# Temporal variation in the reproductive success of *Cacicus haemorrhous* (Linnaeus) (Aves, Icterinae) in an Atlantic Forest reserve in Southeast Brazil

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ABSTRACT. For colonial bird species, egg hatching synchrony has been considered an important factor in their reproductive success. The Red-rumped Cacique, *Cacicus haemorrhous* (Linnaeus, 1766), is a Passeriformes species (Icterinae) that reproduces in colonies in which groups of females lay their eggs at different periods during the reproductive season. The objective of this study was to evaluate if there was a variation in the reproductive success among *C. haemorrhous* females groups that lay eggs in different periods along the reproductive season. A total of 192 nests from four colonies were monitored at Parque Estadual do Rio Doce, Minas Gerais state, Brazil, and used to calculate the nest survival probability in different periods (early and late) of the 2001 reproductive season. The results showed that females that reproduced at the beginning of the reproductive period had higher reproductive success than those that reproduced later. Predation was the main cause of nests loss (48,4%), and an increase in predation rate was observed as the reproductive period advanced.
KEY WORDS. Birds, hatching synchrony.

RESUMO. **Variação temporal no sucesso reprodutivo de *Cacicus haemorrhous* (Linnaeus) (Aves, Icterinae) em uma reserva de Floresta Atlântica no sudeste do Brasil.** Para espécies de aves coloniais a sincronia de eclosão dos ovos tem sido considerada um fator que influencia o sucesso reprodutivo. O Guaxe, *Cacicus haemorrhous* (Linnaeus, 1766), é uma espécie de Passeriformes (Icterinae) que se reproduz em colônias com grupos de fêmeas fazendo a postura em diferentes períodos ao longo da estação reprodutiva. O objetivo deste estudo foi avaliar se há uma variação no sucesso reprodutivo de *C. haemorrhous* entre esses grupos de fêmeas que fazem a postura em diferentes períodos ao longo da estação reprodutiva. Quatro colônias totalizando 192 ninhos foram monitoradas no Parque Estadual do Rio Doce, Minas Gerais, Brasil, calculando-se a probabilidade de sobrevivência dos ninhos em relação a diferentes períodos (cedo e tardio) ao longo da estação reprodutiva de 2001. Constatou-se que fêmeas que reproduziram mais cedo na estação reprodutiva obtiveram maior sucesso reprodutivo do que fêmeas que reproduziram mais tarde. A predação foi a principal causa de perda de ninhos (48,4%), sendo observado um aumento nas taxas de predação com o avanço da estação reprodutiva.
PALAVRAS CHAVE. Mata Atlântica, sincronia de eclosão, sucesso reprodutivo.

According to Brown (1975), the ecological consequences of individual spacing or grouping behavior must be studied in order to detect and estimate the selection pressures affecting individuals within a population. Brown (1975) reports that the wide generality of evolutionary convergence in social systems suggests that individual behaviors in a social system are susceptible to selection pressures.

Seasonal declines in reproductive success have been particularly well documented in birds (Wittenberger & Hunt 1985, Daan *et al*. 1990, Westneat 1992). This decline may be related to the breeding timing, but may also be caused by variation in phenotypical quality between earlier and late breeders (Verhulst *et al*. 1995). Westneat (1992) reports that in *Agelaius phoeniceus* (Linnaeus, 1766) (Icterinae) females reproducing earlier in the season obtained a higher total reproductive success in the seasons monitored. According to Westneat (1992), breeding synchrony is widely thought to be a population' adaptative response to consistent ecological conditions, however, there is considerable uncertainty about which ecological factors are most important. The choice of the best relative moment to reproduce may be important when age and prior occupancy play a role in territory establishment (Sandell & Smith 1991). To understand the role of phenotypical variations in the reproductive period in an evolutionary context, it is necessary to establish if there is a causal relationship between reproduction timing and reproductive success (Daan *et al*. 1990, Hochachka 1990).

