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Biparental Care in a Generalist Raptor, the Chimango Caracara in Central Argentina

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ABSTRACT.—The allocation of parental care behaviors between the sexes may be influenced by the species' mating system, degree of sexual size dimorphism, and predictability of food resources. Biparental care (i.e., both parents contributing to raising young) has been documented in raptors, including those with minimal sexual size dimorphism and/or whose food resources are unpredictable in time (e.g., scavengers). The Chimango Caracara (*Milvago chimango*) is a common raptor with slight sexual size dimorphism and a scavenging lifestyle. During two breeding seasons, we performed focal observations at nests in a Chimango Caracara colony in central Argentina to assess the division of labor between the sexes. For males and females separately, we measured the time spent incubating and brooding, and the food delivery rate to nestlings; then we used GLMMs to assess various factors that may influence these behaviors, including parental sex, time of day, clutch or brood size, and nestlings' age. We used GLMMs to test the influence of time spent brooding and food delivery rate (both parents combined for these variables) on nest success and productivity. Although both sexes contributed to all parental care activities, females spent more time incubating and brooding than males. Brooding time decreased as nestlings aged. Food delivery rate did not differ between the sexes. Food delivery rate was higher during the middle of nestlings' development but declined thereafter. Nest success and productivity were higher at nests with higher food delivery rates. Adults spent more time incubating and brooding during morning and midday, and food delivery rate was higher during the afternoon.

KEY WORDS: *behavior; breeding biology; division of roles; food delivery rate; incubation; scavenger.*

CUIDADO BIPARENTAL EN UN RAPAZ GENERALISTA, MILVAGO CHIMANGO, EN EL CENTRO DE ARGENTINA

RESUMEN.—La división de roles entre sexos en el cuidado parental puede estar determinada por el sistema de apareamiento, el grado de dimorfismo sexual de tamaño y la predictibilidad de los recursos alimenticios. El cuidado biparental, en el que ambos progenitores contribuyen a la crianza de la descendencia, se ha documentado en rapaces, incluso en aquellas con escaso o nulo dimorfismo sexual de tamaño y/o cuyos recursos alimenticios son impredecibles en el tiempo, por ejemplo, las aves carroñeras. *Milvago chimango* es un ave rapaz común que presenta un ligero dimorfismo sexual de tamaño y tiene un estilo de vida carroñero. Durante dos temporadas reproductivas, se realizaron observaciones focales en los nidos de una colonia de *M. chimango* en el centro de Argentina para evaluar la división de

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tareas entre sexos. Para machos y hembras por separado, medimos el tiempo dedicado a la incubación y a la cría, y la tasa de aporte de alimento a los polluelos. Utilizamos modelos lineales generalizados mixtos (GLMM por sus siglas en inglés) para evaluar diversos factores que pueden influir en estos comportamientos, incluyendo el sexo de los progenitores, la hora del día, el tamaño de la puesta o la nidada, y la edad de los polluelos. Se utilizaron GLMM para comprobar la influencia del tiempo de cría y la tasa de aporte de alimento (de ambos adultos combinados) en el éxito y la productividad del nido. Aunque ambos sexos contribuyeron a todas las actividades de cuidado parental, las hembras pasaron más tiempo incubando y criando que los machos. El tiempo de cría disminuyó a medida que aumentaba la edad de los polluelos. No encontramos diferencias en la tasa de aporte de alimento entre sexos. La tasa de aporte de alimento fue mayor en la mitad del período de desarrollo del polluelo, pero disminuyó a partir de entonces. El éxito y la productividad de los nidos fueron mayores en los nidos con tasas de alimentación más elevadas. Los adultos pasaron un mayor porcentaje de tiempo incubando y cuidando a los polluelos durante la mañana y el mediodía, y la tasa de aporte de alimento fue mayor durante la tarde.

[Traducción de los autores editada]

INTRODUCTION

Parental care includes the group of behaviors performed by parents aimed at increasing offspring survival and, thus, parents' biological fitness (Clutton-Brock 1991, Royle et al. 2012, Mock 2022). In birds, parental care can have strong effects on reproductive parameters, which influence population dynamics and demography at a local scale (Newton 1998, Mock 2022). Parental care includes activities such as nest building, incubation, rearing of nestlings (provisioning and feeding), brooding and shading, nest defense, and partner-feeding (Clutton-Brock 1991, Mock 2022). Although most aspects of parental care in birds are usually performed by both members of a breeding pair, effort and activities differ between males and females in some species (Cockburn 2006, Webb et al. 2010). Equal sharing of parental duties (biparental care) is usually associated with monogamy (Lack 1968), and the absence of either color or size dimorphism (Remeš et al. 2015).

