



The influence of parental behavior on vulnerability to nest predation in tropical thrushes of an Andean cloud forest

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The Skutch hypothesis predicts that parental activity around the nest may attract the attention of predators and thus, in the tropics where predation pressure may be high, selection favors reduced parental activity. This hypothesis has been questioned by studies demonstrating that parents can decrease the risk of nest predation through nest defense. The link between parental activity and predation risk may be further confounded by nest site characteristics. We examined the effects of parental behavior and nest site on clutch survival in two sympatric tropical thrushes (*Myadestes ralloides* and *Turdus leucops*). We compared survival rates of clutches in three treatments: 1) natural nests at the incubation stage, 2) unattended nests (un-manipulated nests of the same species, with clutches unattended by parents), and 3) exposed clutches (eggs exposed in unconcealed positions, unprotected by the nest). Parental activity had a positive effect on clutch survival, which was revealed by significantly higher survival rate of clutches in attended nests compared to unattended nests. The effect of nest site was less clear: clutches in unattended natural nests survived better than clutches in exposed sites selected by humans, but results were insignificant. We propose that parent birds can exclude a group of opportunistic predators, that are able to destroy unattended clutches. Nest site characteristics may be less important in determining clutch survival in the tropics, where predator guilds are more diverse, making completely safe sites difficult to find. Our results challenge Skutch's hypothesis and point to the need for more data from tropical latitudes.

Factors such as nest site and parental care are known to affect predation rates on bird nests, though the relative importance of each is often unclear (Weidinger 2002, Thompson 2007), and few studies have been carried out in tropical environments. Skutch (1949) proposed a proximate mechanism connecting the risk of nest predation, parental activity, and clutch size, and argued that parental activity at the nest, which may attract the attention of nest predators, is reduced in tropical birds caring for smaller broods, thus alleviating predation pressure. Studies that have directly or indirectly tested the Skutch's hypothesis have yielded an array of contradicting results (reviewed by Martin et al. 2000a, b). Correlational studies cannot control for the dual effect of parental activity: parents can either decrease the risk of nest predation through nest defense or, conversely, increase the risk of predation by disclosing the position of the nest, and it is difficult to separate both effects (Weidinger 2002). Additionally, nest defense tends to progressively increase during the breeding cycle (Redondo 1989, Thompson 2007), which may counterbalance an increased conspicuousness of the nest during the nestling stage. The interpretation of correlative studies may be further complicated by the covariance of nest predation risk, nest site characteristics, and the stage of the breeding cycle, thus producing the so called "nest site effect" – an increased mortality at the beginning of the reproductive

cycle when predators destroy poorly concealed nests (Dixon 1978, Miller and Johnson 1978, Martin et al. 2000b, Muchai and du Plessis 2005, Thompson 2007).

An important advancement in the attempt to test the importance of parental care on nest survival was the experimental procedure developed by Cresswell (1997). He compared survival rates in natural (active) nests vs the same nests in their original positions, but unattended by parent birds (nestlings had already fledged or the nest had been abandoned after predation). The study was the first convincing demonstration that parental nest defense is important for nest survival, even in small passerines. More recently, Fontaine and co-workers (2007) examined the relative importance of nest site and parental behavior comparing survivability of natural nests in 13 species vs artificial nests baited with eggs and unattended by adult birds. They found a significantly higher survivability among natural nests, however, they refrained from suggesting this as evidence for the protective role of parental behavior since using artificial nests and nest sites selected by humans may have introduced additional factors that were not controlled for.

In the present study we use Cresswell's (1997) method and compare survival rates of clutches in naturally active nests of neotropical thrushes to inactive but un-manipulated nests of the same species. We expected that a difference in

survival rates between these groups would reveal if the activity of adult birds increased nest predation (as predicted by the Skutch's hypothesis) or rather decreased nest predation due to parental defense (Cresswell 1997). Similarly, in order to test the effect of the nest site on clutch survivability, we compare survival rates of clutches in nests unattended by parents to clutches placed in exposed locations.

Methods

We conducted our research at the Yanayacu Biological Station (00° 35' 57" S, 77° 53' 27" W) between February and May of 2004 and 2005, in undisturbed cloud forest on the eastern slopes of the Ecuadorian Andes at elevations ranging 2 050–2 200 m above sea level. The study area is protected by Cabañas San Isidro, and encompasses about 500 ha of primary habitat contiguous with the 188 000 ha Antisana Reserve. Nests and sites with exposed clutches were dispersed in about 235 ha plot (an ellipse with axes of length 1 and 3 km). Potential nest predators include numerous species of birds, micromammalia (*Rodentia* and *Insectivora*), squirrels, mustelids, coatis, monkeys, and snakes (snakes are rather rare in comparison with forests at lower elevations). One nest at this site (not during this study; see Greeney and Halupka 2008) was destroyed by army ants (*Labidus* sp.: *Formicidae*, *Ecitoninae*).