The red-rumped cacique (*C. haemorrhous*) is an exclusively Neotropical Icterinae species that occurs throughout the Amazon Region; southeast and central-west of Brazil; east of the Andes; Colombia; Paraguay and northeast Argentina (Parkes 1970, Sick 1997). It inhabits humid tropical forests, including deciduous and gallery forests. It is common in canopies and forest edges, river banks and clearings (Feekes 1981, Ridgely & Tudor 1989). It is a species that reproduces in colonies, weaving nests in a bag form, suspended from the extremity of branches from tall and smooth trunk trees in the middle of the forest and forest edges or in branches suspended over water (Feekes 1981, Sick 1997). In colonies with a large number of nests it is possible to observe groups of females laying eggs at different periods during the reproductive season (Duca & Marini 2004), and showing different levels of temporal aggregation.

The objective of this study was to evaluate if there is variation in the reproductive success among *C. haemorrhous* females groups that lay eggs in different periods during the reproductive season.

## MATERIAL AND METHODS

### Study area

The study was conducted in Parque Estadual do Rio Doce (PERD), Minas Gerais State, located between 19º48'-19º29'S and 42º38'-48º28'W, in the Rio Doce Valley, southeast Brazil. The Park has 35,974 ha area, with altitudes varying from 230 to 515m above sea level (Cetec 1981 *apud* Tundisi & Saijo 1997). The presence of 38 lakes occupying 6% of the Park's total area characterize the landscape. The climate is humid tropical, with a rainy season from October to March, and a dry season from April to September.

According to Veloso *et al*. (1991) the Park vegetation is named "Sub-mountainous Semi-deciduous Seasonal Forest". Outside the Park's limits, there is a predominance of *Eucalyptus* spp, and also pasture lands, agricultural land and forest fragments (Sif 1990).

### Data collection

Four colonies were monitored at three-day intervals during the reproductive season of 2001. A map of the colonies location was elaborated, in which each nest was plotted and received an identification number. During visits, nests' contents were inspected. For each nest, the following data were recorded: initial and final nest construction dates; eggs' laying and hatching, dates and the dates when the nestlings left the nest, or when the nest was either abandoned or predated. This monitoring objetive was to evaluate nests' success.

Nests were considered successful when at least one nestling left the nest. Nests that were found empty without any sign of damage in their structure caused by predation, and those with nestlings aged over 21 days were considered successful. When found empty before the nestling's age of 21 days, usually presenting traces of predatory actions, such as damage to nest structure, blood traces and/or feathers, the nest was considered predated. Nests containing dead nestlings with signs of aggression, such as injuries and beak marks, were also considered predated. Nests were considered abandoned when eggs remained (intact) in the nest for more than 25 days. Nests found with dead nestlings without any signs of aggression were considered abandoned. Other causes of nestling losses were nest falling and nest destruction due to rainfall or other unknown factors. Nests abandoned before eggs were layed were not considered in the reproductive success analysis.

### Data analyses

Each of the four colonies monitored was divided into two periods: early period and late period, creating groups of females according to the laying date. Those females which laid within the first 15 days counted from the day of the record of the first egg, were grouped into the early period, and those females which laid from the $16^{th}$ day onwards were grouped into the late period. For each of these two periods, the following were calculated: nest survival during incubation (%NsI); nest survival during nestling period (%NsN) and nest survival from start of incubation to fledgling (%Ns), according to Mayfield's (1961, 1975) protocol.

For three of the four colonies monitored it was possible to establish more than two periods of laying. The "late period" of these three colonies was divided into three sub-periods, forming four periods (early, late 1, late 2 and late 3). The first three periods (early, late 1 and late 2) corresponded to the first three two-week periods, counting from the day the first females layed an egg. The fourth period (late 3) corresponded to the group of females that laid 45 days (6 weeks) after the first egg was laid. For each period it was also calculated nest survival probabilities (Mayfield 1961, 1975).

### Statistical analyses

The Mann-Whitney was applied to evaluate if there is any significant difference between nest survival probabilities (%Ns) of the females, which reproduced in different periods (early and late) during the reproductive season. This test was also applied to assess if eggs survival probability (%SnI) was different from the nestling survival probability (%NsN) referring to each of the two periods (early and late) previously considered.