Among raptors, sex-specific division of parental care is often associated with the degree of sexual size dimorphism. Species with dramatic sexual size dimorphism usually exhibit the most extreme division of parental duties (i.e., the female incubates the eggs and broods and feeds the offspring, while the male provides the food; Remeš et al. 2015, Keeley and Bechard 2017). In contrast, among raptors exhibiting slight or no sexual size dimorphism, the division of parental care duties is often minimal (Margalida and Bertran 2000, Margalida et al. 2007, Rollack et al. 2013). Biparental care is predicted to occur when extensive care by both parents is necessary for successful rearing of young (Margalida and Bertran 2000) and when food is spatially and temporally unpredictable, as is the case for avian scavengers (Newton 1979, Margalida and Bertran 2000).

Parental care activities may vary during the 24-hr cycle and across the breeding season, and/or according to clutch size, brood size, and nestling age (Clutton-Brock 1991, Tinbergen and Williams 2002, Coe et al. 2015). For example, incubation, a key behavior that affects offspring survival, is influenced by environmental temperature (Nord and Nilsson 2016). Parents regulate egg temperature to optimize embryonic development and to ensure hatching (Haftorn 1988). Incubation behavior may differ during the 24-hr cycle due to changes in environmental temperature (Tinbergen and Williams 2002, Zuberogoitia et al. 2018) or predation risk (Fontaine and Martin 2006). Similarly, during the early nestling period, when nestlings cannot thermoregulate, parents adjust nest attentiveness behaviors such as brooding and/or shading in response to heat or cold stress (Coe et al. 2015, Clauser and McRae 2017). Additionally, parents may adjust feeding behaviors to the number and age of the nestlings (Collopy 1984, Clutton-Brock 1991). The energetic needs of nestlings change throughout their growth period, increasing until asymptotic growth has been reached and declining thereafter (Ricklefs 1968, Holthuijzen 1990).

Avian scavengers (e.g., vultures and some eagles) often exhibit minimal dimorphism and biparental care (Bassi et al. 2017, Morant Etxebarria et al. 2019). Understanding factors that influence parental care behaviors in avian scavengers should enhance our comprehension of their breeding biology. We studied parental care in the Chimango Caracara (*Milvago chimango*, hereafter chimango), an excellent model species because it is a generalist raptor/scavenger that shows minimal sexual-size dimorphism and is common across its geographic range (Solaro and Sarasola 2018, 2023). To date, no studies have examined parental care in the

chimango; thus, our specific objectives were to (1) describe nest-focused parental care across the incubation and nestling periods, (2) quantify possible sex-related differences in parental care behaviors, (3) examine whether parental care behaviors differ according to time of day, clutch or brood size, or nestlings' age, and (4) assess the influence of parental care behaviors on nest success and productivity.

METHODS

Study Area. We studied parental care behaviors at a breeding colony of Chimango Caracaras located in a 0.5 km² suburban residential area (La Cuesta del Sur; 36°43'S, 64°16'W) in La Pampa Province, Argentina. The colony consisted of approximately 80–90 nests each year (Solaro and Sarasola 2018, 2023). This suburban area has intense pedestrian and vehicular traffic, and the yards are characterized by small grass plots with native species such as *caldén* (*Neltuma caldenia*), *molle* (*Schinus fasciculatus*), and *chañar* (*Geoffroea decorticans*), and exotic species such as eucalyptus (*Eucalyptus* spp.) and pine (*Pinus* spp.). Situated in an ecotone between the Pampas (grasslands) and the Espinal (rough pastures, thorny bush and *caldén* forests) ecoregions, this area experiences hot and wet summers and cold and dry winters (Cabrera 1976). Average annual temperature and precipitation are 16°C and 600 mm, respectively. Sunrise during summer occurs between 0600–0630 H and sunset occurs between 2015–2045 H.

Study Species. The Chimango Caracara is one of the most abundant and common raptors in southern South America (Bierregaard et al. 2022). This generalist predator and facultative scavenger nests in a wide variety of habitats and exhibits little sexual size dimorphism, with females being only 10–20 g heavier (3–6%) than males (Solaro and Sarasola 2018, 2023). However, adult males and females are easily distinguished by sexual dichromatism of the exposed skin: the tarsi and cere are yellow in males and bluish and pinkish, respectively, in females (Sarasola et al. 2011). In central Argentina, chimangos lay 2–3 eggs in October, which are incubated for 26–32 d, starting with the first egg, and nestlings fledge at 32–41 d during December and January (Solaro and Sarasola 2015, 2023).

Data Collection. We studied Chimango Caracaras during two breeding seasons, from October through January (austral spring and summer) of 2016 and 2017. We located chimango nests during incubation, and we estimated hatching date by monitoring nests

every 3 d (Sutherland 2006). Monitoring ceased when nestlings fledged from the nest.

