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Nest survival for two species of manakins (Pipridae) in lowland Ecuador

Thomas B. Ryder, Renata Durães, Wendy P. Tori, José R. Hidalgo, Bette A. Loiselle and John G. Blake

T. B. Ryder (correspondence), R. Durães, W. P. Tori, J. R. Hidalgo, B. A. Loiselle and J. G. Blake, Dept. of Biology and Whitney R. Harris World Ecology Center, University of Missouri-St. Louis, 1 University Blvd., St. Louis, MO 63121. E-mail: pipridae@umsl.edu

Estimates of reproductive success are essential to understand life-history strategies, yet tropical species remain understudied relative to their temperate counterparts. Here, we report nest survival probabilities for two manakin species (Pipridae). We monitored 61 wire-tailed manakin *Pipra filicauda* and 45 blue-crowned manakin *Lepidothrix coronata* nests during three breeding seasons. Both species suffered high nest failure (84%). We modeled the effects of year, nest height, nest age (for *P. filicauda* only), as well as nest manipulation on daily survival rates (DSR) using program MARK. DSR decreased with nest age in *P. filicauda* whereas a constant survival model was best fitted for *L. coronata*. Average DSR was 89% for *P. filicauda* and 85% for *L. coronata*. This study reports some of the lowest nest survival rates among tropical passerines and poses important questions about population maintenance.

The primary cause of nest mortality in birds is predation (Ricklefs 1969) and the most common metric used to measure reproductive success is nest survival (Oniki 1979, Skutch 1985), despite the implied limitations associated with multiple-brooded species (Schmidt and Whelan 1999). Nest predation may be higher among tropical than among temperate birds (Ricklefs 1969, Martin 1996), and predation likely has played a significant role in the evolution of clutch size, reproductive tactics, nest architecture and life history trade-offs of tropical taxa (Martin et al. 2000).

Most previous estimates of nest survival of tropical species relied on experiments with artificial nests (e.g., Mezquida and Marone 2004), and relatively few estimates were based on natural nests (e.g., Robinson et al. 2000, Roper 2005). Artificial nests may not, however, provide accurate survival estimates (see Robinson et al. 2005). Thus, the future contribution of artificial nests studies to theory necessitates improved experiments to better reflect biological reality (Major and Kendal 1996). The use of nest in close-to-natural conditions, with fewer artificial components, (e.g., real nests with attending females and replica eggs) constitutes a significant experimental improvement more likely to reflect biological reality. Moreover, comparison of natural (non-manipulated) and manipulated nests tests the underlying assumption of the artificial approach while concurrently validating the use of experimental approaches to measure nest survival.

Nest survival variation exists both within and among species (Robinson et al. 2000) and is an important component for understanding predation pressures within a system. Probability of nest survival is often influenced by site-specific nest attributes (Martin and Roper 1988). Recently developed techniques allow incorporation of such relevant covariates into estimates of survival (Dinsmore et al. 2002, Rotella et al. 2004) and permit biologists to evaluate questions while generating more biologically meaningful survival estimates (Grand et al. 2006).

Here, we estimate nest survival for blue-crowned manakin *Lepidothrix coronata,* and wire-tailed manakin *Pipra filicauda,* in an Ecuadorian rainforest using both natural nests (non-manipulated) and nests which had their eggs replaced but were attended by females (manipulated nests). We modeled daily survival rate for nests of each species over three breeding seasons (2004–2006) using program MARK (White and Burnham 1999).

Methods

Manakins are sub-oscine passerines in the family Pipridae and typically suffer high nest predation (Skutch 1985). Like most manakin species, *P. filicauda* and *L. coronata* build small open-cup nests comprised of fungal rhizomorphs, leaf material and spider webs (Snow 2004, Hidalgo et al. 2008). Nests of both species are similar in size and position, but differ in height (Hidalgo et al. 2008).