To evaluate if nest survival probability (%Ns) was significantly different when considering four periods (early, late 1, late 2 and late 3) in the reproductive season, a Kruskall-Wallis test was applied. This same test was used to verify if there was a significant difference in the predation rate between the four periods previously considered.

To check if the relation between success and failure in the two different periods (early and late) was the same in forest and swamp habitats, a Fisher Exact Test was applied.

A level of significance equal to 5% was applied to test if there is any relation among the variables. All tests were applied according to OTT (1988) and TRIOLA (1999) and conducted in a Statistica statistical package (STATSOFT 1995).

## RESULTS

Females of period 1 (early) had significantly higher reproductive success than females of period 2 (late) (Mann-Whitney, Z = 2.309, p = 0.021) (Tab. I, Fig. 1). This was also observed when the late period was sub-divided generating four sub-periods (Kruskall-Wallis, H = 52.006, d.f. = 3, p < 0.001), reinforcing the previous analysis (Tab. II, Fig. 2). Thus, those females that reproduced earlier in the reproductive season presented higher success than those that reproduced later.

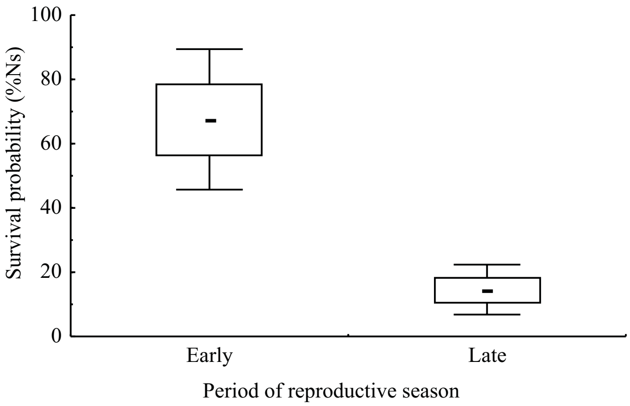


Figure 1. *Cacicus haemorrhous* nests survival probability (%Ns) from start of incubation to fledgling at two periods (early and late) in the reproductive season.

Table I. Number of unsuccessful and successful nests and nest survival probability (%Ns) of *Cacicus haemorrhous* from egg laying to fledgling period with regard to different groups of females at different periods (early and late) of egg laying.

| Colony | Period | Number of failed nests | Number of successful nests | %Ns |
|---|---|---|---|---|
| 1 | Early | 6 | 10 | 62,80 |
| | Late | 13 | 2 | 10,13 |
| 2 | Early | 8 | 6 | 43,97 |
| | Late | 16 | 1 | 6,26 |
| 3 | Early | 1 | 26 | 96,77 |
| | Late | 38 | 9 | 18,68 |
| 4 | Early | 12 | 17 | 66,68 |
| | Late | 20 | 7 | 23,26 |

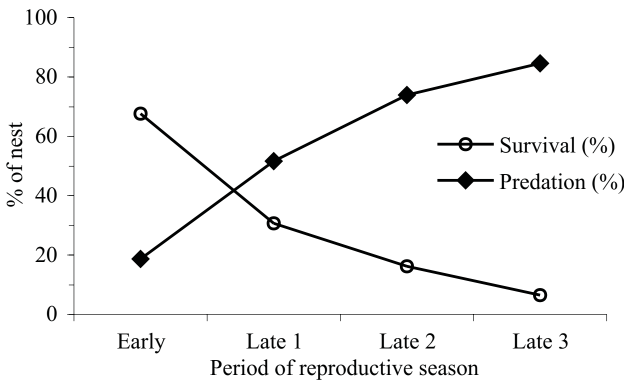


Figure 2. Nest survival probability (%Ns) of *Cacicus haemorrhous* from start of incubation to fledgling, and rate of nest predation (%) at four periods in the reproductive season.

