

Breeding Performance and Effects of Nest Site Features on Nest Survival of Chestnut-Capped Blackbird *Chrysomus ruficapillus* (Passeriformes: Icteridae)

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The Chestnut-capped Blackbird *Chrysomus ruficapillus* is a neotropical species that nests in wetlands, which are abundant in South America. However, many of these wetlands face threats of disappearance and degradation, with potential consequences for the species inhabiting them. Here, we carried out a detailed study of the breeding biology of this species and examined variables that influence daily nest survival rates (DSR). We described nest site features, nest morphometry, breeding parameters, estimated the growth curves of nestlings, and recorded the causes of nest failure. We evaluated the effects of nest site features, nest morphometry, nest age and timing of breeding season on the DSR of Chestnut-capped Blackbirds. We expected that DSR would increase with greater nests and higher nest concealment at the beginning of the breeding season. Additionally, we predicted that larger nests would have higher nest survival. We studied the breeding performance of 138 nests in a wetland in central Argentina over three consecutive breeding seasons. Nests were placed 80 ± 21.53 cm above the water. The clutch size was 2.75 ± 0.67 eggs ($n = 84$ nests), and the brood size was 2.28 ± 0.79 nestlings ($n = 49$ nests). The most frequent cause of nest failures was predation (60%). The daily nest survival rate (DSR) was 0.96, and the cumulative probability of nest survival in a 29-day breeding cycle was 0.31 ($n = 85$ nests). As expected, we found a positive association between nest height above the water and DSR, suggesting that nests built further away from the water have increased survival rates. However, we found no effects of nest morphometry or the timing of breeding season on DSR. We emphasize the importance of understanding the breeding performance and the influence of nest site features on the survival of species inhabiting wetlands to implement actions to conserve and protect the population.

Key words: Breeding cycle, Daily survival rates, Neotropical region, Icteridae

BACKGROUND

Nest survival in birds, a crucial aspect of breeding success, is susceptible to multiple factors. Identifying these factors is vital for understanding

their life histories, habitat preferences, and population dynamics (Zurita et al. 2017; Barocas et al. 2023) and for informing conservation strategies for bird species (Kolada et al. 2009; Anteau et al. 2012). In particular, it is important to study the factors affecting wetland

species that are vulnerable to numerous threats arising from the degradation of these ecosystems (Webb et al. 2010; Barocas et al. 2023).

Factors influencing nest survival may be related to: i) breeding adults, such as adult age and breeding experience (Moreno-Rueda 2003), body condition (Öst and Steele 2010) and nest defense behaviors (Remeš 2005; Brussee et al. 2016), ii) nest predators, such as nest predator abundance (Vazquez and Amico 2023; Browne et al. 2023) and type of predator (Remeš 2005), and iii) environmental conditions, related to the moment of the breeding cycle (Grant et al. 2005), the nest features (Mainwaring et al. 2014), weather conditions (Mwangi et al. 2018; Grudinskaya et al. 2022), and food availability (Mwangi et al. 2018; Grames et al. 2023).

Nest-site features are thought to play an important role in the breeding performance of birds. Many studies have indicated that nest-site features are positively associated with nest survival (Remeš 2005; Newlon and Saab 2011; Mainwaring et al. 2014). A nest that is well-covered by vegetation and positioned relatively high above the ground may reduce the chances of predators visually locating it and help evade terrestrial predators (Remeš 2005; Graña Grilli and Montalti 2014). This, in turn, increases the probability of nest survival (Fernández and Mermoz 2000). Several hypotheses have been proposed to explain how nest site selection reduces predation. The total-foliage hypothesis (or nest concealment hypothesis) predicts that predation will decline in areas with greater overall vegetation density, as this reduces nest detection chances by some predators (Martin 1993; Borgmann and Conway 2015). This hypothesis has been supported by numerous studies. For instance, Zhao et al. (2020) found a positive relationship between nest concealment and nest survival in Chinese grouse (*Tetrastes sewerzawi*), suggesting that this species may be select nesting sites to avoid visual avian predators. Similarly, Liu et al. (2021) showed a strong and positive association between nest concealment and nest survival across all studied species on the Tibet Plateau. However, some studies report that nest-site features do not significantly influence nest survival (Burhans et al. 2002; Fogarty et al. 2017; Smith et al. 2018). Most studies suggest that such differences depend on predator type (e.g., olfactory vs. visual). Species facing olfactory and nocturnal predators (e.g., reptiles and mammals) may experience decreased breeding performance when these predators reach their nests (Berkunsky et al. 2011; Oswald et al. 2020). Another important variable potentially associated with nest survival and breeding performance is nest morphometry. Most studies describe nest size using length and width as key parameters (Heenan and Seymour 2011; Windsor et al. 2013; Lambrechts et al. 2017). The previous

studies suggest that the species with larger nests tend to have larger clutch sizes (Slagsvold 1989; Wiebe and Swift 2001). Larger nests may offer advantages, such as better temperature and humidity regulation, reduced overcrowding of offspring, easier cleaning, and a lower risk of offspring falling out of the nest (Møller et al. 2014). The clutch size hypothesis proposes that larger nests can accommodate more eggs and nestlings compared to smaller nests, assuming a similar mean egg size among individuals (Suárez et al. 2005; Møller et al. 2014). Thus, breeding performance is often positively associated with nest size (Windsor et al. 2013; Møller et al. 2014). Despite these advantages, large nests may also carry risks, as their increased size can make them more easily detectable to visual predators (Soler et al. 1998; de Neve and Soler 2002; Mainwaring et al. 2014).