We performed focal observations at all nests using a spotting scope (20–60×), for 4–6 continuous hours during each observation period, at a distance of 40–50 m from each nest. Observations were performed by four different observers who were previously trained in recognition of the different parental care behaviors as well as in identification of male and female chimangos. During observation periods we recorded parental care behaviors at the nest, including incubation, brooding/shading, and food provisioning (Gaibani and Csermely 2007). To ensure a balanced distribution of field observations for different times of the day, we established three 5-hr time blocks: morning (0600–1059 H), midday (1100–1559 H), and afternoon (1600–2100 H) (Xirouchakki and Mylonas 2007). After each observation period, we waited until the adult left the nest to check nest status (i.e., number of eggs, number and age of nestlings) with a mirror pole to minimize disturbance to the breeding attempt. We used a photographic guide developed from observations made at nests with known hatching dates to visually estimate nestling age (J. H. Sarasola unpubl. data). We determined that a nest was successful if at least one nestling achieved 80% of mean age at first flight (Steenhof and Newton 2007), which is 30 d post-hatching for chimangos (Solaro and Sarasola 2023). Likewise, we defined productivity as the number of young that achieved that same age, 30 d post-hatching.

To understand division of labor between sexes, we calculated the percentage of time devoted to incubation by each parent as the time spent in incubation divided by the amount of time each parent was actually at the nest. Similarly, during the nestling period, we measured the percentage of time spent brooding/shading the nestling(s) by each parent, again taking into account the time each adult was at the nest. We calculated food delivery rates by dividing the number of food deliveries to the nest made by each parent by the total number of hours that the nest was observed. All time measurements were recorded using a stopwatch, to the nearest second.

Statistical Analyses. To examine the influence of several variables on the different parental care behaviors at nests, we used the following approach: for incubation, we modeled the percentage of time spent in incubation as a function of parental sex (male, female), time of day (morning, midday, afternoon), and clutch size, and the interactions of parental sex with time of day. For the nestling period, we modeled the percentage of time spent

Table 1. Reproductive parameters for Chimango Caracara nests observed during the breeding season in 2016 and 2017. Successful nests are those in which at least one young reached the age of 30 d post hatching. Fledgling success = percentage of hatchlings that reached that same age, the age at which we defined productivity, assuming those young actually fledged. Data are presented either as total number, or as mean \pm SE, and percentages are indicated as %.

Year	Nest Attempts	Clutch Size	Brood Size	Successful Nests <i>n</i> (%)	Number of Fledglings per Nest Attempt	Fledgling Success
2016	30	2.19 \pm 0.11	1.75 \pm 0.24	17 (56.7%)	0.80 \pm 0.62	71.3%
2017	40	2.32 \pm 0.18	1.87 \pm 0.13	23 (57.5%)	0.87 \pm 0.43	76.2%
Both	70	2.29 \pm 0.12 ^a	1.81 \pm 0.11 ^b	40 (57.1%)	0.84 \pm 0.58	74.3% ^c

^a *n* = 33 nests.

^b *n* = 37 nests.

^c *n* = 128 hatchlings.

brooding/shading as a function of parental sex, time of day, brood size, and nestling age, and the interactions of parental sex with time of day. Lastly, we modeled food delivery rate as a function of parental sex, time of day, brood size, and nestling age and the interaction of parental sex with time of day. When modeling food delivery rate, a quadratic term was included in addition to the linear term to test for a higher feeding rate at intermediate ages before the known pre-fledging period of weight reduction (Holthuijzen 1990, Galmes et al. 2018). Some nests were observed more than once in each year, but because we never observed the same nest during both the incubation and the nestling periods in the same year, and because most parents could not be identified from one year to another, we included nest identity and year (2016 or 2017), each as a random effect, in all models.

The percentage of time each adult spent in incubation and brooding/shading were modeled as response (dependent) variables with a beta distribution and link function logit. Food delivery rate was modeled as the response (dependent) variable with a Poisson distribution (checking for overdispersion in the model) and log link function. We performed generalized linear mixed models (GLMMs) using the package *glmmTMB* (Douma and Weedon 2019) for the models with incubation and brooding/shading, and the package *lme4* (Bates et al. 2015) for the models with food delivery rate.

We also wished to determine influence of care by both parents on nest success and productivity. Because we never observed the same nest during both the incubation and the nestling periods in the same year, we only modeled these parameters using behaviors performed during the nestling period. We combined the percentage of time spent brooding/shading for males and females (total brooding

time) and the number of food deliveries by both parents per hour of observation (total food delivery rate). We modeled nest success (binomial distribution, link function = logit) and productivity (Poisson, link function = log) using multivariate GLMMs with *lme4* (Bates et al. 2015). In all models, we added the estimated hatching date as a numeric variable (days from the first recorded hatching date of the colony of the season) to account for possible negative effects of breeding late in the nesting season for chimangos (Solaro and Sarasola 2023).

