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ARTICLE

Effects of intrinsic and time-specific factors on daily nest survival of birds in a semiarid area of South America (Caatinga)

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ABSTRACT: Nest predation is a determinant of reproductive success of tropical birds and its effects can vary in space, time and due to intrinsic factors of the species. In this study, we conducted a preliminary investigation on changes in the risk of nest predation on Caatinga birds due to intrinsic factors (nest type and taxonomic group) and time-specific factors (breeding season and nest abundance). We located and monitored bird nests during the breeding seasons of 2012 (n = 33 nests) and 2013 (n = 45) in a mixed landscape of anthropogenic and natural sites. We use the MARK program that uses known-fate models to calculate Daily Nest Survival Estimates (DNS) and evaluate the effect of covariates on DNS estimates. Predation was the main cause of nest loss (n = 54). In the analysis of intrinsic factors, the best model included the type of nest to explain variation in estimates. DNS declined across the breeding season for all nest types, but estimates of closed nests (between 0.996 and 0.851) were higher than those of open nests (between 0.985 and 0.629). For time-specific factors, the best models for each breeding season included the quadratic effect of nest abundance to explain the variation in DNS. There was an inverse relationship between the abundance of nests and nest predation. The high importance of predation and the effect of the type of nest showed that the reproductive success of the birds studied is due to similar factors to those found in other Neotropical environments. On the other hand, locally-specific effects, such as low reproductive success and inverse relationship between abundance and nest predation risk, demonstrate the need for further exploration of this theme within the Caatinga avifauna.

KEY-WORDS: avian, density-dependence, predation, reproductive success.

INTRODUCTION

Interactions such as predation, competition and brood parasitism may result in temporal and spatial variations in reproductive success in birds (Gates & Gysel 1978, Martin 1995, Woodworth 1999). Among these, predation is the primary cause of nest mortality (Ricklefs 1969), especially for Neotropical birds (França & Marini 2009b, Marini *et al.* 2009a, Dias & Macedo 2011), and can result in the loss of some 70% of passerine clutches (Robinson *et al.* 2000, Stutchbury & Morton 2001). The high impact of nest predation on breeding success of Neotropical birds makes this interaction an important part of the dynamics of bird populations in these environments, and knowledge of its operation is key for effective conservation (Stutchbury & Morton 2001).

Fluctuations in nest predation rates may be related to time-specific factors that vary across the breeding season, during nest development or between breeding seasons (Martin *et al.* 2000, Roos 2002, Peak *et al.* 2004, Thompson-III 2007, Wilson *et al.* 2007, França & Marini 2009b). Predation rates can also be determined by spatially varying factors, for example, between different types of habitat, variation in nest building sites and density of co-specific nests (Burhans *et al.* 2002, Roos 2002, Peak *et al.* 2004, Mahon & Martin 2006, Aguilar *et al.* 2008). Finally, predation rates may be linked to intrinsic reproductive factors such as nest type, parental behavior or even morphological and behavioral patterns inherent to taxonomic order of the prey species (Martin & Clobert 1996, Martin *et al.* 2000, Robinson *et al.* 2000, Borges & Marini 2010, Dias *et al.* 2010).

In northeastern Brazil the xeric vegetation type (Caatinga) is characterized by high seasonality, irregularity and lack of rain (Prado 2003, Silva *et al.* 2003, Leal *et al.* 2005), all of which can both regulate and restrict the breeding season for birds (Cavalcanti 2014), and result in time-dependent fluctuations in nest predation rates. Bird breeding in Caatinga seems to be scheduled to coincide with the rainy season (Nascimento *et al.* 2000, Telino-Júnior *et al.* 2005, Roos *et al.* 2006) when, over a short time period, many species simultaneously invest in nest production (Cavalcanti 2014). This temporal concentration of breeding activity generates resource availability peaks for nest predators and can result in density-dependent relationships between predator and prey (Aguilar *et al.* 2008). In addition to extrinsic factors, some intrinsic factors may be important sources of variation in nest predation rates in the Caatinga. The high local richness of bird species in Caatinga (from 70 to 145 species: Santos 2004, Farias *et al.* 2005, Olmos *et al.* 2005, Telino-Júnior *et al.* 2005, Farias 2007, Araujo & Rodrigues 2011) when compared to other semi-arid environments (*e.g.* n ≤ 25, northeastern Venezuela, Poulin *et al.* 1993; n ≤ 54, western Mexico, Del-R & Butterfield 1999; n ≤ 61, northcentral Chile, Jaksic & Lazo 1999) can result in greater variability of such intrinsic factors as nest type, breeding and social behavior, and generate particular predation patterns not found in other tropical semiarid areas.

