Nesting success of birds from Brazilian Atlantic Forest fragments

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ABSTRACT: Several aspects of the ecology of tropical birds remain unresolved both descriptively and experimentally, in spite of the high diversity of birds and the high deforestation rates. Here, I evaluate, apparently for the first time, nesting success and predation levels of open and closed-cupped nesting birds in an avian community from Atlantic Forest fragments in southeastern Brazil. The monitoring of 257 nests of more than 22 species from 1995 to 1999 revealed that overall apparent nest success (42.4%) was in the upper range for tropical species. Daily survival rates (DSR) for 18 species ranged from 0.900–0.987. Total average survival probability was 55.9 for open cup and 60.1% for closed nests. There was no evidence for an edge effect on the success of either open cup or closed nests. Against predictions, apparent success of closed nests (43.6%) did not differ from open cup nests (38.1%). However, there were differences in apparent success within three types of closed nests. Closed nests higher above the ground had greater apparent nest success than lower nests, but this pattern did not occur for open cup nests. This study demonstrates that some patterns of nesting success might not hold for all Neotropical sites, especially disturbed ones.

KEY-WORDS: breeding, Mayfield, nest, predation, survival.

INTRODUCTION

Low nesting success has been proposed as a key reason for the decline of bird populations in fragmented landscapes (Gates & Gysel 1978, Robinson 1989, Robinson *et al.* 1995). Most studies however, have evaluated nest predation and brood parasitism rates in temperate forest fragments, and little is known about nesting success of birds in Neotropical forests (Skutch 1985, Robinson *et al.* 2000, Young *et al.* 2008, Brawn *et al.* 2011), though exceptions for some species (*e.g.* Snow 1962, Aguilar *et al.* 2000) and some artificial nest studies do exist (Tabarelli & Mantovani 1997, Leite & Marini 1999, Duca *et al.* 2001). Tests of edge effects on the success of natural nests are scarce in the Neotropics (*e.g.* França & Marini 2009), and a meta-analysis of 20 Neotropical forest nest predation studies revealed no support for an edge effect (Vetter *et al.* 2013). Studies with artificial nests alone have provided mixed evidence for edge effect on nest survival in the Neotropics, with the majority showing no effect (Melo & Marini 1997, Duca *et al.* 2001, França & Marini 2009, but see Tabarelli & Mantovani 1997). Thus, our knowledge on the cumulative effect of forest fragmentation on nest success in the Neotropics remains incomplete.

In addition, we still lack descriptive and experimental tests of several aspects of the ecology of tropical birds both in natural and disturbed habitats (Martin 1996). For example, few studies of nesting success in the Neotropical region have large sample sizes that can be used to test proposed patterns and existing hypotheses, such as the higher predation levels in the tropics compared to temperate regions (Martin 1993, Robinson *et al.* 2000). Also, differences in the predation rates between open cup and closed nests (Lack 1948, Martin & Li 1992) or across nest heights (Reynolds & Knapton 1984, Robinson *et al.* 2000, Santo *et al.* 2003) are seldom tested in tropical areas (Mezquida & Marone 2001, Auer *et al.* 2007). Thus, it remains unclear if patterns influencing nest success that were demonstrated primarily in temperate areas, apply more broadly to tropical regions.

Habitat disturbance can alter predator communities, the contact rates between predators and nests, and thus nest predation rates (Borges & Marini 2010). This is particularly alarming given the high deforestation rates across several biomes. For example, primary Atlantic Forest cover is currently estimated at 11.4–16% (Ribeiro *et al.* 2009), and a high percentage of Atlantic Forest birds are threatened (*e.g.* 10% in Brazil, review in Marini & Garcia 2005). Thus, information on avian nest success and the factors that influence it are not only desirable, but also urgent as deforestation continues to fragment

Atlantic Forest (Tabarelli *et al.* 2005) and other biomes.

This study evaluates nesting success and predation levels of open cup and closed nesting birds from Atlantic Forest fragments in southeastern Brazil, apparently for the first time. I tested the following hypotheses: 1) that nest predation is higher along borders than in the interior of forest fragments; 2) that nest predation varies according to nest structure, being higher for open-cup than for closed nests; and 3) that nest predation varies with nest height above the ground, being lower at greater heights.

