 2022), which aligns with the timing of juvenile dispersal observed in this study.

The PFDP was longer for young Chaco eagles with poorer body conditions, which is consistent with the OSH (Holekamp 1986, Walls & Kenward 1995). Specifically, this finding suggests that individuals that reach a specific physical condition depart the natal area to benefit from the advantages of early dispersal, such as having more time to explore potential territories for breeding. Furthermore, the PFDP was longer in females, which is consistent with other studies (Kenward et al. 1993, Weston et al. 2018, but see Scherler et al. 2023) and is probably related to the slower development of flight skills of young females (or longer ontogenic phase, sensu Weston et al. 2018). Indeed, the larger sex needs more resources and time to develop (Kenward et al. 1993, Ducatez & Field 2021, Gallego-García & Sarasola 2025), and the sex that establishes the territories is usually driven to depart their natal areas first due to a scarcity of resources (Martens et al. 2018). If male Chaco eagles were the ones establishing the territories, then the fact that

they disperse earlier overall (and irrespective of their body condition) would make sense, as opposed to females, which need to be in a better body condition in order to end their PFDP earlier (but see Hemery et al. 2023). However, given that Chaco eagles are estimated to reach sexual maturity at 4–5 yr of age (Sarasola et al. 2022), the adaptive advantage of early dispersal remains unclear. Furthermore, there is no information on which sex establishes the reproductive territories in this species.

Additionally, juvenile Chaco eagles born in the Monte Desert ecoregion exhibited shorter PFDPs compared to those from the Espinal ecoregion. As no direct ecological or behavioral explanation is immediately apparent for this difference, further investigation is warranted to identify the underlying factors influencing earlier independence in juveniles from the less structurally complex Monte Desert ecoregion. The fact that body condition at fledging only affects the duration of the PFDP of individuals born in the Espinal ecoregion, but not that of those born in the Monte Desert ecoregion, deserves further

habitat quality and food availability analyses. For instance, poorly provisioned juveniles have been known to delay dispersal due to reduced competitiveness (Fattebert et al. 2019, Scherler et al. 2023).

4.2. Ranging areas during the PFDP

Young Chaco eagles in better body condition occupied larger ranging areas, a fact that has already been shown during the dispersal phase. Young individuals in good physical condition tend to travel longer distances during their early life, probably due to more efficient flight performance (Ferrer 1993, Delgado et al. 2010, Rémy et al. 2011). In addition, male Chaco eagles occupied larger areas than females during the PFDP. At first, this result could be seen as unexpected, since females often disperse farther than males in most bird species (Greenwood 1980); thus, the movements inside the natal area during the PFDP should resemble those during dispersal. However, faster developmental rates (and flying skill acquisition) of males would also enable them to explore larger areas during the course of their PFDP (Weston et al. 2018). In fact, higher movement activity of males during the PFDP has already been described for golden eagles *A. chrysaetos* (Zimmermann 2021), although the causes of this behavior are not clear. Additionally, we cannot discard a possible sex-mediated difference in foraging spatial strategies and/or flight performances in varied environmental conditions, due to sex differences in morphology and wing loading characteristics (see Clay et al. 2020), which might explain why BCI has a more pronounced effect on the ranging areas of males than on those of females.

Juvenile Chaco eagles born in the Monte Desert ecoregion had smaller ranging areas than those born in the Espinal ecoregion. Home range size is closely related to food supply and access (Marzluff et al. 1997, Clouet et al. 1999, Gallego et al. 2023). Chaco eagles are large, soaring raptors that are known to prefer open woodlands and savannahs for hunting (Sarasola et al. 2022). We expect that eagles living in the Espinal ecoregion, an area with denser woodlands and thus less availability of potential areas for hunting (or 'key areas', sensu Mirski et al. 2021), need a larger home range to compensate for this limited food access (Marzluff et al. 1997, Tucker et al. 2019). This behavior is also consistent with other species worldwide (Moss et al. 2014, Gallego et al. 2023) but has rarely been studied for juveniles during the PFDP (Zimmermann 2021). Last, the unexpected and opposing effects of body condition on the ranging areas across ecoregions

warrant further investigation, particularly through the exploration of alternative hypotheses at a microhabitat scale. Factors such as the availability of perches or artificially generated open patches (e.g. areas resulting from forest clear-cutting) may play a critical role. As with other large eagles, the Chaco eagle's foraging strategy is probably related to perch-hunting (or sit-and-wait) rather than flight-hunting (see Rudebeck 1950, Nadjafzadeh et al. 2016), so a lower availability of hunting perches would potentially cause the ranging areas of the Chaco eagles to increase.