In addition, the variables that affect nest survival and breeding performance can change throughout the breeding season (Grant et al. 2005). Nest survival may increase as the breeding season advances because of increased vegetation cover providing greater nest concealment (Little et al. 2015; MacDonald et al. 2016). Conversely, nest survival may decrease due to an increase in the community of predators (Martin 2002; Liebezeit et al. 2009). As nest density usually increases in the middle of the breeding season attracting more nest predators, nest survival may be higher for earlier and later nests (Weintraub 2013; Shitikov et al. 2018). The effect of high density in the middle of the breeding season may also be beneficial, as predators have access to other prey in addition to specific species (Smith and Wilson 2010). Moreover, reduced predation may be explained by nest defense; in colonial species, a greater number of adults may be vigilant about nests and warn about predators (Welty 2010; Magrath et al. 2010). Concomitantly, these variables that change as the season progresses also vary with the age of the nest, which may affect nest survival. For instance, the most vulnerable nests are lost early in incubation (Dinsmore et al. 2002), and daily nest survival may decrease during incubation (Grant et al. 2005). This decline may result from adult birds leaving cues when they visit their nests, which predators can use to locate them (Skutch 1985; Conway and Martin 2000; Martin et al. 2000). Therefore, we consider these variables essential for explaining bird nest survival. Understanding these factors allows us to identify temporal patterns that enhance our knowledge of predator-prey interactions, avian life histories, and other aspects of population dynamics (Grant et al. 2005).

Finally, breeding is often considered to be the most demanding life history moment for birds. During the breeding season, the parents must maximize both their own and their offspring's survival by regulating

the trade-off in energy, time, and effort (Lack 1968; Stearns 1992). Most bird species exhibit asynchronous hatching within a clutch, with hatching occurring over 24 hours or more, leading to the establishment of a brood hierarchy (Lack 1954). Asynchronous hatching generally occurs when incubation starts before the last egg is laid, making the timing of the start of incubation a key factor in controlling the competitive hierarchy within avian broods (Ricklefs 1993; Lord et al. 2011; Węgrzyn et al. 2023). In passerines, females usually start incubating when the penultimate egg is laid (Nice 1954; Wang and Beissinger 2009; Skutch 2021). This hatching pattern creates a size-age hierarchy within broods, where later-hatched nestlings are disadvantaged in competitive situations due to their smaller size, younger age, and delayed development compared to their earlier-hatched siblings (Mock and Parker 1997; Soler 2001; Scott Johnson et al. 2009). Therefore, evaluating this variation is important for understanding nestling development rates, their conditions, and offspring fitness (Roff 1996; McCarty 2001).

In this study, we examined the variables that may influence the nest survival of the Chestnut-capped Blackbird (*Chrysomus ruficapillus*). This icterid species is common and locally abundant in South America. It inhabits freshwater marshes and reedy lake margins from French Guiana to Argentina (Fraga 2020). Like some other icterid species, they build their nests in emergent aquatic vegetation, where the distance between the nest and the water likely increases the probability of survival. Additionally, the vegetation in marshes is usually abundant, which may provide greater concealment for the nests from visual predators (Graña Grilli and Montalti 2014; Fraga 2020). In Argentina, the breeding season extends from October to March, with the highest concentration of nests occurring in the early months of the season (De la Peña 2015). First, we estimated the species' descriptive breeding parameters and nestling growth curves. Second, we evaluated if daily nest survival rates (DSR) were affected by nest site features, nest morphometry and time-specific variables. We expected that nest survival would increase in higher nests with higher nest concealment at the beginning of the breeding season. Additionally, we predicted that larger nests would have higher nest survival.

MATERIALS AND METHODS

Study area and specie

This study was undertaken in a wetland of the Middle Parana River in Santa Fe province, Argentina (31°38'10"N, 60°40'31"W). The area corresponds

to a University Ecological Reserve managed by the Universidad Nacional del Litoral of Argentina and the Foundation for Habitat and Development of Argentina. This wetland spans 20 hectares and features a dynamic water regime, with permanent water bodies and semipermanent areas during drought seasons. It lies within the Delta and Islands of the Paraná River ecoregion (Burkart et al. 1999), characterized by heterogeneity that sustains rich biodiversity (Morrone 2001). The climate is subtropical-humid, with mean annual temperatures around 19°C (Iriondo et al. 2007).

The study area includes different types of habitat following the criteria proposed by Lorenzón et al. (2016), such as open water, floating macrophytes (e.g., *Pistia stratiotes*, *Salvinia* spp.), emergent macrophytes (e.g., *Echinochloa* sp., *Sagittaria montevidensis*), shrublands (e.g., *Solanum glaucophyllum*, *Sesbania virgata*) and gallery forests (e.g., *Erythrina crista-galli*, *Salix humboldtiana*, *Tessaria integrifolia*).

Additionally, potential nest predators in our study area include the southern crested caracara (*Caracara plancus*), roadside hawk (*Rupornis magnirostris*), guira cuckoo (*Guira guira*), great kiskadee (*Pitangus sulphuratus*), and American kestrel (*Falco sparverius*); snakes (e.g., *Philodryas* spp.); and rodents (e.g., *Oxymycterus* spp.).