Most studies evaluating nest predation in seasonal Neotropics have occurred in the Cerrado (*e.g.* Francisco 2006, Carvalho *et al.* 2007, Aguilar *et al.* 2008, França & Marini 2009b, Marini *et al.* 2009a, Borges & Marini 2010, Marini *et al.* 2010, Hoffmann & Rodrigues 2011, Marini *et al.* 2012). Caatinga weather conditions are more severe than those of the Cerrado, with higher rates of solar radiation, average annual temperature and potential evapotranspiration, and lower relative humidity rates and annual precipitation (Prado 2003). Avian ecology and conservation from the Caatinga are considered the least-known among Brazilian ecoregions (Marini & Garcia 2005). In view of the lack of information concerning factors influencing predation risk of bird nests in seasonal Neotropical environments, the present study aimed to test the following hypotheses: (1) closed nests are less likely to suffer predation than open nests (as has been reported in other humid and seasonal tropical environments in the Neotropics - Oniki 1979, Purcell & Verner 1999, Robinson *et al.* 2000); (2) the risk of nest predation varies between bird taxonomic Orders (Borges & Marini 2010); (3) the abundance of active nests is related to daily fluctuations in predation risk (Ackerman *et al.* 2004, Paiva 2008, Elmberg & Pöysä 2011).

METHODS

Study area

The Caatinga ecoregion occurs in northeastern Brazil at altitudes ranging from 0–600 m. The average annual temperature varies between 24 and 28°C and total annual rainfall from 250–1000 mm, with a high water deficit for most of the year (Prado 2003). Natural vegetation consists mainly of woody and herbaceous species, small and completely deciduous during the dry season (Velloso *et al.* 2002, Prado 2003). The study presented here occurred in an area of Caatinga (5°03'54''S; 37°24'03''W, 76 m a.s.l.), in the state of Rio Grande do Norte, in the *Depressão Sertaneja Setentrional* (Dry Northern Depression) region (Velloso *et al.* 2002). The study area encompasses some 400 ha, and comprises a mixed landscape of areas of native Caatinga vegetation and human-use areas with different levels and types of impacts. Nest sampling occurred in the areas disturbed by perennial or seasonal plant cultivation, areas where local beekeeping occurred and in abandoned areas of agricultural experiments.

Data sampling and analysis

We conducted active searches for bird nests at likely nesting sites to calculate the estimates of Daily Nest Survival (DNS) and daily nest abundance in the study area. Nests were searched for between March and May 2012, and between February and June 2013. Nests were also located by following individuals exhibiting behavior indicating the nearby presence of a nest. Found nests were visited at regular intervals of three and four days until they became inactive. For each nest we identified the incubator species and classified nest type (open or closed). During each monitoring event we recorded the date, nest status (active or inactive) and type of nest contents (empty, eggs or nestlings). We considered a nest successful when at least one of the nestlings survived long enough to fledge and leave the nest. Nest status was defined as preyed upon when all the eggs or nestlings disappeared from the nest before the minimum period required for hatching or nestling departure had ended, and/or when obvious signs of predation on eggs or nestlings were observed. This form of search and nest monitoring procedure is commonly used in studies estimating reproductive success (*e.g.* Johnson *et al.* 2006, França *et al.* 2009, Marini *et al.* 2012).

