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Timing of nest predation events during incubation for six passerine species in the austral Chaco

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ABSTRACT

We analysed the temporal occurrence (day–night) and timing of nest predation events during incubation for six common passerine species breeding in austral Chaco, a temperate South American habitat. We recorded time of predation events and incubation parental care activity using temperature sensors (data validated by field observations of nest fate) for 187 nests. The temporal occurrence of 35 predation events (77% during the day and 23% overnight) suggests a predator assemblage likely dominated by diurnal predators. Greater nest parental activity occurred early in the morning (06 00–09 00h) and late afternoon (17 00–20 00h), coinciding with a greater number of predation events. However, the relationship between the number of parental trips to a nest and its incidence on nest predation was not significant. Likewise, for Golden-billed Saltator, with parental activity and predation patterns similar to those of the group of species as a whole, nest parental activity was not significantly related to nest success/predation fate during incubation. Even though patterns of parental activity and predation events throughout the day seem alike, the lack of statistical relationship between such variables casts doubts regarding the influence of nest predation on parental behaviours during incubation in the species studied here.

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Incubation; nest monitoring; avian parental activity; Chacoan birds

Introduction

Nest predation is one of the most important causes of nest failure in passerine birds (Nice 1957; Ricklefs 1969; Lima 2009), and is considered one of the main factors affecting reproductive ecology in this group (Martin 1993, 1995). Since the 1950s, accumulated empirical evidence shows that clutch size and other life history traits such as nest site selection, nestling growth rate, and other behavioural and reproductive traits are highly influenced by the risk of nest predation and nest predation per se (Skutch 1949; Ghalambor and Martin 2001, 2002; Fontaine and Martin 2006; Schmidt *et al.* 2006; Eggers *et al.* 2008; Peluc *et al.* 2008; Zanette *et al.* 2011). The underlying mechanism relates to the ability of predators to cue on adult activity at the nest to find them, and on the capability of birds to adjust their behaviours and parental activity at the nest to avoid attracting visually oriented predators to it. For example, birds select more hidden nest sites, and reduce parental activity at the nest when visually oriented predators are close (e.g. Eggers *et al.* 2006, 2008; Peluc *et al.* 2008). This mechanism would entail that most nest predation events occur during daylight hours, when birds are active (Roper and Goldstein 1997; Libsch *et al.* 2008).

To date, the few studies that have analysed the timing of nest predation events show contradictory results. Some studies have shown predation primarily during night-time (Stake and Cimprich 2003; Carter *et al.* 2007), or reported predator assemblages dominated by nocturnal species (e.g. Roper and Goldstein 1997). In other cases, predation events are more frequently observed during daytime (Robinson *et al.* 2005; King and Degraaf 2006; Libsch *et al.* 2008). However, these results are geographically constrained to north temperate areas or the tropics. In south temperate zones, although rates of nest predation are relatively high (e.g. unpub. data; Mezquida *et al.* 2004; Auer *et al.* 2007; Vergara-Tabares and Peluc 2013), and nest predation appears to be a strong influence on life history traits (Ghalambor and Martin 2001; Ghalambor *et al.* 2013), information regarding the timing of nest predation events is rare.

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Supplemental data for this article can be accessed here.

In this study we analysed the temporal occurrence (day–night) and timing of nest predation events, and nest parental activity during the incubation of six common passerine species breeding in mountain Chaco woodland. Additionally, we examined the relationship between timing of nest predation events and incubation activity during the day.

Methods

Data collection

We conducted the study within 90 ha of a fairly well-preserved forest, comprising Chaco mountain woodland habitat (Cabrera 1971). The study site is located at 650 m a.s.l., 15 km east of Rio Ceballos (31°10.685′ S, 64°15.668′ W), Córdoba, Argentina. The climate is seasonal, temperate and semiarid, with a mean annual temperature of 18.9°C (18–39°C during the breeding season), and 650 mm/year of precipitation, concentrated in the summer.