Natural nests

We studied nests of two species of thrushes (Turdidae): Andean solitaire *Myadestes ralloides*, and pale-eyed thrush *Turdus leucops* which are both widespread in Andean cloud forests. In our study area both species reproduce predominantly from Dec. to June. Nests included in the present study were found in 2004 and 2005. Modal clutch size in both species is two eggs and the breeding cycle (from egg laying to fledging) lasts about one month (Greeney and Halupka 2008, Halupka and Greeney 2009).

Nests (11 of Andean solitaires and 22 of pale-eyed thrushes) were found by flushing incubating adults and searching vegetation. We pooled nests of the two species into one sample of "natural nests." In the field it is possible to discriminate between empty nests of Andean solitaires and pale-eyed thrushes by the presence of fern scales in nest lining in the former species (Greeney and Halupka 2008). In both species, survival of nests (39% and 41%, respectively, from the beginning of incubation to fledging), behavior of parent birds (i.e. persistent incubation and flushing upon very close approach of the observer), nest height, and other characteristics of nest sites are very similar (Greeney and Halupka 2008, Halupka and Greeney 2009). Thus it is likely that, from the point of view of potential predators, nests of both species constitute a homogeneous group.

To ensure that data are comparable across treatments, in the "natural nests" group only the incubation stage (without the day of hatching) was included in the analysis. After hatching the nest contents are no longer "passive" (as in "unattended" and "exposed" treatments), and the relative

vulnerability of the nest to predation may be affected by nestling behaviors such as movement or begging (Platzen and Magrath 2004, Thompson 2007).

Nests were checked every 1–5 d. The date of predation was assigned as the mid-point between the last two visits (Mayfield 1975). Two nests were depredated and we can be sure that in both cases it happened within the incubation stage: at one nest the predator left egg shell fragments and in the other nest predation took place before the expected day of hatching (timing was known since the nest was found at the onset of incubation). If hatching occurred between consecutive nest checks, we counted d. of exposure to the day preceding the hatching d. (determined using the stage of nestlings development as a cue). In one nest parent birds deserted the clutch, and we included only nest-day when eggs were still incubated in the analysis.

Unattended nests

We placed 39 replicates of clutches consisting of two zebra finch *Taeniopygia guttata* eggs placed into unattended thrush nests. We used 12 nests that had been previously, in the same breeding season, monitored until fledging or had been plundered by predators. The remaining 27 nests were thrush nests found empty but in a good repair (such nests may be reused by thrushes, even after long periods of inactivity; pers. obs.).

Clutches were exposed for 17 d (roughly the period of clutch completion and incubation), each checked every 3–6 d. If the eggs were damaged or had disappeared, the nest was considered depredated. To define the date of predation, we used the same procedure as for natural nests.

The zebra finch egg is about two-thirds the size of thrush eggs, and also thinner-shelled. We did not, however, observe instances that suggested zebra finch eggs were destroyed by insects or other animals that do not normally forage on eggs. In addition, using zebra finch eggs in nest predation experiments is advisable (Roper 1992, Martin et al. 2000b) compared to quail *Coturnix coturnix* eggs, which are known to be too hard-shelled or too large for some opportunistic nest predators. The difference in color of natural and experimental clutches might be potential confounding factor: white zebra finch eggs appeared to be easier to spot (at least for humans) than bluish eggs of pale-eyed thrushes or white, rusty-flecked eggs of Andean solitaires. On the other hand, another open-nester common in our study site, the chestnut-capped brush finch *Buarremon brunneinucha*, has snowy-white eggs (HFG unpubl. data). Bright white objects are common in the forest understory as many fungi produce fruiting bodies of this color, thus it is not likely that this color attracts particular attention.

Another source of possible bias that we did not control for was possible re-visitation of previously depredated nests by predators with good spatial memory. This factor was not controlled for in other similar studies (Cresswell 1997, Martin et al. 2000b), and at the current state of knowledge it is difficult to judge if the problem is serious.

Exposed clutches

To examine the potential effects of the nest and nest site, 20 clutches of two zebra finch eggs were exposed in places that we subjectively perceived as easy to access and not concealed. We chose sites that were similar to naturally built nests of these species. Nine clutches were placed on fallen tree trunks, another 8 in shallow hollows in the bark on standing trunks, and the remaining 4 on banks. We avoided places where, during heavy rains, water may have jeopardized the eggs. Exposed clutches were checked from a distance to avoid attracting attention of possible predators, every 2–3 d during 17 d of exposure, or until they were destroyed. The date of predation was determined in the same manner as for natural nests. All exposed clutches were located within our study area and we conducted the experiment in Mar.–Apr. 2005, in parallel with monitoring natural nests.