All data analyses were performed with the program MARK (Dinsmore *et al.* 2002). We used capture-recapture models based on known-fate models to generate the estimates of Daily Nest Survival (DNS), and evaluate the effects of temporal and intrinsic covariates on these estimates. To create models, we combined covariates considered to affect the variation in nest survival. The covariates considered were: (1) linear and quadratic effects of the breeding season on the probability of DNS (season and season^2); (2) linear and quadratic effects of nest abundance on the estimates of DNS (nest and nest^2); (3) effect of nest type, either open or closed nests (type) and; (4) effect of taxonomic Order (Columbiformes, Passeriformes and Psittaciformes) of the species under investigation. We used a method that compared a null model with a set of candidate models. We created candidate models by combining covariates thought to explain the variation in DNS. For the covariate *nest abundance*, we used our records of the number of active nests from daily monitoring. Monitoring events occurred at fixed intervals of three and four days, and during this time a pair of researchers sought new nests. Daily monitoring occurred from 4 to 6 h/day.

To select the best model among the set of candidate models, we ordered models with the Akaike Information Criterion (Burnham & Anderson 1998). Models with best fit were those with the lowest AIC and also models with ΔAICc ≤ 2, as these are considered to possess substantial support to explain part of the within-data variation (Burnham & Anderson 1998). We estimated reproductive success through the logistic function of the best model, using a period of 27 days between egg laying and nestling flight. This period is within the 24 to 28 days range of development for seven of the fully monitored nests from the study, and is similar to durations reported by other studies on Neotropical passerines (Lopes & Marini 2005a, Medeiros & Marini 2007, Duca & Marini 2011).

We conducted two analyses of candidate models to test the study hypotheses and the different data types collected in the two breeding seasons. The first analysis considered only data from the first breeding season, and evaluated the effect of intrinsic factors on estimates of DNS. This was the only season in which we sampled closed nests. The second analysis considered only open nests for the two breeding seasons, to evaluate the effect of temporally varying factors on estimates of DNS.

RESULTS

The main factor influencing reproductive success in the study area was nest predation (n = 54 predated nests and 24 successful). To test for intrinsic factors we analyzed 33 nests sampled in 2012. The candidate model with the best support for the observed variation included the covariates *reproductive period* and *nest type* (Table 1). The next models in the adjustment order were not able to explain the variance in the data (ΔAICc ≥ 3.53). The best fit model explained 70% of variance from the set of candidate models.

TABLE 1. Candidate models considered for evaluating the effect of intrinsic factors in the variation of DNS (Daily Nest Survival) estimates in the 2012 breeding season at the Caatinga, Brazil. Selection was based on Akaike Information Criterion with correction for small samples (AIC$_c$). The *w*-AIC$_c$ is the support of each model in relation to the set of candidate models. K represents the number of parameters of each model.

Model	**AIC$_c$**	**ΔAIC$_c$**	***w*-AIC$_c$**	**K**	**Deviance**
Season + type	104.44	0.00	0.70	3	98.36
Season + order + type	107.98	3.53	0.11	6	95.70
Season + order	108.76	4.32	0.08	5	98.56
Type	109.88	5.44	0.04	2	105.85
Constant	110.63	6.18	0.03	1	108.62
Order	112.55	8.10	0.01	4	104.41
Type + order	113.09	8.64	0.00	5	102.89

According to the best fitting model, the DNS for closed and open nests decreased as the breeding season progressed, but closed nests had higher values (Figure 1). In the first 10 days of the breeding season, the DNS estimates tended to decrease at a lower rate (closed nests = 0.996 to 0.992, open nests = 0.985 to 0.972) than in the last 10 days (closed nests = 0.917 to 0.851, open nests = 0.767 to 0.629; Figure 1). Closed nests had high estimates of reproductive success early in the season (69.8%), and values up to 5.3 times lower at the end of the season (13.2%). Reproductive success for open nests ranged from 30.5% at the beginning of the season and close to zero at the end (Figure 2). The difference between nest types ranged from around 56% at breeding season start to 13% at the end.