Research was conducted at Tiputini biodiversity station (TBS, 00°38′S, 76°08′W), Orellana Province, eastern Ecuador. TBS is a 650-ha biological station adjacent to the greater Yasuní National Park (see Ryder et al. 2006 for a detailed site description). We searched for nests between Nov. and March, in 2003–2004, 2004–2005, and 2005–2006 (2004, 2005, and 2006 hereafter). Nests were located via systematic searches within two 100-ha study plots as well as off the study plots. We supplemented systematic searching by following radio-tagged females to their nests. Radio transmitters did not affect the mating behavior of females, as tagged females built nests, copulated, incubated eggs and raised young (pers. obs.). Nests were checked approximately every three days (mean ± SD interval: 2.6 ± 1.4 d), following Martin and Geupel (1993). Monitoring of nests may increase the probability of predation, so we took precautionary measures to minimize our impact (see Robinson et al. 2000).

During the second field season, we modified our sampling regime to meet other goals of our research (i.e., blood collection for paternity analyses). This entailed replacing real eggs with plaster replicas, which were readily accepted by females and did not changes their incubation behavior (for details see Tori et al. 2006). Fake eggs were left in nests until the real eggs hatched in the laboratory (3–16 d), after which hatchlings were returned to the appropriate nest.

Rates of nest success were estimated using the daily-survival estimator available in program MARK (White and Burnham 1999). DSR was then used to estimate cumulative probabilities for nest survival. Duration of nesting stages was based on nests followed for the complete incubation period (i.e., nest found in lay and reached hatching) and/or complete nestling period (from hatching to fledging). Incubation was assumed to last 16 days for both species (*L. coronata*: range 16–17, n = 2; *P. filicauda*: range 16–19, n = 6), while the nestling period was assumed to last 14 days for *L. coronata* (range 13–14, n = 3), and 15 days for *P. filicauda* (range 13–18, n = 4).

Using MARK, we first built models that examined species differences; upon not finding substantial differences in nest survival rates between species (see Results), we then combined data from both species to increase statistical power when incorporating the manipulation covariate. Within species, we built models incorporating combinations of individual covariates (year and nest height, in meters, for both species, and also age of nest, in days), for *P. filicauda*, and compared them to the null-hypothesis model of constant survival, S(.). Models with the nest-age covariate were built following Rotella (2005), allowing DSR to vary following a trend in accordance with nest age. Covariates were unstandardized and mean values were used to fill out missing cells (i.e., three missing height values for *P. filicauda*). The default options of sin (for constant survival models) or logit link function (for models including covariates) and 2nd part variance estimation were adopted. Estimates for specific models were obtained using beta parameters and back transformation following Dinsmore et al. (2002) and Rotella (2005). Models were compared based on AICc, which corrects for small sample sizes (Burnham and Anderson 2002). The model with the lowest AICc value was considered to have the best fit; models with AICc values differing by ≤ 2.00 units were considered equally supported, in which case the model with the fewest parameters was chosen. Means and estimates are presented ± SE.

Results

We monitored 9 *P. filicauda* nests in 2004, 22 in 2005, and 30 in 2006, for a total of 61 nests and 525 exposure days. Six *L. coronata* nests were monitored in 2004, 13 in 2005, and 26 in 2006, for a total of 45 nests and 292 exposure days. We determined the fate of 97 out of 106 total nests, 89 (84%) of which failed; most nests were depredated (70%, n = 74), 11% (n = 12) were abandoned during incubation, and 3% (n = 3) failed from unknown causes. Among nests lost to predation, 70% (n = 52) were depredated during the incubation and 28% (n = 21) during the nestling phase; phase of the remaining depredated nest was not determined.

Species and nest manipulation effects

Models including species, or species and year as covariates, performed as well as general models that combined data between species and across years (ΔAICc < 0.61). Seventy-three of 96 nests (76%; 40 *P. filicauda* and 33 *L. coronata* nests) had their eggs replaced with plaster eggs. DSR for non-manipulated nests was higher than for manipulated nests (MARK: manipulated, 0.873 ± 0.014, non-manipulated, 0.887 ± 0.024). However, models that incorporated manipulation as a covariate performed as well (S(manipulation + species): ΔAICc = 1.93) or worse (S(manipulation): ΔAICc = 2.05; S(manipulation + species + year): ΔAICc = 2.37) than the general model S(.). Because only nests in incubation were manipulated, we further examined the effect of manipulation by estimating the cumulative survival probabilities of these two nest treatments. MARK does not allow for stage specific survival, so we used the traditional Mayfield approach (Mayfield 1975), and compared the cumulative survival estimates using the program CONTRAST (Hines and Sauer 1989). We found no significant effect of manipulation (manipulated 0.057 ± 0.01, non-manipulated = 0.079 ± 0.02, $\chi^2 = 0.741$, df = 1, P = 0.389).