In all cases, we used automated model selection with the *MuMIn* package (Barton 2009), and models were compared based on Akaike's information criterion adjusted for small sample size (AIC_c, Burnham and Anderson 2004). If candidate models had Δ AIC_c \leq 2, they were considered to be equally plausible given the data. All statistical procedures were carried out using R statistical software (R Core Team 2021). Results are presented as mean \pm SE.

RESULTS

We conducted observations at a total of 70 Chimango Caracara nests during the two breeding seasons (30 in 2016, 40 in 2017), for a total observation time of 315 hr (Supplemental Material Table S1). Reproductive parameters were similar between the two years; nest success of the studied chimango population for both years combined was 57.1%, and 74.3% of all hatchlings reached the age when we assumed successful fledging (hatchling alive at 30 d post-hatching = fledgling success; Table 1). The first recorded hatching date of the colony was 7 November in 2016 and 11 November in 2017.

Division of Parental Roles. The best model that explained variation in the percentage of time spent incubating included parental sex and time of day

Table 2. Percentage of time spent in parental care behaviors by adult Chimango Caracaras, according to time of the day (morning: 0600–1059 H; midday: 1100–1559 H; afternoon: 1600–2100 H) and sex (♀ = female; ♂ = male; pooled = both sexes). Values are given as mean ± SE; *n* represents the number of nests observed during the specified time of day. All percentages are calculated based on the total time that either adult chimango was actually present at the nest. “Pooled” refers to percentages that were calculated based on the total time the nest was observed.

Time of Day	Sex and <i>n</i>	Parental Care Activities		
		Incubation (% Time)	Brooding (% Time)	Food Delivery Rate (Deliveries/hr)
Morning	♀	60.2 ± 11.0	72.9 ± 7.2	0.1 ± 0.1
	♂	39.8 ± 11.0	27.2 ± 7.2	0.2 ± 0.1
	Pooled	70.4 ± 7.3	24.4 ± 6.5	0.3 ± 0.2
	<i>n</i>	12	11	11
Midday	♀	55.0 ± 10.4	52.8 ± 14.1	0.3 ± 0.1
	♂	45.0 ± 10.4	47.3 ± 14.1	0.2 ± 0.1
	Pooled	73.9 ± 8.0	20.4 ± 9.8	0.5 ± 0.1
	<i>n</i>	10	12	12
Afternoon	♀	59.3 ± 9.6	45.6 ± 12.1	0.5 ± 0.1
	♂	40.7 ± 9.6	54.4 ± 12.1	0.6 ± 0.2
	Pooled	65.3 ± 9.5	15.4 ± 7.2	0.9 ± 0.1
	<i>n</i>	11	14	14

(Table S2). Females spent a greater percentage of time ($59.0 \pm 6.1\%$) incubating the eggs than males ($41.0 \pm 6.1\%$; Table 2). For both sexes combined, the percentage of time spent in incubation was higher during morning and midday than in the afternoon (Table 2).

The percentage of time spent brooding/shading nestlings was best explained by parental sex, time of the day, and age of the nestlings (Table 3, S3). Females spent a greater percentage of time brooding/shading nestlings ($58.4 \pm 8.6\%$) than males ($41.6 \pm 8.6\%$; Table 2). For both sexes combined,

the percentage of time devoted to brooding/shading was higher during morning and midday than during the afternoon (Table 2) and decreased with increasing age of the offspring (Table 3).

The best model to explain the variation in food delivery rates included the time of day, nestling age and the quadratic term of nestling age (Table 3, S4) but did not include sex, indicating that food delivery rates did not differ between males and females. For both sexes combined, food delivery rates were higher in the afternoon than in the morning and midday (Table 2). Also, the food delivery rate for

Table 3. Coefficient estimates and standard errors for each parameter from the top models explaining parental care behaviors of Chimango Caracara (percentage of time in incubation, percentage of time spent brooding/shading, and food delivery rate), as a function of the different covariates described at each stage, at nests in a suburban residential area in La Pampa Province, Argentina (*n* = 30 nests in 2016, 40 nests in 2017). Dash indicates that the covariate did not appear in the best model. NA indicates that the covariate was not included *a priori* in the model (i.e., during incubation, nestlings are not present and thus brood size and nestling age cannot be included). TOD indicates time of the day.

Variable	Incubation		Brooding/Shading		Food Delivery	
	Estimate	SE	Estimate	SE	Estimate	SE
<i>Sex</i> ^a : male	-0.923	0.321	-0.671	0.122	-	-
<i>TOD</i> ^b : morning	0.130	0.043	0.609	0.071	-0.694	0.331
<i>TOD</i> ^b : midday	0.171	0.032	0.389	0.057	-0.577	0.286
<i>Brood size</i>	NA	NA	-	-	-	-
<i>Nestling age</i>	NA	NA	-0.323	0.049	0.212	0.084
<i>Nestling age</i> ²	NA	NA	NA	NA	-0.014	0.002

^a Coefficient estimates for sex are relative to sex = female.