METHODS

Study area

I conducted this study at the "*Área de Proteção Especial para fins de Preservação dos Mananciais do Barreiro*" (Barreiro therein), owned by *COPASA (Companhia de Saneamento de Minas Gerais)* and located within the municipality of Belo Horizonte, state of Minas Gerais (20°02' – 20°00'S; 43°59' – 44°00'W) (Marini 2010). From 1995 to 2000, I monitored nests at two forest fragments of 50 and 200 ha at the Barreiro. The forests have a 15–25 m high canopy, with and estimated successional stage of approximately 150 years (CETEC 1993). These forest fragments exist in an area of transition between the Atlantic Forest and the Cerrado Biomes. However, the community composition of bird species is more characteristic of the Atlantic Forest. The landscape around the forests is composed mostly of grasslands and Cerrado (around 2000 ha), surrounded by urbanized areas of Belo Horizonte and neighboring cities (Marini 2010). The climate of the region has warm and rainy summers and dry and cool winters with most precipitation falling between October and March. Temperatures generally vary between 9°C and 37°C (Source: *"Estações Climáticas da Mutuca e Catarina"* monitored by COPASA and M*BR – Minerações Brasileiras Reunidas*).

Field methods

I began nest searches usually in July, mostly along ravines and roadbeds, but also inside forests away from these landmarks. To mark nests, I placed a pink plastic tape approximately 5–10 m from them. I made several visits every 3–5 days to monitor nests and determine their fate, assuming that nest content (eggs or nestlings; active or inactive) and status (hatching, fledging and predation) occurred at the midpoint between nest checks, following Mayfield (1961, 1975). Nest monitoring scheme and the classification of nest fate followed standard procedures largely accepted and used in studies of nest success (Mayfield 1961, 1975, Robinson *et al.* 2000, Lopes &

Marini 2005). Thus, a nest was considered successful when at least one bird fledged, and predated when all its contents had disappeared before the expected time of nest fledging. Part nest losses were disregarded since predators usually take the entire nest content (Ricklefs 1969, Martin 1993). A nest was considered abandoned when eggs remained in the nest for a time period that was longer than expected for the species or when nestlings were found dead without signs of predation.

Most nests had their height above the ground measured with a tape (to the nearest cm) and all nests were classified as open-cup or closed. To enable statistical analysis, I divided nests into two classes of height above the ground: up to 1 m and more than 1 m, and performed separate tests for open-cup and closed nests. Then, closed nests were subdivided in cavity in the ground (usually narrow 0.5–1.0 meter-long cavities in ravine walls), domed pensile (globular or elongated closed nests with a side entrance) or domed on or close to the ground (globular closed nests with a side entrance). I also classified most nests in five groups with respect to distance to the forest edge: up to 50 m, 51–100 m, 101–150 m, 151–200 m and greater than 200 m.

Statistical analyses

Reproductive success was calculated in two ways: 1) apparent predation rates (*i.e.* simple percentage of predated nests); and 2) daily survival rates (DSR) (Mayfield 1961, 1975). I applied Chi-square tests to test if apparent predation rates of nests 1) varied with distance from the edge to the interior of forest fragments; 2) differed between open-cup and closed nests; and 3) varied with nest height above the ground. Multivariate analyses where not possible to use since two parameters (nest height and distance to the edge) where not estimated for all nests due to logistical constraints in the field, reducing sample sizes even further. Sample sizes were too small to calculate predation rates at different stages (eggs or nestlings) of the nest cycle for different species. Nests of unidentified species (Pipridae sp., Formicariidae sp., *Turdus* sp., 10 unknown) were usually depredated before the owner of the nest was identified. Since all these nests were depredated earlier in the nest cycle, to avoid overestimating nest success of all species of open-cup and all closed nests they were used for the estimate of average survival probability and average apparent success. However, the nests of Pipridae are probably from Blue Manakin, *Chiroxiphia caudata*. All nests belong to Passeriformes, except for the nest of Crescent-chested Puffbird, *Malacoptila striata*. Nomenclature follows Brazilian Ornithological Records Committee - CBRO (Piacentini *et al.* 2015).

I calculated daily survival rates (DSR) (Mayfield

estimates) based on Mayfield (1961, 1975) and Hensler & Nichols (1981). I did not calculate these estimates individually for unidentified nests since they could not be ascribed to any species, and would have little biological relevance as such. However, I calculated these estimates for Formicariidae, Pipridae and *Turdus* sp. since the number of days of their nest cycle is likely consistent between members of a bird genus (Bennett & Owens 2002, del Hoyo *et al.* 2017). Detailed nesting biology of species with small sample sizes is provided in Marini *et al.* (2007) and with larger sample sizes (Gray-hooded Flycatcher *Mionectes rufiventris*, Euler's Flycatcher *Lathrotriccus euleri*, Yellow-olive Flycatcher *Tolmomyias sulphurescens*

and Sepia-capped Flycatcher *Leptopogon amaurocephalus*) in Aguilar *et al.* (1999, 2000), Anciães *et al.* (2012), and Aguilar (2001).