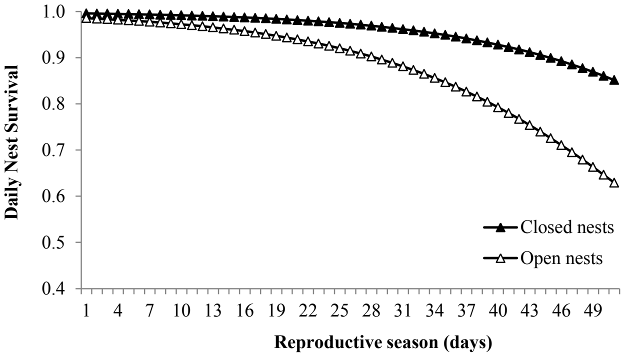

FIGURE 1. Daily Nest Survival (DNS) estimates for open and closed nests during the first breeding season (2012) at Caatinga, Brazil. Results are based on analyses of the best fitting candidate models. Linear equation of the best model: DNS = 4.286 -0.074 (breeding season) + 1.216 (type of nest).

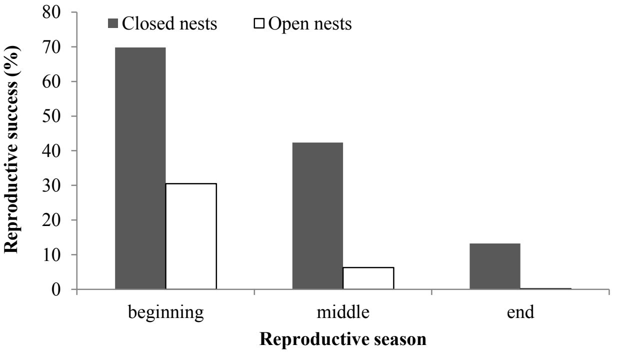

FIGURE 2. Reproductive success estimation (%) for open and closed nests according to three nesting start dates during the breeding season (beginning, middle and end), with a period of 27 days between egg laying and fledgling flight.

Evaluation of the effect of time-dependent factors was based on 24 and 45 open nests from the 2012 and 2013 breeding seasons, respectively. During the first breeding season, seven nests were successful and 17 were preyed upon. Two candidate models showed substantial support to explain the variation in DNS estimates, and the best model was that one which considered the effects of the covariate *nest abundance* (Table 2). The best model was affected by the quadratic effect of nest abundance, while in the second model (ΔAIC_c = 0.84), DNS was affected by the linear effect of breeding season. The best model explained 44% of variance considered by the set of candidate models, and the two best models together explained 73% of the variation (Table 2). We present the results of the best model (nests^2) for discussion. During the 2013 breeding season 14 nests were successful and 31 were predated. In this analysis the best adjusted model was also that one which considered the quadratic effect on the nest abundance to explain variations in DNS (Table 2). The next model in the adjustment order (ΔAIC_c = 7.27), and the null model (ΔAIC_c = 8.87), had no support for explaining the variations in the data. The best fitted model explained 94% of variance considered by the set of candidate models (Table 2). We used the best model (nest^2) to generate the estimates of DNS.

DNS tended to increase during periods of low daily nest abundance records. During the 2012 breeding season, DNS ranged from 0.743 to 0.946 with 5 to 10 active nests per day being recorded. In the 2013 breeding season DNS ranged from 0.831 to 0.952 with 2 to 7 active nests per day being recorded (Figure 3). In periods of higher recorded nest abundance, DNS tended to decrease in the 2012 breeding season, but was more constant in 2013. During the 2012 breeding season, DNS decreased from 0.969 to 0.919, with 17 to 22 active nests recorded daily, while in 2013 DNS values oscillated between 0.977 and 0.975, with 13 to 18 active nests recorded daily (Figure 3). Reproductive success estimates for open nests

TABLE 2. Candidate models considered for evaluating the effect of covariates for time-specific variation of DNS (Daily Nest Survival) estimates for open nests during two studied breeding seasons in Caatinga, Brazil. Selection was based on Akaike Information Criterion with correction for small samples (AIC_c). The *w*-AIC_c is the support of each model in relation to the set of candidate models. K represents the number of parameters of each model.