During the 2015–2016 period, the area was affected by extreme climatic conditions associated with the El Niño phenomenon, which caused abundant precipitation, intense storms and flooding (Contreras et al. 2021; Aliaga and Piccolo 2021). During this period, the principal lagoon expanded in area and increased in depth. The water levels significantly decreased at the end of 2017, and the drought continued until October 2018. Beginning in November 2018, the water levels experienced a rapid rise, ranging from 20 cm to 1.5 m. Consequently, parts of the marshes were populated by emergent macrophytes (e.g., *Echinochloa* sp.) that persisted until the water levels decreased at the end of summer.

The Chestnut-capped Blackbird is an omnivorous passerine. Its diet includes seeds, insects, spiders, and can also feed on cultivated rice seeds (Del Barco et al. 2006; Fraga 2020). This species inhabits wetlands, marshes, rice fields, wet grasslands and agricultural fields, and it invades recently flooded areas. The species is sexually dichromatic and dimorphic in size. Male Chestnut-capped Blackbirds (18.5 cm, 41.3 g) are black overall with a chestnut crown and throat, while females are olivaceous brown, faintly streaked with dusky (17.1 cm, 32.2 g) (Fraga 2020). This species is gregarious in all seasons, colonial in its breeding habits, and polygynous. During breeding season, males sing and built nests to exhibit themselves to females.

If a female accepts a nest, she lines it with thin fibers. Some nests, however, are not selected by any female, so they remain unfinished and the occupied ones. These unoccupied nests may be deeper than occupied nests (Jaramillo and Burke 1999; Fraga 2020). Females incubate and mainly feed the nestlings, while males defend colonies against predators (Fraga 2020). Furthermore, the species is parasitized by the Shiny Cowbird (*Molothrus bonariensis*), with approximately 50% of nests being parasitized in Argentina (Blanco 1995; Lyon 1997).

Nest monitoring and breeding parameters

We searched for active nests during three breeding seasons (September to January of 2016–2017, 2017–2018, and 2018–2019). On discovery, nests were monitored every 1–2 days from the start of the egg-laying stage until either failure or fledging of the young. We defined a nesting attempt as successful when at least one nestling fledged. Failed nests were those that were completely lost during the incubation or nestling stage (Martin and Geupel 1993). We calculated the average and range of clutch size (number of eggs per nest when the clutch is complete), the average and range of brood size (number of nestlings hatched), and the average and range of brood size at fledging (number of nestlings fledged that were alive at the time of fledging).

If nests were found during the building stage, we monitored them to determine the date of clutch initiation (the day the first egg was laid). In cases where clutch initiation dates were unknown, we established them indirectly by calculating the time elapsed since hatching dates for nests found during the incubation stage. We defined the duration of the breeding season as the interval between the earliest and the latest laying dates (Weatherhead 2005; Vengerov 2012). To estimate breeding cycle duration, we summed three components: 1) the laying stage duration, calculated from the beginning of the first egg when the clutch was completed; 2) the incubation stage duration, calculated from the beginning of incubation (when the clutch was completed) to the hatching of the first egg (determined only for those nests for both egg laying and hatching dates were known); and 3) the nestling stage, calculated from the hatching of the first egg to the fledging of the first nestling (determined when the day of fledging was known).

Eggs were numbered with indelible ink according to their order of appearance. Maximum length (A) and breadth (B) were measured with a caliper (to the nearest 1 mm). Egg mass was measured with a weighing scale during each visit the laying stage (precision of 0.1 g). Egg volume (V) was calculated using the formula

provided by Hoyt (1979): $V = 0.541AB^2$. To estimate egg size and weight at the population level, we use the average egg size for each nest with a complete to avoid pseudoreplication. To describe the nestling's growth, we took measures such as body mass (weighing scale with a precision of 0.1 g), length of the beak, head + beak, wing, tarsus, tibia, and total body length at different nestling ages using a caliper (to the nearest 1 mm) and a precision scale (precision of 0.1 g). These measurements were made at ages 0 to 3, 4 to 7, and 8 to 11 days after hatching. Hatchlings were marked with indelible ink of different colors on their legs to establish their hatching sequence, and they were weighed every 2 days. Nestlings were assigned letters corresponding to their hatching order, so that nestling A was the first to hatch out, nestling B the second, and so on (C). They were monitored until fledging. Close to the fledging age, we approached cautiously to avoid premature abandonment of the nest. At older ages, we confirmed the nestlings' presence but did not remove them from the nest for measurements.

Nests were classified according to the type of failure: I) predated nests, when eggs and/or nestlings disappeared between consecutive visits and there was no more parental activity near the nest; II) deserted nests without recognizable causes, when eggs were cold or nestlings were dead, and no further parental activity was observed; III) weather-affected nests when cold eggs or dead nestlings were found following weather events such as rain or storms; and IV) deserted nests due to brood parasitism, when all eggs in parasitized nests were damaged, and no further parental activity was observed. When possible, dead nestlings were collected for subsequent laboratory analysis (e.g., diet).

Nest morphometry and nest site features measurements

We recorded nest morphometry based on external width and length, as well as its depth as well egg chamber, measured using a ruler and a measuring tape (to the nearest 1 cm).