The study species were Golden-billed Saltator (*Saltator aurantiirostris*; Thraupidae), Creamy-bellied Thrush (*Turdus amaurochalinus*; Turdidae), Chiguanco Thrush (*Turdus chiguanco*; Turdidae), Rufous-bellied Thrush (*Turdus rufiventris*; Turdidae), Red-crested Finch (*Coryphospingus cucullatus*; Thraupidae), and Variable Antshrike (*Thamnophilus caerulescens*; Thamnophilidae). These are common bird species (Dardanelli *et al*. 2006), that build cup-nests at similar heights (1–3.5 m), and use the same array of plant species as substrates. During incubation, females attend nests and incubate exclusively in all species (with the exception of Variable Antshrike), whereas males may guard the nest.

Nest monitoring and inference of nest predation events

We searched for and monitored nests from October to February (the main breeding season in this system) during three consecutive periods: 2011–2012, 2012–2013 and 2013–2014. In all nests found prior to the nestling stage, we placed a temperature sensor (HOBO Temp, RH, 2x External (C) 1999; Onset Computer Corp., Pocasset, MA) to record parental care activities and capture the time of predation events during incubation. The sensors provide an indirect measure of nest parental activity by means of contrasting changes in nest temperature with ambient temperature (Joyce *et al*. 2001). Ambient temperature tends to be stable and mostly lower than nest temperature, whereas nest temperature changes abruptly in relation to parental incubation. We validated the method comparing direct observations of nest parental activity with activity patterns recorded from sensors. Indefinite interruptions of nest temperature changes would reflect the absence of parental activity (Duncan-Rastogi *et al*. 2006; Libsch *et al*. 2008), and we interpreted them as predation events. In all cases we verified that the sudden absence from a nest was not the result of desertion or death of the adult (registering evidence of nest predation such as broken eggs, partial nest destruction, etc.). We analysed the distribution of nest predation events during the day (0600h and 2100h) and night (2100h and 0600h), in accordance with daylight hours in the study area (sunrise–sunset).

To evaluate the relatedness between time of day and occurrence of predation events, we quantified events within five 3-h periods between 0600 and 2100h. At each nest we averaged the per period number of trips to and from the nest during the days that the nest was monitored and until predation/hatching occurred, which resulted in five values per nest. We then calculated another average which included the average number of trips per period for all the nests monitored (all species combined). We ended up obtaining an average number of trips for five time periods.

Statistical analysis

We performed a binomial exact test (Conover 1980) to evaluate whether the proportion of nest predations between day and night departed from the expected proportion of 0.5. We used a chi-square test to identify whether there were significant differences between the number of nest predation events among time periods during the day, using INFOSTAT (Di Rienzo *et al*. 2002). To evaluate the temporal distribution of predation events we performed a circular statistic, the Rayleigh test, on adjusted data to unify angular distribution (using R software, CircStats package, R Core Team 2015). This is a test of uniformity that assesses the significance of the mean resultant length. We compared the number of parental trips among time periods with a Kruskal–Wallis test (H) (Di Rienzo *et al*. 2002). To evaluate the relationship between nest parental activity and incubation fate, we performed a logistic regression on data from the Golden-billed Saltator, the species with the greatest number of nests observed (n = 20). A parental activity index (i.e. the rate between the number of bouts during the day prior to the predation event or hatching and the time length between the first and last trip from/to the nest during the day) was the independent variable. Nest fate (failure/predation or success/hatch) was included as a binomial response. We transformed the independent variable with a logit function in R and assumed a binomial distribution of the error. In all analysis we used a significance level of 0.05.

Results and discussion

We monitored 187 nests (Table S1), and recorded 35 predation events during incubation, from which significantly more events occurred during the day than overnight (observed success proportion = 0.77, P = 0.002; Figure 1). Moreover, predation events were concentrated during the early morning hours (0600–0900h) and afternoon (1500–2100h; χ^2 = 10.72, P = 0.030; Figure 2(a)).

The Rayleigh test of uniformity results were non-significant (Z = 0.126, P = 0.579), indicating that the distribution of the timing of predation events is not unimodal throughout the day.