4.3. Overlap in ranging areas by juveniles born in the same territory

Ranging areas during the PFDP of juveniles born in the same breeding territory but in different years had a high degree of overlap. A possible explanation could link the coincidence of ranging areas to an absence (or scarcity) of adequate habitat, which is a common factor limiting the populations of birds and raptors (Newton 1998, Negro et al. 2007) and a proven threat for Chaco eagle populations (Fandiño & Pautasso 2013, Sarasola et al. 2022). Alternatively, this overlap during successive years may mean that the ranging areas are heavily affected by habitat or other time-persistent characteristics (e.g. food abundance) that make them repeatable by Chaco eagles year after year, irrespective of climate conditions or individual relatedness. Given that breeding pair substitutions among Chaco eagles are not unusual (Canal et al. 2025), this finding highlights this species' strong range consistency during the PFDP.

4.4. Conservation implications

More than half of all raptor species worldwide are currently showing declines in global populations and high sensitivity to anthropogenic threats (McClure et al. 2018). Most species show a high mortality rate during the PFDP (Wiens et al. 2006, Cox et al. 2014, Naef-Daenzer & Gruebler 2016), and preliminary data suggest that the Chaco eagle is no exception (authors' unpubl. data). Therefore, a better understanding of post-fledging ranging areas and the drivers of their variation is crucial for the implementation of effective conservation policies (Morrison & Wood 2009, Serano 2018, Gallego-García & Sarasola 2025).

Traditionally, raptor research and conservation efforts have primarily focused on breeding home range areas and nest sites (e.g. Tanferna et al. 2013). How-

ever, our study highlights the need to protect areas used by Chaco eagle juveniles during their first months of life, well after fledging (i.e. after the reproductive season). Any measure to protect this threatened bird of prey should be extended in space (beyond breeding areas) and time (not only focusing on the breeding season) to ensure the long-term conservation of this and any other endangered bird species (Ramos et al. 2019).

Furthermore, the pronounced range consistency observed among Chaco eagles in this study highlights the urgent need for targeted research and conservation initiatives aimed at identifying and mitigating the main causes of anthropogenic mortality affecting this Endangered species. The vulnerability of Chaco eagle populations to habitat fragmentation and loss (Fandiño & Pautasso 2013), electrocution in power line pylons (Sarasola et al. 2020), and drowning in water reservoirs (Sarasola et al. 2022) should be taken into account when designing effective conservation plans to ensure the long-term persistence of its populations.

4.5. Future research

Apart from the aforementioned drivers of variation found in our study, we encountered high inter-individual differences in the timing of dispersal and in the ranging areas used during the PFDP. It is well known that individual decisions affect the movements patterns within a given population (Spiegel et al. 2017). These differences may induce changes in movement behavior and may be mediated by specific environmental characteristics of the natal areas at different scales (Fattebert et al. 2019, Spatz et al. 2022) or by other intrinsic attributes, such as personality (Patrick et al. 2017). Similar to other studies, we assumed that body condition was constant during the PFDP. Future work could accommodate temporal variation in body condition to better understand the factors shaping the PFDP in this species. We therefore advocate for a more detailed investigation into the complex, interactive effects of environmental and intrinsic variables on the development of this understudied life-history stage in raptors. Such knowledge will be critical for improving conservation strategies that aim to mitigate the challenges these species currently face.