Table II. *Cacicus haemorrhous* nest survival probability (%Ns) from egg laying to fledgling during four periods (early, late 1, late 2 and late 3) of the reproductive season.

| Period | %Ns | | |
|---|---|---|---|
| | Colony 2 | Colony 3 | Colony 4 |
| Early | 43,97 (n = 14) | 96,77 (n = 27) | 66,66 (n = 29) |
| Late 1 | 27,55 (n = 4) | 37,02 (n = 19) | 47,83 (n = 6) |
| Late 2 | 1,09 (n = 4) | 0,30 (n = 11) | 47,33 (n = 8) |
| Late 3 | 2,12 (n = 9) | 15,52 (n = 17) | 1,93 (n = 13) |

The predation rate was significantly different (Kruskall-Wallis, H = 8.436, d.f. = 3, p = 0.038) in the four periods, being observed an increase in the predation rate and a decrease of nest survival probability as the reproductive season progressed (Tab. III, Fig. 2).

Table III. *Cacicus haemorrhous* nests parameters of predation at four periods (early, late 1, late 2 and late 3) of the reproductive season.

| Period | No. predated eggs (%) | No. predated nestlings (%) | Total predation (%) |
|---|---|---|---|
| Early | 4 (5,7) | 9 (12,8) | 13 (18,6) |
| Late 1 | 4 (13,8) | 11 (37,9) | 15 (51,7) |
| Late 2 | 10 (43,5) | 7 (30,4) | 17 (73,9) |
| Late 3 | 22 (56,4) | 11 (28,2) | 33 (84,6) |
| Total | 40 (24,8) | 38 (23,6) | 78 (48,4) |

The colonies were analyzed in two different environments (forest area and swamp area). In order to test if the impact of the reproductive periods (early and late) was the same in both environments, the same analyses were applied taking into account the environment observed. In both, the forest (Fisher Exact Test, $p < 0.001$) and the swamp (Fisher Exact Test, $p < 0.001$) environment, the results were identical to the previous tests. Thus, even within different environments there was a difference in the success between early and late breeders, with higher reproductive success found for females that reproduced earlier in the season.

It was evaluated if there was a significant difference in nest survivorship between the two nest phases (incubation and nestling) in relation to the groups of females that reproduce in different periods (early and late) (Tab. IV). It was verified that the incubation phase had significantly higher survivorship, but only for the groups of females that reproduced in the second period (late) (Mann-Whitney, $Z = 2.309$, $p = 0.021$), not being significant for groups of females that reproduced in the first period (early) of the reproductive season (Mann-Whitney, $Z = 1.443$, $p = 0.149$).

Table IV. *Cacicus haemorrhous* nest survival probability during incubation (%NsI) and nestling period (%NsN) at two periods (early and late) of the reproductive season.

| Colony | Early | | Late | |
|---|---|---|---|---|
| | %NsI | %NsN | %NsI | %NsN |
| 1 | 82,13 | 76,47 | 80,33 | 12,61 |
| 2 | 92,76 | 47,40 | 76,97 | 8,13 |
| 3 | 100,00 | 96,77 | 55,15 | 33,88 |
| 4 | 89,74 | 74,30 | 52,90 | 43,97 |

## DISCUSSION

The results presented here showed that (1) there is a decline in nest survival probability and an increase in predation rate with the progress of the reproductive season; (2) temporal aggregation seemed to influence reproductive success more than the characteristics of the environment. These results suggest that *C. haemorrhous* benefited from temporal aggregation and that these benefits have a strong effect on the reproductive success of the species in the study area.

The seasonal decline in the reproductive success has been particularly well documented in birds (Birkhead & Nettleship 1982, Verhulst *et al*. 1995, Morbey & Ydenberg 1997, 2000, Massoni & Reboreda 2001). It is considered that reproductive synchronism is a consequence of joint timing by many individual females. However, one uncertainty about synchrony is whether females time their nesting in order to be synchronous, or are synchronous because each individual starts breeding during a short period of time when environmental conditions are good (Westneat 1992). Our results suggest that the reproductive temporal aggregation observed in *C. haemorrhous* was more associated to a behavioral characteristic than conditioned to physical variables of habitats when considering colonies in forest and swamp environments. This does not imply that climatic variables (precipitation and temperature) do not influence the temporal distribution of nests. Apparently, the reproductive synchronism in *C. haemorrhous* was in the first instance, a behavioral answer to nest predation pressure.