We measured nest height above the water using a measuring tape (to the nearest 1 cm), and identified each nest support plant. Nest concealment was determined by assessing its visibility from a distance of 1 m in each of the four cardinal directions (N, E, S, W) as well as from directly above. If the nest was visible, it was assigned the value 1. These five measurements were averaged to generate a concealment index for each nest, with values ranging from 0 (completely concealed, not visible from any of the five sides) to 1 (completely visible, visible from all sides) (King et al. 1998). All measurements were performed by the same observer to ensure

consistency.

Data analysis

Three breeding performances were assessed: A) hatching success, defined as the proportion of eggs that hatched from eggs that survived to the end of incubation; B) fledging success, defined as the proportion of nestlings present in the nest on the last check before fledging; and C) breeding success, defined as the proportion of nesting attempts in which at least one young fledged. A nesting attempt was classified as successful if at least one host young fledged.

We estimated the frequency of parasitism as the proportion of parasitized nests and the intensity of parasitism at the incubation stage as the number of parasitic eggs per nest.

For different analyses, we used nest morphometry variables, including the external width, external length, and depth of the nest, and nest site features, such as the height above the water and nest concealment. Moreover, we used clutch size and brood size as breeding parameters.

We tested for differences in breeding parameters between breeding seasons using the non-parametric Kruskal-Wallis test (Kw).

We modeled the daily nest survival rates (DSR) of Chestnut-capped Blackbird using the RMark package (Laake 2013), which interfaces with Program MARK (White and Burnham 1999). DSR was modeled as a function of the nest site features, nest morphometry, nest age (day 0 = date on which the first egg in the clutch was laid), and time of breeding (the first egg of each nest was laid, compared to the date the first egg was laid in the season; day 1 = 01 October) (Dinsmore et al. 2002). We evaluated relationships between independent variables using the Spearman correlation coefficient (r). Since $r < 0.70$ in all cases, no variable was removed from the analysis. We used Akaike's Information Criterion adjusted for small sample size (AICc) to compare competing models of Chestnut-capped Blackbird nest survival and to select the best-fitting model (Burnham and Anderson 2002). The AICc weight of a model (WeightAICc, w_i) indicated the relative likelihood that specific model is the best of all tested models (Burnham and Anderson 2002). The effects of covariates on a model were considered meaningful when the 95% confidence intervals of β coefficients did not overlap zero.

To assess whether there were significant differences in nestlings' body mass among different hatching orders, an analysis of variance (ANOVA) was conducted. Before performing the ANOVA, homogeneity of variances and normality of residuals

were checked. Post hoc Tukey tests (Tukey's honest significant difference test) were conducted for pairwise comparisons between nestlings. We used non-linear mixed models (NLMM) (nlme package; Pinheiro and Bates 2022) to estimate nestling growth curves for body mass as a function of nestling age. The curves were fitted to Richard's equation (Tjørve and Tjørve 2017). Richard's model using parameterization A , K , ti , and d , where A is the upper asymptote (*i.e.*, predicted adult size), K maximum relative growth rate, ti age at the inflection point, and D shape parameter (Tjørve and Tjørve 2017). We modeled body mass growth and estimated the curves for each hatching order, considering nestling and nest identity as random effect factors to estimate curve parameters (Svigelj et al. 2019). Nestlings showing signs of starvation were excluded for growth analyses.

We considered an alpha of 0.05 for decision making on variables effects. All values are reported as means \pm SD.

RESULTS

Breeding parameters

During the three breeding seasons, a total of 138 nests of Chestnut-capped Blackbird were monitored (4 in 2016–2017, 16 in 2017–2018, and 118 in 2018–2019). The earliest clutch was initiated on October 1, and the latest on December 28. The peaks of clutch initiation occurred in November and December (Fig. 1).

The breeding cycle of the Chestnut-capped Blackbird lasted 29.07 ± 1.12 days. The egg-laying stage lasted 3.09 ± 0.42 days ($n = 84$ nests), the incubation stage lasted 13.25 ± 1.20 days ($n = 84$ nests), and the nestling stage lasted 13 ± 0.73 days ($n = 49$ nests).

Clutch size was 2.75 ± 0.67 eggs per nest (mode = 3, range = 1–4, $n = 84$ nests). Clutch size did not vary significantly among years (KW = 2.41, $df = 2$, $p = 0.30$). Egg dimensions were as follows: the maximum length was 22.75 ± 1.31 mm, the greatest breadth was 16.21 ± 9.81 mm, the mean volume was 30.27 ± 2.33 cm³, and the egg mass was 3.29 ± 0.40 g ($n = 224$ eggs from 84 nests).

Brood size was 2.28 ± 0.79 nestlings per nest (mode = 3, range = 1–3; $n = 49$ nests). Brood size (2016–2017 and 2018–2019 of breeding seasons) did not vary significantly between years (KW = 0.09, $df = 1$, $p = 0.76$). In the 2017–2018 breeding season, none of the nests reached the nestling stage.

Brood size at fledging was 1.60 ± 0.64 fledglings per nest (mode = 1, range = 1–3; $n = 38$ nests). Brood size (2016–2017 and 2018–2019 of breeding seasons)

did not vary significantly between years (KW = 1.20, *d.f.* = 1, *p* = 0.27).