Acknowledgements. We thank The Center for Conservation Biology (CCB) and Hawk Mountain Sanctuary Association for funding of the GPS devices and their location data. This article is part of the PhD thesis of D.G.G., who holds a docto-

ral fellowship from CONICET (Argentinian National Scientific and Technical Research Council). The Peregrine Fund, The Whitley Fund for Nature, and The Rufford Foundation provided funding for fieldwork (i.e. nest monitoring to tag fledglings with GPS devices). We thank the numerous volunteers, researchers, and field technicians who took part in the monitoring of nests and in the tagging of the Chaco eagle nestlings. 'I can fly higher than an eagle, for you are the wind beneath my wings' — Bette Midler.

LITERATURE CITED

- ✦ Awade M, Candia-Gallardo C, Cornelius C, Metzger JP (2017) High emigration propensity and low mortality on transfer drives female-biased dispersal of *Pyriglena leucoptera* in fragmented landscapes. PLOS ONE 12: e0170493
- Azpiroz AB, Cortés GD (2014) On the status of crowned eagle *Buteogallus coronatus* in Uruguay. Bull Br Ornithol Club 134:110–115
- Balbontín J, Ferrer M (2005) Factors affecting the length of the post-fledging period in the Bonelli's eagle *Hieraetus fasciatus*. Ardea 93:189–198
- ✦ Barbar F, Capdevielle A, Encabo M (2016) Direct persecution of crowned eagles (*Buteogallus coronatus*) in Argentina: a new call for their conservation. J Raptor Res 50: 115–120
- ✦ Bartoń K (2009) MuMIn: multi-model inference. <http://r-forge.r-project.org/projects/mumin/>
- ✦ Bates D, Mächler D, Bolker DB, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67(1):1–48
- Bellocq MI, Bonaventura SM, Marcelino FN, Sabatini M (1998) Habitat use of crowned eagles (*Harpyhaliaetus coronatus*) in the southern limits of the species' range. J Raptor Res 32:312–314
- ✦ Birdlife International (2024) Species factsheet: crowned solitary eagle *Buteogallus coronatus*. <https://datazone.birdlife.org/species/factsheet/crowned-solitary-eagle-buteogallus-coronatus>
- ✦ Börger L, Dalziel BD, Fryxell JM (2008) Are there general mechanisms of animal home range behavior? A review and prospects for future research. Ecol Lett 11:637–650
- ✦ Burnham K, Anderson D (2004) Model selection and multi-model inference. Springer-Verlag, New York, NY
- ✦ Busso CA, Fernández OA (2018) Arid and semiarid rangelands of Argentina. In: Gaur MK, Squires VR (eds) Climate variability impacts on land use and livelihoods in drylands. Springer International Publishing, Cham, p 261–291
- ✦ Calabrese JM, Fleming CH, Gurarie E (2016) ctmm: an R package for analyzing animal relocation data as a continuous-time stochastic process. Methods Ecol Evol 7: 1124–1132
- ✦ Calabrese JM, Fleming CH, Noonan MJ, Dong X (2021) ctmmweb: a graphical user interface for autocorrelation-informed home range estimation. Wildl Soc Bull 45: 162–169
- ✦ Canal D, Negro JJ, Sarasola JH (2025) Non-invasive DNA monitoring unveils the reproductive strategy of an endangered and elusive top predator, the Chaco Eagle. Glob Ecol Conserv 60:e0306
- ✦ Clay TA, Joo R, Weimerskirch H, Phillips RA and others (2020) Sex-specific effects of wind on the flight decisions