^b Coefficient estimates for TOD are relative to TOD = afternoon.

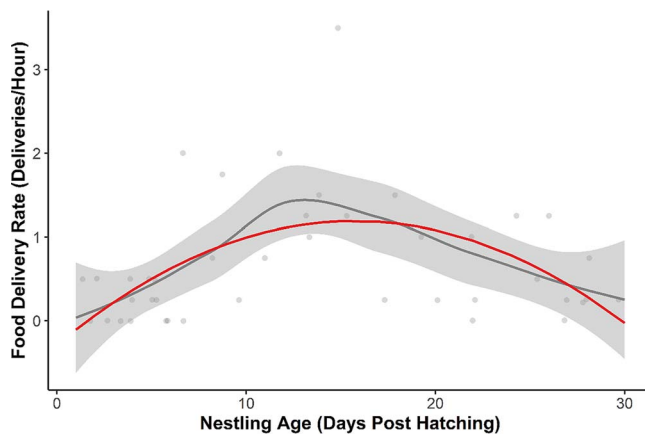


Figure 1. Food delivery rates for male and female Chimango Caracaras as a function of nestling age, at a breeding colony in a suburban area of central Argentina. Food delivery rates were calculated at 37 nest attempts observed during the combined breeding seasons of 2016 and 2017. The gray line corresponds to the predictions from the quadratic model, and the gray area corresponds to the 95% confidence interval. The red line represents a simulation of the quadratic relationship between the response variable (number of prey deliveries per hour) and the predictor variable (age of the nestlings).

both sexes combined (quadratic relationship) was lower during the early days of the nestling period, reached a peak during the middle of the nestling period, and declined thereafter (Fig. 1).

Effect of Parental Care Activities on Reproductive Parameters. The total percentage of time spent brooding/shading by both parents combined at nests observed throughout the nestling period had no apparent influence on nest success or productivity (Table S5, S6). However, both nest success (estimate: 1.75 ± 0.63) and productivity (estimate: 0.35 ± 0.12) were higher at nests where both parents delivered food at a higher rate.

Hatching date and year were not important variables in any of the final models for any analyses (Table S5, S6).

DISCUSSION

Ours is the first study of parental care behaviors in the Chimango Caracara. At the nests we observed, parental care efforts were independent of clutch or brood size, but both parents adjusted their behaviors to meet the age-specific needs of nestlings (Ricklefs 1968, Galmes et al. 2018). During daylight hours when they were actually at the nest, females allocated a greater percentage of time to incubation and to brooding/shading than males, similar to many other raptors, including avian scavengers (Newton 1979, Keeley and Bechard 2017). Food provisioning rates were similar for females and males, which is in line

with other scavenging raptors that show little sexual size dimorphism (Rollack et al. 2013).

Time spent brooding/shading by the parents decreased with nestling age, as predicted, similar to other avian scavengers (Margalida and Bertran 2000). When nestlings are newly hatched, the presence of adults at the nest is important to protect the young from predation, one of the main causes of offspring mortality in raptors (Newton 1998). As nestlings grow, their size may make them too large for certain predators, reducing the nestlings' need for parental protection. Similarly, during the first weeks after hatching, when nestlings cannot thermoregulate, regular protection from extreme temperatures by the adults is essential to their survival (Beecham and Kochert 1975, Visser 1998, Durant 2002).

Food provisioning rates were similar for both sexes, as has been shown for other scavenging raptors that show little sexual size dimorphism (Brunton 1988, Margalida and Bertran 2000, Rollack et al. 2013). Parental food delivery rates showed an overall quadratic relationship with nestling age, in line with other avian species (Ricklefs 1968, Holthuijzen 1990, Galmes et al. 2018). Food delivery rates increased with the nestling age during the first days post-hatching, likely due to higher energy demands of the nestlings during the early days of growth (Ricklefs 1968, Xirouchakis and Mylonas 2007). However, after the central days of the nestling period, food delivery rates declined. The most important energy requirements

of nestlings are a sum of maintenance (proportional to the age of the nestling) and growth rate (which decreases with the age of nestlings; Ricklefs 1968). Because maintenance is more costly when the nestling is more developed and maximum growth rates occur during the first days post-hatching, energetic requirements of nestlings will be higher during the central days of the nestling period (Ricklefs 1968); thus, parents adjust food delivery rates to meet those needs. Increasing energetic requirements of nestlings, together with decreasing needs for parental defense and brooding, may cause females initially focused on incubation and shading to devote more time to securing food, resulting in food delivery rates similar to those of males (Collopy 1984, Margalida and Bertran 2000). Finally, at our study nests, food delivery rate had a positive influence on nest success and productivity even after controlling for the possible effect of hatching date (Solaro and Sarasola 2023).