The mean body mass for the hatching orders A, B, and C were 11.52 ± 7.32 g (range: 1.80–31.00 g), 9.93 ± 5.63 g (range: 2.05–27.00 g), and 6.65 ± 4.33 g (range: 1.70–17.00 g), respectively. The body mass of nestlings varied significantly across these hatching orders ($F = 6.88$, *d.f.* = 2, *p* = 0.0001). Post hoc comparisons using Tukey’s HSD test revealed that there was no significant difference between the body masses of A and B nestlings (*p* = 0.23). However, significant differences were found between A and C (*p* = 0.0009) and between B and C nestlings (*p* = 0.05).

By fitting Richard’s curves to the body mass data of the Chestnut-capped Blackbird nestlings, we estimated the growth parameters for each hatching order (Table 1). These parameters were then used to

predict the growth curves at different ages (Fig. 2). The estimated body masses at hatching for nestlings A, B, and C are 1.76 g, 1.71 g, and 1.67 g, respectively. The curve indicates that few C nestlings (marginal nestlings) survive beyond seven days in the nest (Fig. 2). We sampled regurgitated and the stomach contents of dead nestlings found in the nests (*n* = 4). The items identified included seeds of *Echinochloa* sp., insects (Odonata, Diptera, Coleoptera, Hymenoptera and Orthoptera), and Mollusca.

Nest morphometry and nest site features

The nests were cup-shaped, built by males using wet plant fibers intertwined and lined with aquatic plants. Nest external height, external width, and depth measured 11.55 ± 2.01 cm (range = 9–18 cm), 11.54

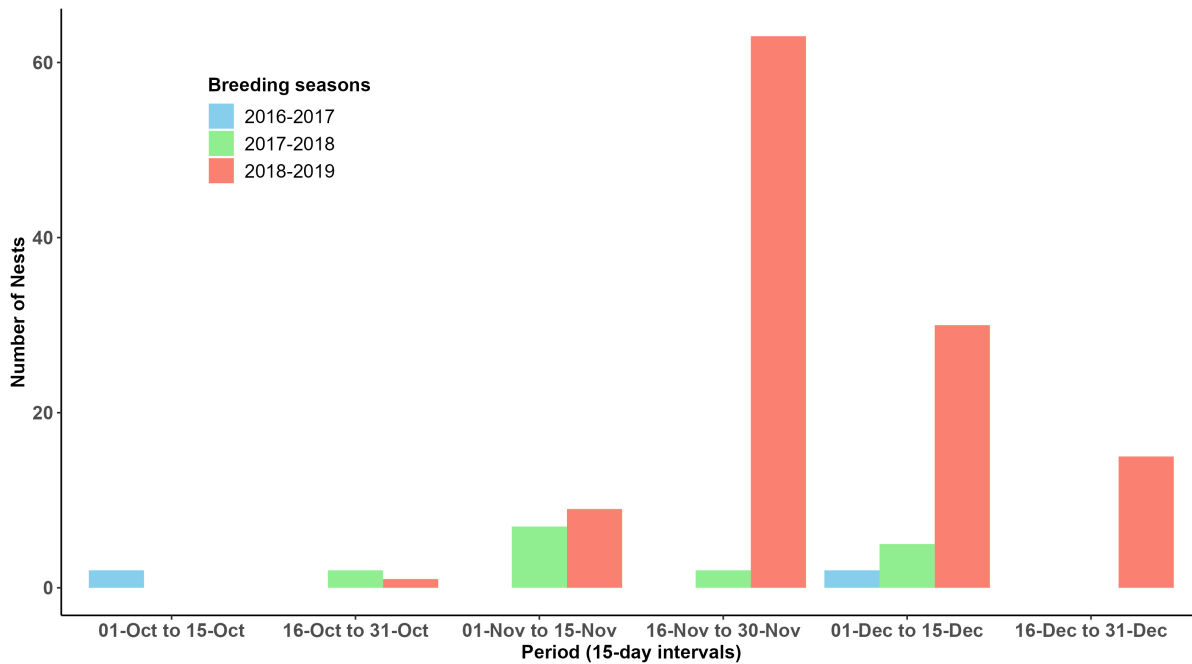


Fig. 1. Distribution of Chestnut-capped Blackbird (*Chrysomus ruficapillus*) nests initiated each month during three breeding seasons (2016–2019) in a wetland in Argentina.

Table 1. Richard’s growth curve parameters for body mass of Chestnut-capped Blackbird (*Chrysomus ruficapillus*) (*n* = 109 nestlings from 51 nests). Hatching order of the nestlings: A was the first to hatch out (*n* = 105 nestlings), nestling B the second (*n* = 71), and C the ultimate (*n* = 30)

Hatching order of nestlings	A	K	<i>t</i> _i	<i>d</i>	RD
A-order	36.21 ± 4.16	0.17 ± 0.05	7.13 ± 0.48	1.06 ± 0.30	1.33
B-order	33.97 ± 7.65	0.16 ± 0.09	6.46 ± 0.68	0.98 ± 0.20	1.30
C-order	22.51 ± 7.84	0.37 ± 0.29	5.75 ± 0.72	1.78 ± 1.15	0.84

A = upper asymptote, *t*_i = time in days when maximum growth was reached, K = maximum relative growth rate; *d* = shape parameter, and RD = residual standard deviation for the predicted curve. Values are presented as mean ± SD.