- of a sexually dimorphic soaring bird. *J Anim Ecol* 89: 1811–1823
- Clouet M, Barrau C, Goar JL (1999) The golden eagle (*Aquila chrysaetos*) in the Bale Mountains, Ethiopia. *J Raptor Res* 33:102–109
- ✦ Cox WA, Thompson FR III, Cox AS, Faaborg J (2014) Post-fledging survival in passerine birds and the value of post-fledging studies to conservation: post-fledging survival in passerines. *J Wildl Manag* 78:183–193
- Cramp S, Simmons KEL (1980) The birds of the Western Palearctic, Vol 2. Oxford University Press, Oxford
- ✦ Delgado MM, Penteriani V, Revilla E, Nams VO (2010) The effect of phenotypic traits and external cues on natal dispersal movements. *J Anim Ecol* 79:620–632
- ✦ Ducatez S, Field DJ (2021) Disentangling the avian altricial–precocial spectrum: quantitative assessment of developmental mode, phylogenetic signal, and dimensionality. *Evolution* 75:2717–2735
- ✦ Ellegren H, Sheldon B (1997) New tools for sex identification and the study of sex allocation in birds. *Trends Ecol Evol* 12:255–259
- Fandiño B, Pautasso AA (2013) Distribución, historia natural y conservación de *Harpyhaliaetus coronatus* (Aves: Accipitridae) en el centro-este de Argentina. *Natura Neotropicalis* 44:41–55
- ✦ Fattebert J, Perrig M, Naef-Daenzer B, Gruebler MU (2019) Experimentally disentangling intrinsic and extrinsic drivers of natal dispersal in a nocturnal raptor. *Proc R Soc B* 286:20191537
- ✦ Ferrer M (1992) Regulation of the period of postfledging dependence in the Spanish imperial eagle *Aquila adalberti*. *Ibis* 134:128–133
- ✦ Ferrer M (1993) Ontogeny of dispersal distances in young Spanish imperial eagles. *Behav Ecol Sociobiol* 32: 259–263
- ✦ Fleming CH, Fagan WF, Mueller T, Olson KA, Leimgruber P, Calabrese JM (2015) Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology* 96:1182–1188
- ✦ Gallego D, Sarasola JH (2021) Using drones to reduce human disturbance while monitoring breeding status of an endangered raptor. *Remote Sens Ecol Conserv* 7:550–561
- ✦ Gallego D, McCabe R, Goodrich L (2023) Homeward bound: annual breeding home range size and overlap in broad-winged hawks (*Buteo platypterus*) and the effects of sex, productivity, and ecoregion. *J Field Ornithol* 94:9
- ✦ Gallego-García D, Sarasola JH (2025) Ecological drivers of variation in the extent of the post-fledging dependence period in the largest group of diurnal raptors. *Ibis* 167: 345–356
- ✦ Gallego-García D, Watts BD, Sarasola JH (2025) Case report: independence day, comparison of methods to estimate the onset of dispersal in large territorial birds. *Anim Biotelem* 13:6
- ✦ Galmes MA, Sarasola JH, Grande JM, Vargas FH (2018) Parental care of the endangered Chaco eagle (*Buteogallus coronatus*) in central Argentina. *J Raptor Res* 52: 316–325
- ✦ Green JG (2001) Mass/length residuals: Measures of body condition or generators of spurious results? *Ecology* 82: 1473–1483
- ✦ Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28:1140–1162
- ✦ Hemery A, Mugnier-Lavorel L, Itty C, Duriez O, Besnard A (2023) Timing of departure from natal areas by golden eagles is not constrained by acquisition of flight skills. *J Avian Biol* 2023:e03111