Effects of year, nest age and nest height on nest survival

Daily survival rates for *P. filicauda* nests ranged from 86 to 93%, depending on year; overall DSR for the three years combined was 89% (Table 1) Cumulative probability of nest survival was 0.026 suggesting that ~3% of nests fledge

Table 1. Daily survival rates (DSR) for *P. filicauda* and *L. coronata* nests at TBS, estimated according to the MARK estimators. Mean DSR ± 1 SE for each year, and combined across years.

Year	*P. filicauda*	*L. coronata*
2004	0.930 ± 0.021	0.832 ± 0.059
2005	0.902 ± 0.015	0.845 ± 0.029
2006	0.864 ± 0.023	0.858 ± 0.025
All years	0.891 ± 0.015	0.853 ± 0.022

young. The four models that incorporated effects of age were equally fit and better than models that did not incorporate age (ΔAICc ≤ 2.00, Table 2). Inclusion of year and nest height as covariates improved model performance; however, the age model was chosen because it has the fewest parameters among the best-fit model set (Table 2). The nest-age model had a positive slope ($\beta_{age} = 0.050 \pm 0.021$) indicating a gradual increase in survival with nest age, although confidence intervals around survival estimates are large (Fig. 1).

DSR of *L. coronata* nests ranged between 83 and 85%, depending on year; DSR for the three years combined was 85% (Table 1). Cumulative probability of survival using MARK constant rates was 0.008, meaning a mere 0.8% of nests fledge young. The general model S(.) had equal support compared with either nest height or year models, and was better fit than a model with both variables (Table 2). The general model was chosen because it had the fewest number of parameters.

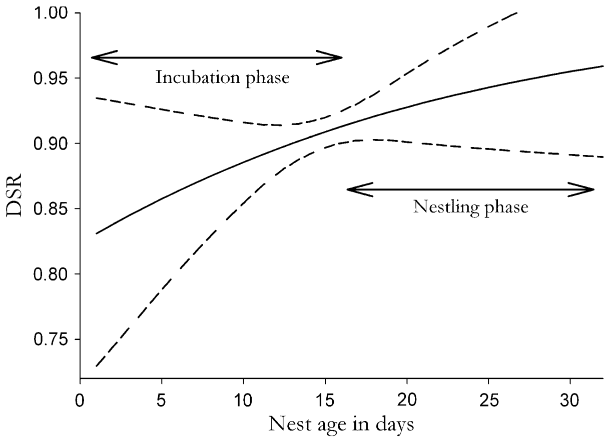

Figure 1. Daily nest survival (DSR) of *Pipra filicauda* nests at TBS, across three breeding seasons, shows a gradual increase with nest age. Solid line represents DSR estimated using beta parameters from the best-fit model incorporating age. Dashed lines represent upper and lower confidence intervals for the estimated DSR.

Discussion

Birds in the tropics and southern hemisphere have been reported to suffer high rates of nest failure, mostly due to predation (Sargent 1993). In this study, nest failure was extremely high for both *P. filicauda* and *L. coronata*, with only 7.5% fledging any young. To our knowledge, these predation rates are among the highest ever recorded for tropical passerines and imply the importance of either high female survival and/or multiple breeding attempts per season to maintain population stability.

