



Special Issue Article: Tropical Insectivores

## Increased abundance, but reduced nest predation in the chestnut-backed antbird in Costa Rican rainforest fragments: surprising impacts of a pervasive snake species



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## ARTICLE INFO

## Article history:

Received 1 April 2014

Received in revised form 8 January 2015

Accepted 17 January 2015

Available online 11 February 2015

## Keywords:

Birds

Costa Rica

Fragmentation

La Selva Biological Station

*Myrmeciza exsul*

Nest predation

Predators

*Pseustes*

## ABSTRACT

Understory insectivorous birds often disappear from fragmented tropical rainforest landscapes before mechanisms such as increased rate of nest depredation can be evaluated. Here, we took advantage of chestnut-backed antbird (*Myrmeciza exsul*), a representative rainforest understory insectivore that persists in fragments (unlike many other understory species), to identify variables influencing nest predation rate and to test the hypothesis that nest predation underlies avian extirpation in tropical fragments. We compared nest predation rates, bird density, and predator identities in three habitats of lowland Caribbean Costa Rica: two fragments, a peninsular reserve (La Selva Biological Station), and unfragmented rainforest. Our results suggest an inversely density-dependent nest predation pattern: In fragments, chestnut-backed antbirds reached their highest density and—contrary to predictions—experienced their lowest nest predation rates; La Selva on the other hand experienced the lowest density and highest predation rate. Because nest predation decreased with fragmentation, it appears not to explain declines of understory insectivores from forest fragments generally. Nest survival models indicated that habitat best explained nest predation likelihood, whereas edge, annual, and nest age effects were unimportant. Video surveillance documented both bird-eating snake (*Pseustes poecilonotus*) causing 80% of nest loss overall (37 of 46 nests) and a larger variety of predators in fragments; thus, landscape factors influenced an understory bird's nest predation. Given the large effect on our focal species, *Pseustes* likely affects other understory nesters, a topic warranting further study. Tropical reserve conservation plans should consider potential impacts of specialized nest predators on vulnerable understory birds.

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## 1. Introduction

Animal extirpation in fragmented tropical forest landscapes is non-random; patterns of guild decline and loss following fragmentation are often predictable (Bierregaard and Lovejoy, 1989; Ferraz et al., 2007). Larger animals, for example, tend to disappear first from fragments due to the bushmeat trade (Duffy, 2003). Another highly vulnerable group includes understory insectivorous birds and ant-following birds (Şekercioğlu et al., 2002; Sigel et al., 2006; Stouffer and Bierregaard, 1995; Stratford and Stouffer, 1999). Whereas patterns of sensitivity have been identified, we still lack demographic or ecological explanations for most avian responses to tropical forest fragmentation or other global change phenomena, hampering conservation efforts (Robinson and Sherry, 2012).

Mechanisms affecting bird populations in fragmented landscapes typically reduce survival or reproduction. Nest predation is one such mechanism that may limit avian populations (Newton, 2003; Ricklefs, 1969) and has long been suspected as a factor threatening bird populations in temperate (Heske et al., 2001) and tropical forest fragments (Oniki, 1979). However, it is generally difficult to generalize about nest predation over broad scales, among birds with different nest structures, or even among similar species (Brawn et al., 2011). Whereas some studies find relatively high nest predation for tropical birds (Robinson et al., 2000), others—especially at higher elevations—find rates similar to those in temperate forests (Martin, 1996; Skutch, 1985). A potential influence on nest predation that remains understudied in the tropics is density dependence (but see Boyle, 2008). Dense territories can increase predators' ability to find the more closely-spaced nests (Martin, 1988; McKellar et al., 2014; Page et al., 1983). Yet bird density and nest predation are not always positively correlated, and multiple life-history traits and contexts are relevant (Ricklefs, 2000; Schmidt and Whelan, 1999).

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Alternatively, in areas of low bird density (e.g. due to factors independent of nest predation), less prey would be available for nest predators, and therefore the nests they depredate would represent a greater proportion of the total, resulting in an inverse relationship.

Elevated nest predation rate may involve altered predator types in fragments or the loss of top down predation pressure, which releases middle-sized predator populations such as snakes, monkeys, or coatimundis; (i.e. mesopredator release; Crooks and Soule, 1999). Identifying predators is central to testing these hypotheses. Because of the infrequency of both predator identification and predictable patterns of nest predation, some have called for more research identifying predators (Lahti, 2009; Robinson and Robinson, 2001) and their ecology (Ribic et al., 2012; Spanhove et al., 2009b; Weatherhead and Blouin-Demers, 2004). Predator identification connects bird demographic patterns with community ecology and trophic dynamics. Nest predator species may respond demographically and behaviorally to land-use change differently from their prey (Thompson, 2007). Predator diversity and abundance is often higher along habitat boundaries such as agriculture/forest edges because both forest-dwelling predators and generalist predators from agricultural habitat can access nests, and this may disproportionately affect small forest fragments (Andrén, 1992; Marini et al., 1995; Møller, 1989; Tewksbury et al., 2006). Nevertheless, Chalfoun et al. (2002) recognized how nest predator responses to fragmentation are complex, taxon-specific, and context-dependent. Explanations of nest predation rate patterns without both descriptive information of avian populations and predator identities are thus risky.