The hypothesis of temporal aggregation as an anti-predator strategy focuses on the increase in efficiency of detection and avoidance of predators and intruders, reducing the probability of nest predation (Robinson 1985, Westneat 1992, Massoni & Reboreda 2001). The benefits deriving from the reproductive synchronism are also accountable from other hypotheses sustained by factors such as the socially facilitated foraging (Brown 1986), seasonal decline in brood size (Westneat 1992, Rodrigues & Crick 1997), nestling growth (Morbey & Ydenberg 2000), and in the dilution of the predator effect (Wittenberger & Hunt 1985). The seasonal decline in the reproductive success of *C. haemorrhous* may also be attributed to a better timing, and survival ability presented by the individuals that reproduce earlier in the season. According to Sandell & Smith (1991), this factor probably is determined by phenotypic traits, age or prior occupancy, all being important dominance predictors.

Yasukawa & Searcy (1981) did not find any evidence that the cooperative defense of the nests is an important factor influencing nest dispersion in *Agelaius phoeniceus* (Icterinae). These authors state that their data favor the hypothesis that females nest asynchronously within territories to minimize competition for male parental care. As *C. haemorrhous*, males do not provide parental care, this factor does not represent a selection pressure against nest synchrony. In fact, the synchrony in breeding is widely thought to be an adaptive response of the population to consistent ecological conditions, such as resource availability and climatic conditions, however, there is considerable uncertainty about which ecological factors are most important (Westneat 1992).

As predation was the main cause of nests loss in this study, it was expected an increase in predation rates along the reproductive season, explaining the decrease of nests survival (%Sn) during the reproductive season. The seasonal increase in predation rates may be related to an absence of predators at the beginning of the colony's activities. Similarly, Massoni & Reboreda (2001) argument that the lack of correlation between the number of nests available and the probability per day of nest predation or desertion could have been confounded by the absence of predators during the initiation of the colony. Probably, there is a time lag between the start of a colony and its detection by predators.

The difference between nest survival probability in the two phases (egg and nestling) is significant only in the second period (late period) of the reproductive season. It reinforces the previously discussed result that females' timing to reproduce in the first period (early period) of the reproductive season is an important factor in obtaining higher reproductive success in the study area. Massoni & Reboreda (2001) report that *Agelaius thilius* (Molina, 1782) (Icterinae) females which started reproduction earlier in the season had higher reproductive success and that there was no significant difference in nest survival probability in both phases (egg and nestling). VERHULST *et al*. (1995), argues that seasonal variation in fledging success was due to quality effects only. This evidence suggests that seasonally declining fledging success was caused by a combination of timing and phenothypical quality effects. Nevertheless, these authors assume that 87% of the seasonal decline in the reproductive success of *Parus major* (Linnaeus, 1758) could be causally related to timing of breeding, and the remaining 13% would be due to quality differences between early- and late-breeding birds. DAAN *et al*. (1990) and HOCHACHKA (1990) state that to understand the role of phenotypic variation in breeding dates in an evolutionary context requires the establishment of a causal relationship between reproduction timing and reproductive success. This effect is clearly observed in *C. haemorrhous*, in which females reproducing earlier achieve a higher reproductive success. However, there is evidence in the literature showing that prior residence and age influence reproduction timing and the spatial position obtained within the colonies (ROBINSON 1986).

The results presented here suggest that the reproductive timing for each female in the reproductive season is an important factor for reproductive success. In the study area, the best moment for of *C. haemorrhous* reproduction was at the beginning of the reproductive season. Reinforcing this conclusion, it is observed that the difference in nest survival probability in the incubation phase and in the nestling period was significant only from the second period (late 1) onwards in the reproductive season.

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