It is difficult to say if the low rates of nest success observed here are typical for manakins, given the limited amount of comparable data in the literature. Cumulative success for *P. mentalis* in Panama, using a constant-rate Mayfield probability, was estimated at 12.3% (Robinson et al. 2000). Other available estimates are based on percentage of successful nests: *Manacus manacus* and *M. aurantiacus* in Central America had 19% and 25% of successful nests (Skutch 1985). However, these apparent survival rates inadequately quantify nest success because they are biased against nests that survive for short periods of time and, thus, are overestimated (Mayfield 1975). If we were to adopt apparent rates of nest survival, our estimates of nest success would increase markedly (10.9% for *P. filicauda* and 4.8% for *L. coronata*), but still be lower than in Skutch's study.

Table 2. Model selection results for nest survival in *P. filicauda* and *L. coronata*. Models are sorted in increasing order according to ΔAICc values. The number of model parameters (K), the model deviance (Dev), the difference between the AICc value for the current model and the model with the lowest AICc (Δ AICc) and model weight (w_i).

Model[a]	K	Dev	ΔAICc[b]	w_i
P. filicauda				
S(year+age)	3	215.815	0.000	0.274
S(height+age)	3	216.347	0.532	0.210
S(age)	2	218.498	0.654	0.198
S(year+height+age)	4	214.731	0.956	0.170
S(year)	2	221.363	3.517	0.047
S(year+height)	3	220.017	4.202	0.034
S(height)	2	222.054	4.209	0.025
S(.)	1	224.648	4.784	0.009
L. coronata				
S(.)	1	161.648	0.000	0.4787
S(height)	2	161.079	1.460	0.2302
S(year)	2	161.486	1.870	0.1878
S(year+height)	3	160.630	3.070	0.1033

[a] Survival of nests was modeled with the incorporation of covariates and compared with the null model of constant survival S(.).
[b] The lowest AICc values was 221.874 for *P. filicauda* and 163.664 for *L. coronata*.

Given that any kind of nest manipulation may reduce nest survival by increasing chances of predator attraction, we examined the effect of our manipulation protocol. Manipulated nests had slightly lower DSR than non-manipulated nests; yet, a model incorporating manipulation as a covariate did not perform better according to the AIC approach. In part, observed differences may reflect the fact that only nests found at the incubation stage were manipulated, while nests found in the nestling stage, when survival probabilities were shown to be higher, were not manipulated. A secondary examination of incubation-specific survival probability using the traditional Mayfield approach, however, also failed to detect survival differences. This may in large part be due to the fact that females incubated the fake eggs normally, and thus the manipulated nests were able to simulate natural nests more realistically than the artificial nests used in previous experimental protocols. A direct experimental comparison with artificial nests would be interesting to further to validate this assertion.

Nest age was shown to influence nest survival: *P. filicauda* daily survival probability gradually increased as the nest aged. In altricial species, nest survival is expected to be lower during the nestling stage because of increased parental activity and noisy begging calls of young. In our study species, although number of female trips increase during the nestling phase, nestlings are completely silent even during feeding bouts. Further, female manakins appear to remain vigilant once eggs hatch, spending long bouts sitting on the cup watching over the nestlings. Nest vigilance is a function of parental investment and females may increase nest defense during the nestling stage (Montgomerie and Weatherhead 1988). Nest vigilance and the relative silence of manakin nestlings may have contributed to the increase in DSR with nest age. Alternatively, DSR may be higher during later nesting stages because more vulnerable nests (e.g., nests located in less concealed sites) get depredated earlier in the nesting cycle.

Nest predation is a major, if not the most important, cause of breeding failure in birds and, along with food limitation and adult survivorship, has been considered an essential force driving the evolution of avian life histories (Ricklefs 1969, Martin 1996). Differences in nest predation rates also have been purported to be one of the causes for the divergent breeding strategies between avian species from northern and southern hemispheres. However, the lack of studies on tropical nesting biology precludes rigorous ecological comparisons (Martin 1996). Here we have shown extremely high nest predation for two species of manakins. Future studies should focus on understanding population regulation given these alarming predation rates. These studies will undoubtedly require linking manakin population dynamics and life history to determine how these species mitigate the effects of such low reproductive output. Regardless, this study contributes to the growing knowledge of nesting biology, reproductive success and causes of nest failure in tropical birds.

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