The temperate-zone literature has abundantly documented increased nest predation and brood parasitism in forest fragments (Donovan et al., 1995; Luck, 2003; Tewksbury et al., 2006), in areas of decreased forest cover (Robinson et al., 1995), and closer to edges (Batory and Baldi, 2004). Effects of the proximity of nests to the habitat border, or edge effects, are also frequently investigated. Recent reviews have both supported (Batory and Baldi, 2004) and rejected (Lahti, 2001) the existence of consistent edge effects on nest predation, but these reviews have often not distinguished between temperate and tropical forests. The relevant tropical literature tends to show either equivocal edge effects (Chiarello et al., 2008; Young et al., 2008) or inverse effects, with lower nest predation rates near edges than in forest interior (as documented in the Afrotropics: Carlson and Hartman, 2001; Spanhove et al., 2009a). Despite invocations of nest predation to explain tropical forest bird population dynamics in fragmented landscapes (Sodhi et al., 2004; Stratford and Robinson, 2005), adequate tests of this mechanism are rare.

Some evidence suggests that tropical forest interior birds experience reduced nesting success in fragments, but most such studies have been criticized. Many have used artificial nests (e.g. Gibbs, 1991; Githiru et al., 2005; Sieving, 1992), which are now widely considered biased and unrepresentative of rates and predators on natural nests in the tropics (Moore and Robinson, 2004; Roper, 1992). Unfortunately, comparative tropical fragment nest predation studies using real nests are few (but see Laurance et al., 2002; Newmark and Stanley, 2011; Young et al., 2008), reflecting the challenge of finding adequate numbers of often cryptic nests on large territories (Robinson et al., 2000). Rapid species loss from fragments exacerbates the problem by preventing tests in many landscapes. Indirect predator-identification techniques such as imprints on plasticine eggs, hair traps, and track plates are increasingly questionable in light of recent camera and video studies (Pietz and Granfors, 2005; Thompson and Burhans, 2003). In the Neotropics, no study to date has adequately identified nest predators with video camera sample sizes per species over ten (Weidinger, 2008), nor made comparisons at the landscape scale.

Anecdotal data suggest the importance of snakes (e.g. *Pseustes poeilonotus*, *Boa constrictor*, and *Spilotes pullatus*) as nest predators, along with diverse birds (e.g. raptors, jays, toucans, oropendolas, antshrikes), monkeys, coatimundis, opossums, and army ants (Reidy, 2009; Riehl and Jara, 2009; Robinson and Robinson, 2001; Robinson et al., 2005; Tarwater, 2008). Although these are invaluable documentations of nest predator diversity, many species were identified only once, and most knowledge comes from Panama.

The present study tested the nest predation decline mechanism within a fragmented Costa Rican landscape, the Sarapiquí (Caribbean) lowlands. Using the chestnut-backed antbird (*Myrmeciza exsul*), an understory insectivorous bird that persists in fragments, we compared nest predation rates and nest predator identities in habitats with varying degrees of fragmentation. We also quantified chestnut-backed antbird population density to test its potential impact on nest predation risk, as previous observations reported high density in a fragment (Woltmann et al., 2010). No single species represents an entire guild, as species are by nature unique, but they can help control for many variables. This single species' occurrence across a landscape along with evidence of moderate declines at La Selva (Sigel et al., 2006) made it a good choice for this investigation. To the extent that its nests and life histories are similar to other understory birds, chestnut-backed antbirds can help us understand, and perhaps even predict other species' persistence or declines. Here, we identified factors related to nest predation that might permit the persistence in fragments of chestnut-backed antbirds, and perhaps other understory birds in general. We hypothesized that nest predator taxa vary spatially and thus influence the nest predation rate. Because we expected nest predator taxa to be more diverse and bird populations to be denser in fragments, we expected nest predation rate also to be highest in fragments, and we predicted elevated nest predation rate near forest edges, based on potential exposure to more predator types.

## 2. Methods

### 2.1. Study species

Chestnut-backed antbirds (family Thamnophilidae) are small, insectivorous understory passerines. Like many antbirds, they forage opportunistically at army-ant swarms, but more often solitarily (Willis and Oniki, 1972). They are resident in lowland rainforests (generally <1000 m elevation) from Honduras to Ecuador, where both sexes defend their territory year-round (Losada-Prado et al., 2014; Woltmann et al., 2010). Chestnut-backed antbirds are monogamous, and they build small, open-cup nests containing 1–2 eggs 10–40 cm off the ground (Greeney et al., 2013). Such nest types are vulnerable to various predators (Sieving, 1992). Care of eggs and nestlings is biparental (Skutch, 1969). Researchers may discover nests using a search image plus the birds' parental behaviors including distinctive alarm calls given near the nest. Genetic and experimental studies indicate that chestnut-backed antbirds disperse extremely poorly (Moore et al., 2008; Woltmann et al., 2012), so colonization ability cannot explain their persistence in isolated forest fragments. Unlike most thamnophilids, chestnut-backed antbirds persist widely in small rainforest fragments (Roberts, 2007; Woltmann et al., 2010), making them suitable for comparative landscape study.

### 2.2. Site description

The Sarapiquí region of Costa Rica lies in the country's northern Caribbean slope of the Cordillera Central Mountains (Fig. 1). Until recently, the area was largely covered by lowland tropical wet forest, which is now a patchwork due to rapid deforestation following

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