Model	AIC_c	ΔAIC_c	*w*-AIC_c	K	Deviance
2012 Breeding season					
Nests^2	60.64	0.00	0.44	3	54.48
Season	61.48	0.83	0.29	2	57.40
Season^2	63.07	2.42	0.13	3	56.91
Nests	63.32	2.67	0.11	2	59.24
Constant	66.84	6.20	0.01	1	64.82
2013 Breeding season					
Nests^2	134.98	0.00	0.94	3	128.92
Nests	142.25	7.26	0.02	2	138.22
Constant	143.85	8.86	0.01	1	141.84
Season	144.23	9.25	0.00	2	140.20
Season^2	144.71	9.72	0.00	3	138.65

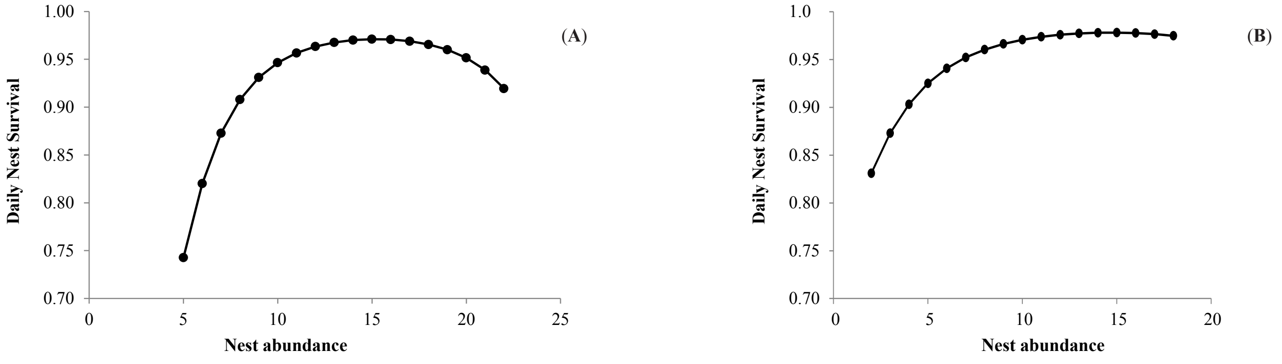

FIGURE 3. Daily Nest Survival (DNS) estimates for open nests with nest abundance considered (quadratic effect), during the 2012 (**A**) and 2013 (**B**) breeding seasons at Caatinga, Brazil. Results are based on the best model from the analysis of candidate models. Linear equation of the best models: (**A**) DNS = -1.928 + 0.715 (nests) -0.023 (nests^2) and (**B**) DNS = 0.841 + 0.403 (nests) -0.014 (nests^2).

were low (Figure 4). During the 2012 breeding season reproductive success ranged from very low to almost zero (7.4 to 0.01% of successful nests). During the 2013 breeding season reproductive success declined from the beginning and middle of the breeding season, then increased again to peak at the end of the season (15.1%).

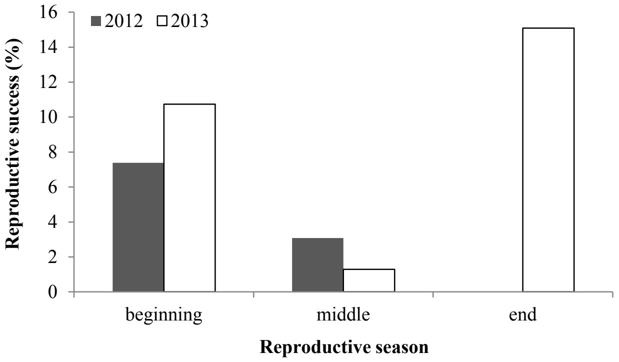

FIGURE 4. Reproductive success estimate (%) with open nests at Caatinga, Brazil, according to three nest start dates (beginning, middle and end) during the 2012 and 2013 breeding seasons, and with a period of 27 days between egg laying and nestling flight.

DISCUSSION

Predation was the main cause of nest failure during this study. This parallels observations made in Cerrado (Carvalho *et al.* 2007, Medeiros & Marini 2007, Aguilar *et al.* 2008, França & Marini 2009a, Borges & Marini 2010), Amazonia (Oniki 1979, Mullner & Linsenmair 2007) and Atlantic Forest (Duca & Marini 2005, Duca & Marini 2008). In our study closed nests had higher success, and this also has been commonly observed in both Neotropical (Oniki 1979, Robinson *et al.* 2000, Duca & Marini 2005, Duca & Marini 2008, Faria *et al.* 2008) and temperate areas (Purcell & Verner 1999). It is assumed that closed nests are under lower predation rates due to the reduced accessibility of nest contents to predators (Oniki 1979). Our data provide evidence that the characteristic feature of the semiarid Caatinga, with high unpredictability in the availability and distribution of rainfall (Prado 2003), is not a factor that changes the overall Neotropical pattern of high nest predation rates on all types of nests.