± 1.83 cm (range = 8–17 cm), and 7.91 ± 1.30 cm (range = 5–13 cm; $n = 138$ nests), respectively. The support plant used in the first two seasons was primarily *Solanum glaucophyllum*. In the last season (2018–2019), 54% of the nests were built on this species, while other plant species were incorporated, including *Schoenoplectus californicus* (7%), *Solanum pilcomayense* (4%), *Persicaria punctatum* (6%), and *Senecio bonariensis* (1%). Furthermore, 28% of the nests were built using more than one plant species for support, often combining the species mentioned above with *Echinochloa* sp. The height above the water level was 80 ± 21.53 cm (range = 38–150 cm), with a nest concealment of 0.52 ± 0.33 (range = 0.2–1; 138 nests).

Breeding performance and causes of nest failures

The mean hatching success per nest during the breeding season was 0.46 ± 0.43 (46%), and

fledging success per nest was 0.32 ± 0.40 (32%). Breeding success was 0.44 ± 0.50 (44%). DSR in the constant model was 0.96 ± 0.08 ($n = 85$ nests), and the probability of nest survival throughout the entire 29-day cycle breeding was 0.31 (31%).

During the first two breeding seasons (2016–2017, 2017–2018), six nests with eggs were monitored, of which four were parasitized by the Shiny Cowbird. The frequency of parasitism was 67% (4/6 nests) with an intensity of parasitism of 2.25 ± 0.96 eggs per nest (range = 1–3). However, during the 2018–2019 breeding season, when the greatest number of nests was recorded ($n = 118$), no parasitic eggs were found. Egg punctures or parasite nestlings were also absent. All four parasitized nests were abandoned, likely after receiving parasitic eggs.

We found 53 nests during the building stage (with fresh material) that later did not proceed to lay, which were not considered failures. Among these nests, 41 were located near nests with laying, and in addition,

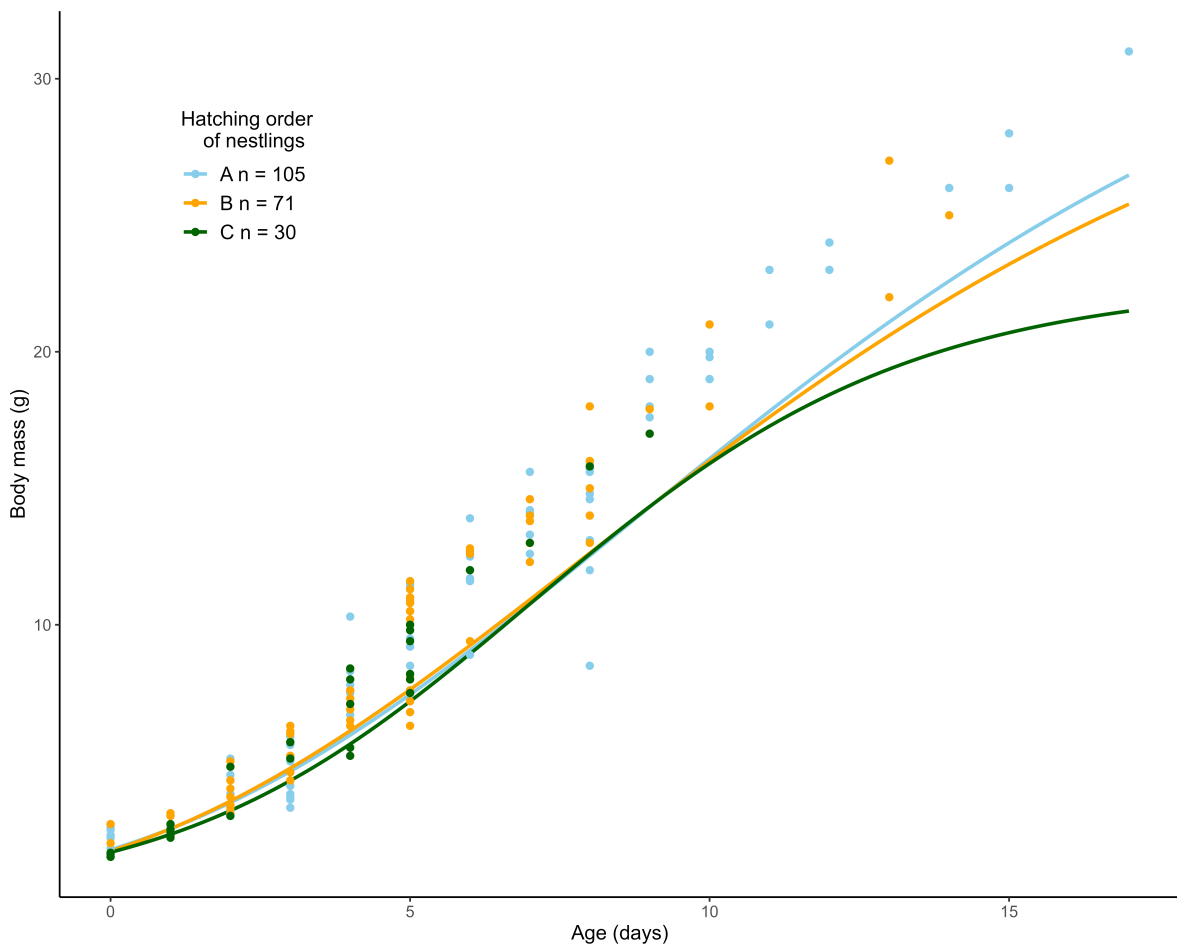


Fig. 2. Growth curve for body mass of Chestnut-capped Blackbird (*Chrysomus ruficapillus*) nestlings. Growth curves were obtained from non-linear mixed models applied to the Richards equation ($n = 109$ nestlings from 51 nests). The lines depict growth by the order of hatching (fixed effects), whereas the points show individual nestlings.

many other nests without laying were observed adjacent to active nests that were not included in the count. During 2017–2018, we found 12 nests in different stages of building. None of the 12 nests were occupied, coinciding with Chestnut-capped adults leaving the study area.