RESULTS

Overall apparent nest success (%), independent of nest structure or location, was of 42.4% (*n* = 257 nests) across 95 open cup nests of at least eight species and 162 closed nests of at least 10 species over the five years of the study (Table 1). Overall apparent nest predation levels, independent of nest structure or location, was 44.7%

Table 1. Sample sizes of nest fates, daily survival rates (DSR) and survival probability following Mayfield (1961, 1975), and apparent success of forest birds with open cup and closed nests.

Species name	Nest fate[a]				Exposure days	Daily survival rates (DSR)	Survival probability % (mean ± SD)	Apparent success (%)[e]
	S	P	A	NC				
Open cup nests								
Lathrotriccus euleri	21	13	1	-	753	0.983	68.5 ± 0.07	60
Platyrinchus mystaceus	2	1	-	-	57	0.983	71.4 ± 0.24	67
Chiroxiphia caudata	1	1	-	-	52	0.981	60.4 ± 0.31	50
Pipridae sp.	1	5	-	-	120	0.958	42.7 ± 0.17	17
Thamnophilus caerulescens	3	3	-	-	104	0.962	50.7 ± 0.18	50
Dysithamnus mentalis	2	5	-	-	98	0.949	48.0 ± 0.16	29
Formicariidae sp.	-	3	1	-	31	0.903	34.9 ± 0.22	0
Conopophaga lineata	3	5	1	-	147	0.966	53.0 ± 0.15	33
Turdus leucomelas	2	5	1	1	134	0.963	48.3 ± 0.16	22
Turdus rufiventris	1	-	-	-	13			100
Turdus sp.	-	5	1	-	46	0.891	34.7 ± 0.17	0
Not identified	1	4	2	-				14
Total open cup nests	47	40	7	1	1555		55.9[f]	49.5[f]
Closed nests								
Malacoptila striata[b]	1	-	-	-	31			100
Philydor rufum[b]	2	1	1	-	77	0.987	71.5 ± 0.24	50
Lochmias nematura[b]	1	-	-	-	9			100
Tersina viridis[b]	2	1	-	-	35	0.971	71.3 ± 0.24	67
Tolmomyias sulphurescens[c]	23	28	8	1	1394	0.980	57.4 ± 0.06	38.3
Leptopogon amaurocephalus[c]	30	25	8	1	1655	0.985	63.3 ± 0.06	46.9
Mionectes rufiventris[c]	7	6	3	2	290	0.979	62.7 ± 0.12	38.9
Todirostrum poliocephalum[c]	1	-	-	-	32			100
Basileuterus culicivorus[d]	-	5	-	-	55	0.909	35.1 ± 0.17	0
Myiothlypis flaveola[d]	-	2	-	-	20	0.900	34.9 ± 0.28	0
Not identified pensile[c]	1	-	1	-				50
Not identified domed[d]	-	1	-	-				0
Total closed nests	62	75	21	4	3598		60.1[f]	38.3[f]

[a] Nest fate: S = success, P = predation, A = abandonment, NC = natural causes.
[b] Cavity inside the ground.
[c] Domed pensile.
[d] Domed on or close to the ground.
[e] Apparent success = all successful nests/all nests.
[f] Average survival probability or average apparent success of all species.

(n = 115 nests). The other 12.9% of failed nests were the result of nest abandonment or other natural causes such as tree falls.

Daily survival rates (DSR) (Mayfield estimates) of 18 species ranged from 0.900 to 0.987 (Table 1). For four species with >18 nests monitored, the daily survival rate ranged from 0.979 to 0.985. Total average survival probability was 55.9% for open cup and 60.1% for closed nests. We refrain from making further comparisons with daily survival rates because sample sizes were too small for most species.

Forest border *vs.* forest interior

Apparent nest success was similar along the edge to interior forest gradient. When open-cup and closed nests were considered together, nest success was similar among the five edge distance categories (χ^2 = 0.425, *df* = 4, P = 0.980). This lack of edge effect was maintained when either open-cup (χ^2 = 0.830, *df* = 3, P = 0.842) or closed (χ^2 = 1.093, *df* = 4, P = 0.895) nests were analyzed separately (Fig. 1).