The mean number of adult trips/h varied significantly between different time periods (H = 17.1; P = 0.0017). We found a higher average value of nest parental activity early in the morning (0600–0900h: X = 6.83; EE = 0.49; n = 27 nests), and in the afternoon (1800–2100h: X = 6.2; EE = 0.39; n = 26 nests). Birds made fewer nest trips between 1500 and 1800h (X = 4.42; EE = 0.6) (Figure 2(a)).

When focusing on the Golden-billed Saltator, the number of predation events did not differ among time periods (χ^2 = 7.78, P = 0.1; Figure 2(b)). Yet the mean number of adult trips/h for such species showed the same pattern as the group of species as a whole (H = 20.59; P < 0.001; n = 20; Figure 2(b)). The logistic regression showed that parental activity at Golden-billed Saltator nests was not significantly related to their fate during incubation (Z = 0.98; P = 0.326).

In this study we report for the first time a pattern of timing of predation events for six common passerine species in the Chaco forest. Although predation occurred both during the day and night, events were concentrated during the daylight hours (Figure 1). This predation pattern contrasts with that observed by Libsch *et al.* (2008) in a tropical system with comparable predation rates, where nest predation occurred during the day and concentrated in the afternoons. Our results also contrast with those by King and Degraaf (2006), who reported nest predation events only during the day for a group of passerine species breeding in northern temperate forests.

In our study system, nest parental activity for all species was greatest in the early morning and late afternoon, and declined at midday. This is a relatively common avian activity pattern during incubation. During the morning greater activity is mostly attributable to the need to forage to replenish energy after overnight incubation, followed by a gradual decrease of activities towards midday/early afternoon, and an increase in nest parental activity during the late afternoon mostly related to foraging prior to the prolonged overnight incubation (Conway and Martin 2000; Deeming 2002).

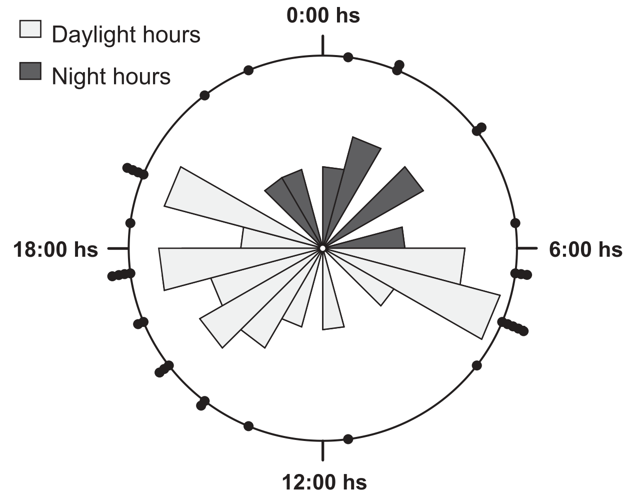

Figure 1. Rose diagram that shows the proportion of nest predation events occurring at a given time period. Dark areas indicate nocturnal events and light areas diurnal events. Points at circle edge represent nest predation events.

In order for nest predation to influence parental care behaviours, it is expected that predation events would occur at hours of greatest nest parental activity (Martin *et al.* 2000; Ghalambor and Martin 2002; Ghalambor *et al.* 2013). Nevertheless, predation events recorded here for six passerine species, even though concentrated in the early morning hours also occurred at night when parental care activity was nil. Moreover, we also recorded predation events during the midday/afternoon hours, when parental activity was relatively low. Furthermore, we did not find a relationship between average activity at a nest and its occurrence of predation for Golden-billed Saltator. Even though we found a coincidence between parental activity patterns and predation events throughout the day, the lack of relationship between such variables evidences a discrepancy. These contradictory results cast doubts regarding the relative influence of nest predation on parental behaviours during incubation, and make the case for more profound examination of the role of nest predation as a selective force on life history traits.