Both male and female chimangos devoted higher percentages of time spent at the nest to incubation and brooding during morning and midday and exhibited higher food provisioning rates during the afternoon. Birds increase the amount of time they spend at the nest when environmental temperatures fall because lowering egg temperatures for a prolonged period could reduce reproductive success (Clark and Wilson 1981, Webb 1987, Williams 1993). Chimango nestlings hatch during summer, when maximum temperatures (often $>35^{\circ}\text{C}$) are reached between 1600–1900 H, while early morning temperatures can fall to 12°C (Cabrera 1976). At our study nests, adult chimangos spent more time attending eggs and nestlings during the cooler part of the day likely to ensure optimized egg and nestling temperatures. Finally, food was delivered primarily during the afternoon. Along with scavenging, chimangos often feed on insects, which show increased activity during the afternoon and before sunset (Joern et al. 1986).

Although we provide new information about parental care in the Chimango Caracara, much of the life history of this common species remains unknown. We encourage further research to address knowledge gaps, particularly to evaluate reproductive success across larger regions of the species distribution. Improving our understanding of all aspects of the chimango's breeding biology across its broad geographic range may have benefits when addressing species-related conservation issues (Buechley and Şekercioğlu 2016, Peisley et al. 2017).

SUPPLEMENTAL MATERIAL (available online).

Table S1: Number of hours Chimango Caracara nests were observed during the breeding season in 2016 and 2017, by reproductive period (incubation

and nestling) and by time of the day: morning (0600–1059 H), midday (1100–1459 H), and afternoon (1500–2100 H). Table S2: Model selection results of GLMM explaining the percent of time adult Chimango Caracaras (*Milvago chimango*) spent incubating at nests in a suburban residential area in La Pampa Province, Argentina ($n = 30$ nests in 2016, 40 nests in 2017). Table S3: Model selection results of GLMM explaining the percent of time adult Chimango Caracaras (*Milvago chimango*) spent brooding/shading nestlings at nests in a suburban residential area in La Pampa Province, Argentina ($n = 30$ nests in 2016, 40 nests in 2017). Table S4: Model selection results of GLMM explaining food delivery rates by adult Chimango Caracaras (*Milvago chimango*) at nests in a suburban residential area in La Pampa Province, Argentina ($n = 30$ nests in 2016, 40 nests in 2017). Table S5: Model selection results of GLMM explaining nest success at Chimango Caracara (*Milvago chimango*) nests in a suburban residential area in La Pampa Province, Argentina. Analysis used nests observed only during the nestling period. Table S6. Model selection results of GLMM explaining nest productivity at Chimango Caracara (*Milvago chimango*) nests in a suburban residential area in La Pampa Province, Argentina. Analysis used nests observed only during the nestling period.

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LITERATURE CITED

- Barton, K. (2009). MuMIn: multi-model inference. <http://r-forge.r-project.org/projects/mumin/>.
- Bassi, E., P. Trotti, M. Brambilla, F. Diana, F. Sartirana, L. Galli, and L. Pedrotti (2017). Parental investment in two large raptors breeding in a high prey density area. *Journal of Ornithology* 158:549–559. doi:10.1007/s10336-016-1407-6.
- Bates, D., D. Mächler, D. B. Bolker, and S. Walker (2015). Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823. doi:10.48550/arXiv.1406.5823.
- Beecham, J. J., and M. N. Kochert (1975). Breeding biology of the Golden Eagle in southwestern Idaho. *Wilson Bulletin* 87:506–513.