- ✦ Holekamp KE (1986) Proximal causes of natal dispersal in Belding's ground squirrels (*Spermophilus beldingi*). *Ecol Monogr* 56:365–391
- ✦ Kenward RE, Marcström V, Karlbom M (1993) Post-nestling behaviour in goshawks, *Accipiter gentilis*. II. Sex differences in sociality and nest-switching. *Anim Behav* 46: 371–378
- ✦ Krüger S, Amar A (2017) Insights into post-fledging dispersal of bearded vultures *Gypaetus barbatus* in southern Africa from GPS satellite telemetry. *Bird Study* 64: 125–131
- ✦ Labocha MK, Hayes JP (2012) Morphometric indices of body condition in birds: a review. *J Ornithol* 153:1–22
- ✦ Lloyd P, Martin TE (2016) Fledgling survival increases with development time and adult survival across north and south temperate zones. *Ibis* 158:135–143
- ✦ López-López P, Gil JA, Alcántara M (2014) Post-fledging dependence period and onset of natal dispersal in bearded vultures (*Gypaetus barbatus*): new insights from GPS satellite telemetry. *J Raptor Res* 48:173–181
- ✦ Martens FR, Pfeiffer MB, Downs CT, Venter JA (2018) Post-fledging movement and spatial ecology of the endangered Cape vulture (*Gyps coprotheres*). *J Ornithol* 159: 913–922
- ✦ Martin TE (2014) A conceptual framework for clutch-size evolution in songbirds. *Am Nat* 183:313–324
- ✦ Martin TE (2015) Age-related mortality explains life history strategies of temperate and tropical songbirds. *Science* 349:966–970
- ✦ Marzluff JM, Knick ST, Vekasy MS, Schueck LS, Zarriello TJ (1997) Spatial use and habitat selection of golden eagles in southwestern Idaho. *Auk* 114:673–687
- ✦ Matthysen E (2005) Density-dependent dispersal in birds and mammals. *Ecography* 28:403–416
- ✦ McCaslin HM, Caughlin TT, Heath JA (2020) Long-distance natal dispersal is relatively frequent and correlated with environmental factors in a widespread raptor. *J Anim Ecol* 89:2077–2088
- ✦ McClure CJW, Westrip JR, Johnson A, Schulwitz SE and others (2018) State of the world's raptors: distributions, threats, and conservation recommendations. *Biol Conserv* 227:390–402
- ✦ Miller TA, Brooks RP, Lazone MJ, Cooper J and others (2017) Summer and winter space use and home range characteristics of golden eagles (*Aquila chrysaetos*) in eastern North America. *Condor* 119:697–719
- ✦ Mirski P, Cenian Z, Dagys M, Daroczi S and others (2021) Sex-, landscape- and climate-dependent patterns of home-range size — a macroscale study on an avian generalist predator. *Ibis* 163:641–657
- ✦ Morales JM, Moorcroft PR, Matthiopoulos J, Frail JL and others (2010) Building the bridge between animal movement and population dynamics. *Philos Trans R Soc B* 365: 2289–2301
- ✦ Morrison JL, Wood PB (2009) Broadening our approaches to studying dispersal in raptors. *J Raptor Res* 43:81–89
- ✦ Moss EH, Hipkiss T, Ecke F, Dettki H and others (2014) Home-range size and examples of post-nesting movements for adult golden eagles (*Aquila chrysaetos*) in boreal Sweden. *J Raptor Res* 48:93–105
- ✦ Nadjafzadeh M, Hofer H, Krone O (2016) Sit-and-wait for large prey: foraging strategy and prey choice of white-tailed eagles. *J Ornithol* 157:165–178