Statistical analysis

We calculated daily survival rates (DSRs) of natural nests during incubation, unattended nests, and exposed clutches using Mayfield's (1975) method. DSRs are presented with standard errors (Johnson 1979). We decided to use the original Mayfield's method because it is quite robust and tolerant for small samples, and performs well when intervals between nest-checks are short (Johnson 1979, Hazler 2004), as in our study. Only two planned comparisons of DSRs were done (natural vs unattended nests and unattended nests vs exposed clutches), thus we proceeded using the test proposed by Johnson (1979). P-values are two-tailed.

Results and discussion

Natural nests during the incubation period survived significantly better than unattended nests ($Z = 3.335$, $P < 0.001$; Table 1). To make sure that pooling natural nests of two species into one sample (see Methods) did not produce biased results, we repeated the analysis including only the nests of pale-eyed thrushes, for which the sample size was sufficient (22 natural nests and 23 unattended nests). Again natural clutches survived better than clutches in unattended nests (respective DSR values were $97.9\% \pm 1.4$ vs $93.3\% \pm 1.4$; $Z = 2.300$, $P = 0.02$).

Our results suggest that parents provide protection for the nest and, at least during incubation, parental activity increases nest survival rather than, as Skutch's (1949) hypothesis predicts, lowering it (Martin et al. 2000a, b). Such findings are consistent with the pattern described by

Fontaine et al. (2007) who also found higher survivability in natural nests compared to artificial nests baited with eggs and unattended by adult birds. The authors interpreted this result very cautiously, suggesting that it might either reflect the importance of parental care or their "inability to adequately simulate nest sites chosen by real birds" (experimental nests used in the study were made by researchers, who also selected nest sites). The former explanation seems to be more likely, however, as in a multi-factorial analysis of survivability Fontaine and co-workers found a marginally significant ($P \leq 0.05$, after controlling for nest type and year) effect of nest attendance by parent birds. Our data, which were collected within one breeding season in an experiment using un-manipulated natural nests of only one type, strengthen such an interpretation. We hypothesize that adult birds are able to exclude a group of opportunistic nest predators that destroy clutches in the absence of adults (Weidinger 2002, Remeš 2005). Parents may also lower vulnerability of the nest to predation simply by concealing eggs during incubation and thus increasing the crypticity of the clutch (Hailman and Woolfenden 1985).

Though Skutch (1949) specifically addressed birds of the humid tropics, few studies thus far have attempted to test predictions of the hypothesis in tropical birds and, surprisingly, most of them yielded negative results. For two Afrotropical warblers, in a study correlating nest predation to adult activity levels (during both incubation and nestling periods), neither the number of parental visits to the nest, nor the proportion of time spent at the nest by parents, explained variability in nest survival (Schaefer et al. 2005). In a similar study in Mexico (Rangel-Salazar et al. 2008), female nest-attentiveness increased survival of nestlings, but the number of parental visits to the nest was lower for successful than for failed nests during incubation. Finally, two experimental studies manipulating number of nestlings in Neotropical, altricial birds revealed that predation risk was not related to brood size (Young 1996, Styrsky et al. 2005). Only in slaty antshrikes *Thamnophilus atrinucha*, studied in Panama, was survival rate of clutches significantly higher in nests unattended by parent birds than in naturally active nests (Roper 2003). Also Libsch et al. (2008) demonstrated that most nest-predation in a lowland, Panamanian forest occurred during the day, which coincides with the time when adult birds are active. Though this result supports Skutch's hypothesis, it remains unclear if predators use cues provided by parental activity.

The survivability of exposed clutches was the lowest, but did not differ significantly from the DSR of unattended nests ($Z = 1.424$, $P = 0.155$; Table 1). The difference between DSRs ($0.941 - 0.902 = 0.039$), suggesting higher mortality of exposed clutches was fairly large, however, and its 95% CI (-0.015 to 0.093) barely overlapping 0, may

Table 1. Survival statistics for three group of clutches.

Treatment	n	Nest-days		DSR	SE
		successful	with predation		
Natural nests	33	160	2	0.9877	0.0087
Unattended nests	39	429	27	0.9408	0.0111
Exposed clutches	20	129	14	0.9021	0.0249

suggest that its insignificance was due to small sample size. Thus nest site characteristics might play some role, though further studies are needed to draw firmer conclusions. In wet tropical areas it is possible that nest sites might be of lesser importance than in the temperate zone, where they can affect nest success (Muchai and du Plessis 2005, Fontaine et al. 2007). In the tropics, where nest predator guilds are more diverse and different predators search for prey using an array of cues and methods of hunting, refuge might be difficult to find (Filliater et al. 1994, Lindell et al. 2004). In such conditions the relative significance of nest defense over nest concealment would be expected to increase (Weidinger 2002).

In conclusion, our study species (thrushes nesting in understory layer of tropical wet forest) parental presence increases survivability of clutches, whereas nest site selection appears to be less important. Other studies separating the protective effects of nest site selection and parental nest attendance are needed to reveal if such a pattern is widespread.

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