Nest structure

Open cup and closed nests had similar nest success, contrary to expectation. Mean nest success over the five years was similar (χ^2 = 3.077, *df* = 1, P = 0.105) between open-cup (49.5%) and closed (38.3%) nests. Nest predation levels were also very similar between closed (46.3%) and open-cup nests (42.1%). However, nest success and nest predation levels varied among different types of closed nests, though small and uneven sample sizes precluded proper statistical analyses. Domed nests on or close to the ground (n = 8 nests of three species) had the highest predation level (100%) and lowest nesting success (0%). Domed pensile nests (n = 145 nests of five species) had intermediate predation levels (40.7%) and nesting success (42.8%), whereas cavity nests inside the
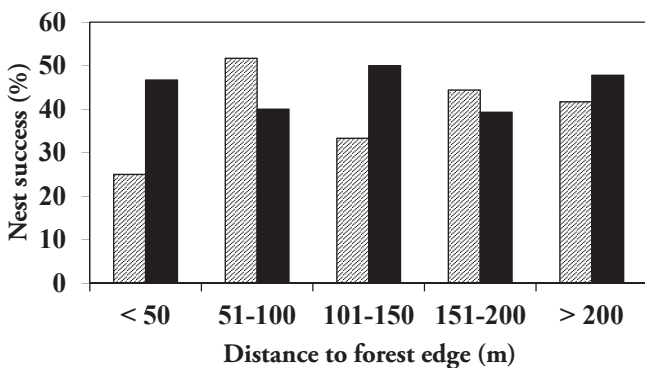

Figure 1. Percentage of open-cup (cross-hatched bars) and closed (solid bars) successful nests at five distances (m) from the forest edge.

ground (n = 9 of four species) had the lowest predation levels (22.2%) and the highest nesting success (66.6%).

For all open cup nests, apparent nest success and predation levels varied little among the five years of study. Nest success varied from 30.0 to 42.9% (mean for the five years = 38.1 ± 5.1%). Nest predation varied from 47.6 to 61.5% (mean for the five years = 53.8 ± 6.4%). Nest losses due to other causes varied from 0 to 12.5%, but in four out of five years ranged from 8.3 to 12.5%.

For all closed nests, nest success had an almost two-fold variation among the five years, from 30 to 56.5% (mean for the five years = 43.6 ± 10.8%). The same pattern occurred with nest predation, which varied from 36.1 to 57.5% (mean for the five years = 43.2 ± 8.7%). Nest losses due to other causes varied almost six-fold, ranging from 4.4 to 25% (mean for the five years = 13.3 ± 7.7%). This last result was mostly due to a very high rate of nest abandonment in 1996 (25%) probably caused by the experimental manipulation of nests of Yellow-olive Flycatcher that year. If nests from 1996 are excluded from the analyses, mean loss to other causes drops to 10.4%.

Nest height above the ground

Nest success varied according to nest height for closed nests, but not for open cup nests. Closed nests higher above the ground (> 1 m) (n = 48) had significantly (χ^2 = 8.47, *df* = 1, P = 0.004) higher nest success than nests lower to the ground (< 1 m) (n = 16). However, open cup nests placed above (n = 34) and below (n = 27) 1 m had similar (χ^2 = 1.57, *df* = 1, P = 0.297) nest success.

DISCUSSION

Overall nest success recorded here is twice as high as average values reported for real nests of Neotropical birds of about 20% (Snow 1962, Oniki 1979, Robinson *et al*. 2000, Mezquida & Marone 2001, Lopes & Marini 2005, Medeiros & Marini 2007). Nest success in Atlantic Forest fragments is higher than that of other Neotropical regions, but most studies were conducted in areas with several levels of habitat fragmentation and degradation. As pointed out by Martin (1996), nest predation rates may be similar between North America and Central and South America. Indeed, few studies with sufficient sample sizes of real nests exist in the Neotropics and temperate South America (but see Martin *et al*. 2000, Borges & Marini 2010, Brawn *et al*. 2011, França *et al*. 2016), and further study is required to test this difference.