- ✦ Naef-Daenzer B, Gruebler MU (2016) Post-fledging survival of altricial birds: ecological determinants and adaptation. *J Field Ornithol* 87:227–250
- ✦ Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A movement ecology paradigm for unifying organismal movement research. *Proc Natl Acad Sci USA* 105:19052–19059
- Negro JJ, Sarasola JH, Barclay JH (2007) Augmenting wild populations and food resources. In: Bird DM, Bildstein KL (eds) *Raptor research and management techniques*. Hancock House, Surrey, p 401–410
- Newton I (1998) *Population limitation in birds*. Academic Press, London
- ✦ Patrick SC, Pinaud D, Weimerskirch H (2017) Boldness predicts an individual's position along an exploration–exploitation foraging trade-off. *J Anim Ecol* 86:1257–1268
- ✦ QGIS.org (2023) QGIS geographic information system. QGIS Association. www.qgis.org
- R Core Team (2024) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna
- ✦ Ramos RF, Silva JP, Carrapato C, Rocha P, Marques PAM, Palmeirim JM (2019) Spatial behaviour of Spanish imperial eagle *Aquila adalberti* juveniles during the dependence period revealed by high-resolution GPS tracking data. *J Ornithol* 160:463–472
- ✦ Rémy A, Le Galliard JF, Gundersen G, Steen H, Andreassen HP (2011) Effects of individual condition and habitat quality on natal dispersal behaviour in a small rodent. *J Anim Ecol* 80:929–937
- ✦ Rivers JW, Johnson JM, Haig SM, Schwarz CJ and others (2014) Resource selection by the California condor (*Gymnogyps californianus*) relative to terrestrial-based habitats and meteorological conditions. *PLOS ONE* 9:e88430
- ✦ Rudebeck G (1950) The choice of prey and modes of hunting of predatory birds with special reference to their selective effect. *Oikos* 2:65–88
- ✦ Russell EM, Yom-Tov Y, Geffen E (2004) Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. *Behav Ecol* 15:831–838
- ✦ Sarasola JH, Negro JJ, Travaini A (2004) Nutritional condition and serum biochemistry for free-living Swainson's hawks wintering in central Argentina. *Comp Biochem Physiol A Mol Integr Physiol* 137:697–701
- ✦ Sarasola JH, Santillán MA, Galmes MA (2010) Crowned eagles rarely prey on livestock in central Argentina: persecution is not justified. *Endang Species Res* 11:207–213
- ✦ Sarasola JH, Grande JM, Negro JJ (2018) *Birds of prey: biology and conservation in the XXI century*. Springer International Publishing, Cham
- ✦ Sarasola JH, Galmes MA, Watts BD (2020) Electrocution on power lines is an important threat for the endangered Chaco eagle (*Buteogallus coronatus*) in Argentina. *J Raptor Res* 54:166–171
- ✦ Sarasola JH, Gallego D, Martínez-Miranzo B (2022) Chaco eagle ecology and conservation. In: DellaSalla D, Goldstein MI (eds) *Imperiled: the encyclopedia of conservation*. Elsevier, Amsterdam, p 102–112
- ✦ Scherler P, Witczak S, Aebischer A, van Bergen V, Catitti B, Gruebler MU (2023) Determinants of departure to natal dispersal across an elevational gradient in a long-lived raptor species. *Ecol Evol* 13:e9603
- ✦ Serrano D (2018) Dispersal in raptors. In: Sarasola JH, Grande JM, Negro JJ (eds) *Birds of prey: biology and conservation in the XXI century*. Springer International Publishing, Cham, p 95–121
- ✦ Spatz T, Katzenberger J, Friess N, Gelpke C and others (2022) Sex, landscape diversity and primary productivity shape the seasonal space use of a migratory European raptor. *J Avian Biol* 2022:e02925
- ✦ Spiegel O, Leu ST, Bull CM, Sih A (2017) What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecol Lett* 20:3–18
- ✦ Steenhof K, Kochert MN, McIntyre CL, Brown JL (2017) Coming to terms about describing golden eagle reproduction. *J Raptor Res* 51:378–390
- ✦ Sur M, Duerr AE, Bell DA, Fisher RN and others (2020) Reliance of individual and environmental drivers of movement of golden eagles. *Ibis* 162:381–399
- ✦ Tanferna A, López-Jiménez L, Blas J, Hiraldo F, Sergio F (2013) Habitat selection by black kite breeders and floaters: implications for conservation management of raptor floaters. *Biol Conserv* 160:1–9
- ✦ Tucker MA, Alexandrou O, Bierregaard RO, Bildstein KL and others (2019) Large birds travel farther in homogeneous environments. *Glob Ecol Biogeogr* 28:576–587
- ✦ Walls SS, Kenward RE (1995) Movements of radiotagged common buzzards *Buteo buteo* in their first year. *Ibis* 137:177–182
- ✦ Weston ED, Whitfield DP, Travis JM, Lambin X (2018) The contribution of flight capability to the post-fledging dependence period of golden eagles. *J Avian Biol* 49:716–726
- ✦ Wiens JD, Noon BR, Reynolds RT (2006) Post-fledging survival of northern goshawks: the importance of prey abundance, weather, and dispersal. *Ecol Appl* 16:406–418
- ✦ Zimmermann SS (2021) *The early life of juvenile golden eagles (Aquila chrysaetos): sex and activity drive fledging time and pre-dispersal exploratory behaviour*. MSc thesis, Albert-Ludwig University, Freiburg

Editorial responsibility: Brendan Godley,

University of Exeter, Cornwall Campus, UK

Reviewed by: F. Angulo, V. Valiati and 1 anonymous referee

Submitted: April 7, 2025; Accepted: August 5, 2025

Proofs received from author(s): October 2, 2025

This article is Open Access under the Creative Commons by Attribution (CC-BY) 4.0 License, <https://creativecommons.org/licenses/by/4.0/deed.en>. Use, distribution and reproduction are unrestricted provided the authors and original publication are credited, and indicate if changes were made