- Bierregaard, R. O., G. M. Kirwan, and P. F. D. Boesman (2022). Chimango Caracara *Daptrius chimango*, version 1.1. In *Birds of the World* (N. D. Sly, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bow.chicar1.01.1.
- Brunton, D. H. (1988). Sexual differences in reproductive effort: Time-activity budgets of monogamous Killdeer, *Charadrius vociferus*. *Animal Behaviour* 36:705–717. doi:10.1016/S0003-3472(88)80153-2.
- Buechley, E. R., and Ç. H. Şekercioğlu (2016). The avian scavenger crisis: Looming extinctions, trophic cascades, and loss of critical ecosystem functions. *Biological Conservation* 198:220–228. doi:10.1016/j.biocon.2016.04.001.
- Burnham, K. P., and D. R. Anderson (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research* 33:261–304. doi:10.1177/0049124104268644.
- Cabrera, A. (1976). Regiones fitogeográficas argentinas. In *Enciclopedia Argentina de Agricultura y Jardinería* (W. F. Kugler, Editor) ACME, Buenos Aires, Argentina. pp. 1–85.
- Clark, A. B., and D. S. Wilson (1981). Avian breeding adaptations: Hatching asynchrony, brood reduction, and nest failure. *Quarterly Review of Biology* 56:253–277. doi:10.1086/412316.
- Clauser, A. J., and S. B. McRae (2017). Plasticity in incubation behavior and shading by King Rails *Rallus elegans* in response to temperature. *Journal of Avian Biology* 48:479–488. doi:10.1111/jav.01056.
- Clutton-Brock, T. H. (1991). *The Evolution of Parental Care*. Princeton University Press, Princeton, NJ, USA.
- Cockburn, A. (2006). Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B: Biological Sciences* 273:1375–1383. doi:10.1098/rspb.2005.3458.
- Coe, B. H., D. L. Beck, S. Y. Chin, C. D. B. Jachowski, and W. A. Hopkins (2015). Local variation in weather conditions influences incubation behavior and temperature in a passerine bird. *Journal of Avian Biology* 46:385–394. doi:10.1111/jav.00581.
- Collopy, M. W. (1984). Parental care and feeding ecology of Golden Eagle nestlings. *The Auk* 101:753–760. doi:10.2307/4086902.
- Douma, J. C., and J. T. Weedon (2019). Analysing continuous proportions in ecology and evolution: A practical introduction to beta and Dirichlet regression. *Methods in Ecology and Evolution* 10:1412–1430. doi:10.1111/2041-210X.13234.
- Durant, J. D. (2002). The influence of hatching order on the thermoregulatory behaviour of Barn Owl *Tyto alba* nestlings. *Avian Science* 2:167–173.
- Fontaine, J. J., and T. E. Martin (2006). Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters* 9:428–434. doi:10.1111/j.1461-0248.2006.00892.x.
- Gaibani, G., and D. Csermely (2007). Behavioral studies. In *Raptor Research and Management Techniques* (D. M. Bird and K. L. Bildstein, Editors). Hancock House Publishers, Blaine, WA, USA. pp. 117–128.
- Galmes, D. A., J. H. Sarasola, J. M. Grande, and F. H. Vargas (2018). Parental care of the endangered Chaco Eagle (*Buteogallus coronatus*) in central Argentina. *Journal of Raptor Research* 52:316–325. doi:10.3356/JRR-16-82.1.
- Haftorn, S. (1988). Incubating female passerines do not let the egg temperature fall below the 'physiological zero temperature' during their absences from the nest. *Ornis Scandinavica* 19:97–110. doi:10.2307/3676458.
- Holthuijzen, A. D. A. (1990). Prey delivery, caching, and retrieval rates in nesting Prairie Falcons. *The Condor* 92:475–484. doi:10.2307/1368244.
- Joern, A., R. Mitschler, and H. O'Leary (1986). Activity and time budgets of three grasshopper species (Orthoptera: Acrididae) from a sandhills grassland. *Journal of the Kansas Entomological Society* 59:1–6.
- Keeley, W. H., and D. J. Bechard (2017). Nesting behavior, provisioning rates, and parental roles of Ferruginous Hawks in New Mexico. *Journal of Raptor Research* 51:397–408. doi:10.3356/JRR-16-85.1.
- Lack, D. (1968). *Ecological Adaptations for Breeding in Birds*. Chapman and Hall, London, UK.
- Margalida, A., and J. Bertran (2000). Breeding behaviour of the Bearded Vulture *Gypaetus barbatus*: Minimal sexual differences in parental activities. *Ibis* 142:225–234. doi:10.1111/j.1474-919X.2000.tb04862.x.
- Margalida, A., L. D. González, R. Sánchez, J. Oria, and L. Prada (2007). Parental behaviour of Spanish Imperial Eagles *Aquila adalberti*: Sexual differences in a moderately dimorphic raptor. *Bird Study* 54:112–119. doi:10.1080/00063650709461462.
- Mock, D. W. (2022). Parental care in birds. *Current Biology* 32:R1132–R1136. doi:10.1016/j.cub.2022.07.039.
- Morant Etxebarria, J., P. López-López, and I. Zuberogoitia Arroyo (2019). Parental investment asymmetries of a globally endangered scavenger: Unravelling the role of gender, weather conditions and stage of the nesting cycle. *Bird Study* 66:329–341. doi:10.1080/00063657.2019.1688251.
- Newton, I. (1979). *Population Ecology of Raptors*. T and AD Poyser Ltd., Berkhamsted, UK.
- Newton, I. (1998). *Population Limitation in Birds*. Academic Press, San Diego, CA, USA.
- Nord, A., and J. Å. Nilsson (2016). Long-term consequences of high incubation temperature in a wild bird population. *Biology Letters* 12:20160087. doi:10.1098/rsbl.2016.0087.
- Peisley, R. K., M. E. Saunders, W. A. Robinson, and G. W. Luck (2017). The role of avian scavengers in the breakdown of carcasses in pastoral landscapes. *Emu-Austral Ornithology* 117:68–77. doi:10.1080/01584197.2016.1271990.
- R Core Team (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Remeš, V., R. P. Freckleton, J. Tökölyi, A. Liker, and T. Székely (2015). The evolution of parental cooperation in birds. *Proceedings of the National Academy of Sciences* 112:13603–13608. doi:10.1073/pnas.1512599112.