Of the 85 remaining nests, 38 (45%) were successful, while 47 (55%) failed due to different causes. The most frequent cause of nest failures was predation ($n = 28$, 60%), followed by desert for unknown causes ($n = 10$, 21%), adverse weather conditions ($n = 5$, 11%), and desert due to brood parasitism ($n = 4$, 8%). Among the failed nests, 36 (77%) failed during the laying incubation stages while 11 (23%) failed during the nestling stage.

Factors influencing nest survival

The best model was the one that included the height above the water level in modeling DSR (Table 2), and this effect different from zero and was positive ($\beta \pm SE$: 0.014 ± 0.007 ; 95% CI: 0.00002–0.02851). The rest of the candidate models that included nest concealment, variables of nest morphometry or temporal effects had no important effect on nest survival (Table 2).

DISCUSSION

In this study, conducted in a wetland in central Argentina, we provide detailed data on the breeding parameters, nest site features, nest morphometry, and nestling growth rates of the Chestnut-capped Blackbird (*Chrysomus ruficapillus*). We also found low nest survival in our study site. Our findings support the prediction that the height of the nest above the water

is a relevant factor associated with nest survival. However, contrary to our prediction, nest concealment, nest morphometry and time of breeding season had no effects on nests of Chestnut-capped Blackbird.

The breeding season length of the Chestnut-capped Blackbird was similar to that recorded in rice paddies (Bello Fallavena 1987; Cirne and López-Iborra 2005) but shorter than in natural wetlands (Costa et al. 2020). These differences may be based on geographic factors. These differences may stem from geographic factors, as the study conducted in Brazil’s tropical climate featured a more favorable and prolonged breeding season (Costa et al. 2020). Moreover, ecological factors such as the availability of support plants, food resources, and fluctuations in water levels may influence the length of the breeding season. In rice paddies, clutch initiation is tied to the growth of rice plants (Bello Fallavena 1987; Cirne and López-Iborra 2005). According to our findings, the 2018–2019 breeding season length may be associated with the growth of *Echinochloa* sp., a key resource for the species. This plant served as both nest support and food source for adults (pers. observ.; Bello Fallavena 1987; Del Barco et al. 2006) and nestlings (as observed in this study).

The average clutch size registered in this study was slightly lower than those reported in studies in natural ecosystems (Klimaitis 1973; Canavelli 1994; Di Giacomo 2005) and similar to studies in rice paddies in Brazil (Cirne and López-Iborra 2005). A modal clutch size of three eggs is common among South American icterids (Jaramillo and Burke 1999). It coincides with a smaller clutch expected for southern temperate species compared with North Hemisphere species (Martin et al. 2000). The morphometry measurements of eggs fall into the reported range (De la Peña 2015).

Our study revealed that early-hatched nestlings

Table 2. Results of models for daily nest survival of Chestnut-capped Blackbird (*Chrysomus ruficapillus*) in Argentina during three breeding seasons (2016–2019), including a null model of constant survival (S(.)). Model with greater support than the null model is in bold

Model	K	AIC _c	ΔAIC _c	w _i	Deviance	Change in Deviance
S(~Height)	2	279.09	0.00	0.390	275.08	-4.15
S(~.)	1	281.23	2.14	0.134	279.23	0.0
S(~NestAge)	2	281.63	2.54	0.109	277.62	-1.61
S(~Time)	2	281.73	2.65	0.104	277.72	-1.51
S(~Conc)	2	282.35	3.27	0.076	278.34	-0.88
S(~Depth)	2	282.36	3.28	0.757	278.35	-0.87
S(~ExtHeight)	2	282.79	3.70	0.061	278.77	-0.45
S(~ExtWidth)	2	283.19	4.10	0.050	279.18	-0.05

K = number of parameters estimated in a model, AIC_c = Akaike Information Criterion (corrected for small sample sizes), ΔAIC_c = differences in AIC_c between models, w_i = model importance weight, Deviance = likelihood difference between each model and the saturated model (hypothetic model with perfect fit), Change in Deviance = the difference between the deviance of a models and the deviance of a null model.

(A–B) reached a larger body mass and showed higher asymptotes and inflexion points in their growth curves than late-hatched nestlings (C-nestlings). Late-hatched nestlings frequently exhibited signs of starvation, making them more vulnerable within the nest and contributing to their lower survival rates. Similarly, in Brazil, Cirne and López-Iborra (2005) found the poorest nestling conditions in the youngest nestlings. Several studies have shown that hatching asynchrony may decrease growth rates (Tuero et al. 2018; Wawrzyniak et al. 2020). Moreover, nestling growth can be influenced by various factors such as food availability, the number of siblings, sex, breeding season, weather conditions, parental age, and quality (Gebhardt-Henrich and Richner 1998; Badyaev et al. 2002; Massemin et al. 2002). These findings are expected because hatching asynchrony in birds influences body mass and, as a consequence, growth rate.