Edge effects on nest success have rarely been tested in the Neotropical region and studies have revealed mixed results. Here, nest success was similar from the edge to the interior of the forests, even though open cup nests

close (< 50 m) to forest border had a tendency of lower nesting success. Sample sizes, however, were low in the < 50 m distance class, and further study is necessary. Similar nest success rates were found for both natural and artificial nests between the edge and interior in a Cerrado reserve in Brazil (França & Marini 2009). One study with artificial nests did not demonstrate an edge effect (Tabarelli & Mantovani 1997), but neither Melo & Marini (1997) nor (Duca *et al.* 2001) found edge effects on nest success. Overall, most of the evidence from both natural and artificial nests in southeast central Brazil points to the lack of edge effects on the probability of avian nest success. Evidence for edge effects on avian nesting success is also mixed in other regions of the world (review in Lahti 2001). Specificities from each region, such as predator community and landscape features, might account for the lack of a general edge effect pattern among studies (Lahti 2001, Vetter *et al.* 2013).

We rejected the prediction that open cup nests have lower nesting success than closed nests (Ricklefs 1969, Oniki 1979). Similarly to our results, Ramo & Busto (1984) and Mezquida & Marone (2001) also did not detect higher nesting success for closed nests. However, closed nests had higher success than open-cup nests at the Brazilian Caatinga (França *et al.* 2016). The decrease in the success of the Yellow-olive Flycatcher in 1996 due to manipulation had little effect on the overall estimate of nest success of closed nests, since these nests represented less than 3% of all closed nests, and predation would have destroyed around half of them anyway. The difference among the three types of closed nests in this study is noteworthy as it reveals that predation pressure and life history constraints differ among them. Only arboreal or aerial predators can depredate a domed pensile nest, whereas a different suite of predators may depredate nests on the ground. For example, birds, primates and snakes have been reported to depredate the pensile nests of Icteridae in the Amazon (Robinson 1985) and in the Atlantic Forests (Duca & Marini 2004). Our results suggest that an open cup-closed nest dichotomy may be too simple to explain biological patterns in nest success and predation among birds.

The average nest survival probabilities (Mayfield) for open cup nests (49.5%) is above most values reported for other Neotropical sites, such as the Cerrado (29.4%) (Borges & Marini 2010), the Caatinga (< 15%) (França *et al.* 2016), and lowland forests in Panama (7.1% for the Dusky Antbird *Cercomacroides tyrannina*) (Robinson *et al.* 2000). Nest survival probabilities (Mayfield) of closed nests (38.3%) is in the range of other closed nesting Neotropical species, such as Ochre-bellied Flycatcher *Mionectes oleagineus* in Central American forests (12.1–51.5%) (Skutch 1985, Robinson *et al.* 2000), the Red-rumped Cacique *Cacicus haemorrhous* in the Atlantic Forest (40.5%) (Duca & Marini 2008), and

closed nests at the Caatinga (seasonal range = 13.2–69.8%) (França *et al.* 2016). Thus, nest success in these forest fragments was average (closed) to high (open cup) compared to other Neotropical sites.

Closed nests were more successful when positioned higher above the ground, but nest success was similar for high and low open cup nests. Similarly, cavity-nesting passerines had higher nesting success when higher above the ground (Li & Martin 1991). Also, the closed nests of Winter Wren *Troglodytes troglodytes* were more successful when higher above the ground (Santo *et al.* 2003). The same pattern, however, has also been found for an open-cup nester, Chipping Sparrow *Spizela passerina* (Reynolds & Knapton 1984). The reason for this difference between open cup and closed nests may be related to the community of predators within the forest fragments of our study site. At least 256 species of mammals, birds, reptiles and arthropods depredate bird nests in the Neotropical region (Menezes & Marini 2017). Among them, snakes, toucans, raptors, small mammals and monkeys could enter or reach inside closed nests and at high densities could increase nest predation rates above average expected values. For example, Black-necked Aracaris (*Pteroglossus aracari*) depredated closed nests of *Cacicus haemorrhous* in the Atlantic Forest (Duca & Marini 2004). Thus, the reason for these high predation rates of closed nests at Atlantic Forest fragments should be investigated further.

This study revealed that some patterns of nesting success found in the literature might not hold for all Neotropical sites, especially disturbed ones such as ours (see also Marini *et al.* 2012). Here, predation levels in the fragmented forests were not different from the levels of most Neotropical studies. Also, closed nest success was similar to that of open cup nests, but there seems to be differences in success among types of closed nests. The breeding biology and ecology of many Neotropical species and ecosystems remains poorly studied (*e.g.* Heming *et al.* 2013), and reproductive success studies in novel systems are still rare (but see França *et al.* 2016). This rarity in tropical regions is probably related to small sample sizes due to low population densities compared to temperate species, high species diversity with varied nest types including many undescribed nests, and the need of field-intensive nest monitoring programs. However, the present study demonstrates how a small amount of new field data from a novel study site can add to the discussion of avian life history.

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