- Ricklefs, R. E. (1968). Patterns of growth in birds. *Ibis* 110:419–451. doi:[10.1111/j.1474-919X.1968.tb00058.x](https://doi.org/10.1111/j.1474-919X.1968.tb00058.x).
- Rollack, C. E., K. Wiebe, D. J. Stoffel, and C. S. Houston (2013). Turkey Vulture breeding behavior studied with trail cameras. *Journal of Raptor Research* 47:153–160. doi:[10.3356/JRR-12-40.1](https://doi.org/10.3356/JRR-12-40.1).
- Royle, N. J., P. T. Smiseth, and D. Kölliker (2012). *The Evolution of Parental Care*. Oxford University Press, Oxford, UK.
- Sarasola, J. H., J. J. Negro, D. J. Bechard, and A. Lanusse (2011). Not as similar as thought: Sexual dichromatism in Chimango Caracaras is expressed in the exposed skin but not in the plumage. *Journal of Ornithology* 152:473–479. doi:[10.1007/s10336-010-0606-9](https://doi.org/10.1007/s10336-010-0606-9).
- Solaro, C., and J. H. Sarasola (2015). Nest-spacing, not human presence, influences the breeding of Chimango Caracaras (*Milvago chimango*) in a peri-urban reserve. *Emu* 115:72–75. doi:[10.1071/MU14038](https://doi.org/10.1071/MU14038).
- Solaro, C., and J. H. Sarasola (2018). Natal dispersal and philopatry of Chimango Caracaras (*Milvago chimango*) in suburban, rural and natural habitats, determined by band recovery and re-sighting data. *Emu* 118:158–165. doi:[10.1080/01584197.2017.1321961](https://doi.org/10.1080/01584197.2017.1321961).
- Solaro, C., and J. H. Sarasola (2023). Breeding performance is explained for coloniality and phenology but not for urbanization in a generalist raptor bird. *Urban Ecosystems* 26:743–753. doi:[10.1007/s11252-022-01319-3](https://doi.org/10.1007/s11252-022-01319-3).
- Steenhof, K., and I. Newton (2007). Assessing nesting success and productivity. In *Raptor Research and Management Techniques* (D. M. Bird and K. L. Bildstein, Editors). Hancock House. Blaine, WA, USA. pp. 181–192.
- Sutherland, W. J. (2006). *Ecological Census Techniques: A Handbook*. Cambridge University Press, Cambridge, UK.
- Tinbergen, J. D., and J. B. Williams (2002). Energetics of incubation. In *Avian Incubation: Behavior, Environment and Evolution* (D. C. Deeming, Editor). Oxford University Press, Oxford, UK. pp. 299–313.
- Visser, G. H. (1998). Development of temperature regulation. In *Avian Growth and Development: Evolution within the Altricial – Precocial Spectrum* (J. D. Starck and R. E. Ricklefs, Editors). Oxford University Press, Oxford, UK.
- Webb, D. R. (1987). Thermal tolerance of avian embryos: A review. *The Condor* 89:874–898. doi:[10.2307/1368537](https://doi.org/10.2307/1368537).
- Webb, T. J., V. A. Olson, T. Székely, and R. P. Freckleton (2010). Who cares? Quantifying the evolution of division of parental effort. *Methods in Ecology and Evolution* 1:221–230. doi:[10.1111/j.2041-210X.2010.00027.x](https://doi.org/10.1111/j.2041-210X.2010.00027.x).
- Williams, J. B. (1993). Energetics of incubation in free-living Orange-Breasted Sunbirds in South Africa. *The Condor* 95:115–126. doi:[10.2307/1369392](https://doi.org/10.2307/1369392).
- Xirouchakakis, S. D., and D. Mylonas (2007). Breeding behaviour and parental care in the Griffon Vulture *Gyps fulvus* on the Island of Crete (Greece). *Ethology Ecology and Evolution* 19:1–26. doi:[10.1080/08927014.2007.9522578](https://doi.org/10.1080/08927014.2007.9522578).
- Zuberogoitia, I., J. E. Martínez, M. Larrea, and J. Zabala (2018). Parental investment of male Peregrine Falcons during incubation: Influence of experience and weather. *Journal of Ornithology* 159:275–282. doi:[10.1007/s10336-017-1503-2](https://doi.org/10.1007/s10336-017-1503-2).

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