Few studies have considered the processes responsible for temporal variation in predation in Neotropical bird nests. Results presented here indicate a temporal effect of nest abundance in the Daily Nest Survival. Predator-prey interactions are commonly considered to be related to density-dependent effects (*e.g.* Gates & Gysel 1978, Oliveira *et al.* 2001, Oro *et al.* 2006), and some of these are involved during nest predation (Gates & Gysel 1978, Bêty *et al.* 2002, Roos 2002, Paiva 2008). In such studies, variation in the risk of nest predation may have arisen from a functional response by predators, so that predation frequency may be directly related to density (Gates & Gysel 1978, Roos 2002, Aguilar *et al.* 2008, Paiva 2008, Dias *et al.* 2010).

Our results have found a different effect to that commonly reported in the literature, and indicate a direct relationship between the abundance of nests and estimates of DNS. In other words, an inverse relationship between the abundance of nests and their risk of predation. This may have climatic links. The breeding season in the Caatinga is among the shortest reported for any seasonal Neotropical environment (Cavalcanti 2014), possibly due to the short rainy season and associated period of adequate food availability. In 2013 the breeding season at the current study site lasted only 87 days (active nests) (Cavalcanti 2014). It is possible that this brevity results in an avian breeding season so short, intense, widespread and temporally contiguous as to generate rapid predator satiation. In such a situation, prey consumption rates may depend simply on the intake ability and digestive capacity of individual predators (Jeschke *et al.* 2002). When satiation is achieved hunting activities decrease, lowering predation rates (Jeschke *et al.* 2002). According to this hypothesis, a rapid predator satiation process may result in the inverse relationship between the abundance and predation rate of nests, as we observed at this Caatinga site.

We recorded low levels of avian reproductive success, and a marked variation between the two study years (2012, 0.01 to 7% and 2013, 10% to 15%). Reports of reproductive success for other seasonal Neotropical areas are generally higher than those recorded (Cerrado - *Suiriri affinis* 32%, *Suiriri islerorum* 10%, Lopes & Marini 2005b; *Elaenia chiriquensis* 33%, Medeiros & Marini 2007; *Tyrannus savana* 52.5%, Marini *et al.* 2009a; *Elaenia cristata* 27.1%, Marini *et al.* 2009b; *Mimus saturninus* 54%, Rodrigues 2009). For some species, breeding success values close to those of the current study have been reported (Amazonia - *Cercomacra tyrannina* 7.1%, Robinson *et al.* 2000; Cerrado - *Volatinia jacarina* 4.7%, Carvalho *et al.* 2007; Cerrado – *S. islerorum* 16.8 and 6.7%, França & Marini 2009b). A study in Cerrado has shown that overall bird community breeding success in areas under high human impact (16.6%) may be less than those in more natural areas (29.4%) (Borges & Marini 2010). We report here the lowest reproductive success values so far encountered in the Neotropics, and this may be a consequence of the high levels of human impact on the study site vegetation, the mosaic nature of the landscape, or the unique nature of Caatinga rainfall patterns. While it is difficult to determine which of these is the dominant cause for the low breeding success observed, these results highlight the vulnerability of local Caatinga bird populations, as heavy nest predation pressure could make human-impacted vegetation fragments potentially inviable, as either population sources or sinks for the local avifauna.

This study is one of the first to establish the current patterns of variation in breeding success for Caatinga birds. The pronounced importance of predation and the effect of the type of nest demonstrated by this study show that breeding success for Caatinga birds are governed by processes similar to those found in other Neotropical environments. On the other hand, the local characteristics of inverse dependence between abundance and nest predation risk, as well as an extremely low rate of breeding success, highlight the need for attention to the unusual nature of the breeding ecology of the Caatinga avifauna.

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