In our study, we found that the nesting success of the Chestnut-capped Blackbird was lower than previously reported (Klimaitis 1973; Cirne and López-Iborra 2005; Costa et al. 2020). These differences may be attributed to variations in nesting sites (wetlands vs. rice paddies), weather conditions, or differences in the composition of the predator community. For example, studies on other *Chrysomus* species, such as the Yellow-hooded Blackbird (*C. icterocephalus*) in Venezuela's llanos showed that nesting success depends on the wet season when food availability and vegetation are abundant (Cruz and Andrews 1989). In addition, Neotropical species generally have lower nesting success than Nearctic species (Martin 1993 1996; Wiersma et al. 2007; Kleindorfer 2007). This trend is likely due to higher predation rates and greater predator diversity in the tropics and Southern Hemisphere (Martin et al. 2006; Menezes and Marini 2017; Matysioková and Remeš 2022). Therefore, the low nesting success may be due to the high predation rate, nest site availability and weather conditions that preclude finding safe nesting sites (Mezquida 2004; Menezes and Marini 2017).

Nest site features observed in this study were similar to previous descriptions (Klimaitis 1973; Cirne and López-Iborra 2005; De la Peña 2015). However, the height of the nest above the water was slightly lower than data reported for natural environments (Klimaitis 1973; Olguín 2017). Like other icterid species, nests were built on low branches, concealed in vegetation, and protected from aerial predators (Graña Grilli and Montalti 2014; Mermoz and Reboreda 1998). Furthermore, overlapping nests were found as mentioned in Klimaitis (1973) and Canavelli (1994). However, the function of these nests with greater external height and depth is unknown. On the

other hand, there were nests built in unsuitable plant species (e.g., *Echinochloa* sp., *Persicaria punctatum*) that were damaged by the fall of these plants during extreme weather conditions (windstorms and rainfall). Previous studies on the Brown-and-yellow Marshbird (*Pseudoleistes virescens*) reported that building nests in certain support plants like exotic thistles, influenced breeding success because some nests fell off their plant supports (Mermoz and Reboreda 1998). Similarly, in the Chestnut-capped Blackbird, the choice of plant species for nest building may affect loss of clutch and/or its nest survival.

Shiny cowbirds (45–50 g; Tuero et al. 2013) parasitized a high frequency (67%) of Chestnut-capped blackbirds (38 g) during the first two breeding seasons and were absent in the following season (≈ 200 total nests). Lyon (1997) reported a high frequency of parasitism in colonies with 10 to 30 nests. In contrast, other studies indicated a low frequency of parasitism (Klimaitis 1973; Canavelli 1994; Cirne and López-Iborra 2005; Costa et al. 2020). Most nests containing parasite eggs were abandoned, consistent with observations by Klimaitis (1973), who suggested that nest abandonment by the female may be a response to the presence of parasitic eggs.

Nest height above the water was positively associated with nest survival, with nests positioned higher above the water exhibiting increased daily survival rates (DSR). Nest predation may vary with nest height, depending on the composition of the predator community in the area (Martin 1988; Menezes and Marini 2017). For instance, avian predators may have difficulty detecting lower nests (Remeš 2005), whereas such nests are more vulnerable to predators that rely on olfactory cues, such as snakes (Kleindorfer et al. 2005; Colombelli-Négrel and Kleindorfer 2009). Previous studies have identified avian predators as threats to this species (Cirne and López-Iborra 2005). Another factor to consider is the distance from the water to the nest. If the water level increases, the nest becomes more vulnerable. In November 2018, the water level in the lagoon of the Ecological Reserve started to increase by 30 cm to 1.5 m. This gradual growth led to the loss of low nests at the beginning of the breeding season (mostly without laying). Toward the end of the breeding season, nests close to the water surface were at risk of becoming wet and flooded. Therefore, nest height in the Chestnut-capped Blackbird may be influenced by both the predatory community and changes in water levels. Further studies are needed to ascertain the critical factors contributing to nest site isolation and protection.

Contrary to expectations, nest concealment and the timing of the breeding season did not affect daily survival rates (DSR). The vegetation covers at our study

site, which remained consistent throughout the breeding season, may have contributed to the lack of variation in DSR between different levels of nest exposure and between earlier and later nests. Additionally, this result might be explained by nest defense behavior. Previous studies have reported that communal mobbing by blackbirds reduces predation risk (Fernández and Mermoz 2000; Yasukawa et al. 2020; Lawson et al. 2023). We suggest that Chestnut-capped Blackbirds can significantly reduce predation rates by defending their nests. Our results also showed no relationship between nest size and DSR. The similarity in blackbird nest architecture suggests that there may be no significant impact on the likelihood of egg survival and the successful fledging of offspring (Lambrechts and Deeming 2024).

CONCLUSIONS

This study enhances our understanding of the biology and breeding success of Chestnut-capped Blackbirds (*Chrysomus ruficapillus*) nesting in natural marshes and rice paddies. Our findings demonstrate that nest height above water is a critical factor associated with nest survival. This insight highlights the importance of identifying nest-site characteristics favorable for breeding in natural wetlands. Given that many wetlands in our region have been modified, we underscore the significance of understanding nesting preferences to support the conservation of species that depend on these habitats. Furthermore, we propose using this species as an ecological indicator to assess wetland conditions and the impacts of environmental changes. This information can also guide the development of conservation and management strategies to mitigate the damage caused by this species in rice paddies.

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