Regarding the predators responsible for the nest losses, it seems plausible that predation events occurring early in the morning are related to visually oriented predators, mostly birds, which cue on nest parental activity. In that regard, it would sound surprising that between 0800 and 1400h, a time period when many nest predatory birds and reptiles are active, we observed an almost complete lack of

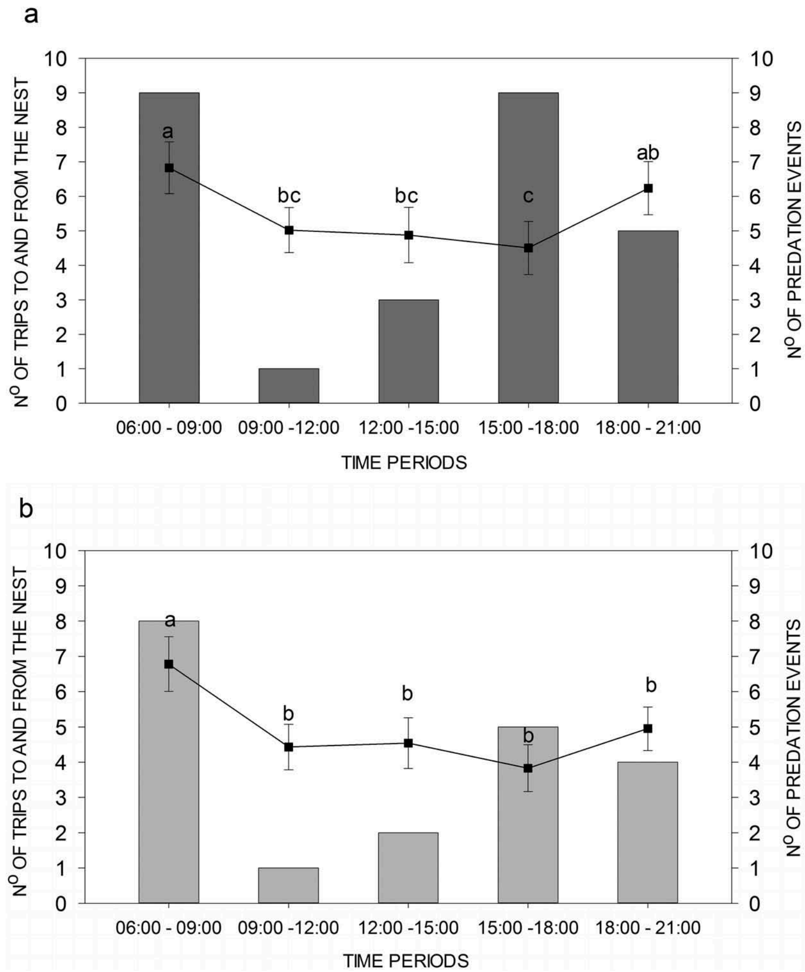

Figure 2. Mean (±SE) number of adult trips to and from the nest within time periods (boxes), and total number of predation events (bars) recorded during incubation for (a) all species combined and (b) Golden-billed Saltator. Letters indicate significant differences among means.

nest predation. Such observation seems to support the idea that lower nest parental activity is related to fewer predation events. On the other hand, the occurrence of predation events with low nest parental activity observed later in the day (1500–2100h; Figure 2(a)) argues against the previous statement. In fact, we found a lack of association between nest parental activity and fate when analysing data on the Golden-billed Saltator. These results seem to contrast with those by Martin *et al.* (2000), that incubating adults of depredated nests had higher activity than individuals from non-predated nests.

Alternatively, the discordant patterns of nest predation and parental activity observed later in the day may be due to a change in the identity of predators active at these hours (mostly not visually oriented, terrestrial and arboreal duelling reptile, small or medium-sized mammal species, mostly active during the late afternoon or even crepuscular; Vergara-Tabares 2011; Schaaf *et al.* 2015). A similar argument may apply to explain the occurrence of nocturnal predation events when parental care activity is nil.

Even though much evidence supports the idea that nest predation is a strong force which shapes a variety of behavioural traits associated with reproduction, our results do not show a clear association between nest parental activity and the occurrence of predation events. Moreover, the noticeable proportion of nocturnal predation events suggests that the role of nest predation by non-visually oriented predators in shaping life history traits deserves examination (e.g. Peluc *et al.* 2008).

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