



Nesting Success of Costa Rican Lowland Rain Forest Birds in Response to Edge and Isolation Effects

Bruce E. Young¹, Thomas W. Sherry, Bryan J. Sigel, and Stefan Woltmann

NatureServe, 1101 Wilson Boulevard, 15th Floor, Arlington, Virginia 22209, U.S.A.

Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, Louisiana 70118, U.S.A.

ABSTRACT

Although open-cup nesting birds generally face increased risk of nest depredation from forest edge predators and brood parasites in fragmented temperate landscapes, little information exists to assess such risks in tropical birds. We compared nesting success of real birds' nests in large and small forest fragments to a control site in Caribbean lowland wet forest of Costa Rica. Pooling across species, nesting success was significantly greater in unfragmented forest than in either small, isolated fragments or the La Selva Biological Reserve, which is at the tip of a forest 'peninsula' embedded in a largely deforested landscape. Nesting success in isolated fragments did not vary according to distance from edge, suggesting that predators in fragments act throughout these forest patches. The case for increased nest predation as a plausible mechanism to explain the documented decline of forest interior bird populations in this fragmented tropical landscape is enhanced by a simple demographic model that suggests nesting success is likely too low to maintain populations at La Selva and in the fragments. The fact that the large (> 1000 ha) La Selva forest reserve is experiencing nest predation rates similar to those in much smaller fragments is cause for concern. Our results make a strong case for additional studies to document the identities of nest predators in both fragmented and unfragmented forests in such tropical forest landscapes.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: forest edge; forest fragmentation; nest predation; nest success; tropical birds; tropical forest.

CONSERVATION BIOLOGISTS HAVE FOCUSED MUCH ATTENTION on the consequences of habitat loss and fragmentation for tropical bird populations (*e.g.*, Thiollay 1997, Bierregaard *et al.* 2001, Stratford & Robinson 2005, Stouffer *et al.* 2006), where the stakes are high due to high species richness. This richness typically declines with decreasing forest patch size (Stratford & Stouffer 1999, Stouffer *et al.* 2006, Ferraz *et al.* 2007) and increasing isolation and time (Ferraz *et al.* 2003, Ferraz *et al.* 2007). Primary mechanisms that drive these patterns in temperate regions are reduced nesting success due to increased nest predators and brood parasites (Wilcove 1985, Wilcove *et al.* 1986, Robinson *et al.* 1995), both associated with edge habitat, as well as reduced pairing success (Lampila *et al.* 2004). Although additional mechanisms of population extirpation appear to operate in tropical landscapes (Sodhi *et al.* 2004, Stratford & Robinson 2005, Lindell *et al.* 2007), the potential detrimental effect of diverse nest predators in fragmented tropical landscapes remains poorly evaluated (Brawn *et al.* 1998, Stratford & Robinson 2005). Thus, an important step to understand tropical forest fragmentation impacts on birds is to address whether or not birds experience reduced nesting success in tropical forest fragments (Bierregaard & Stouffer 1997, Brawn *et al.* 1998).

Based on limited evidence, nest predation appears to increase in fragmented tropical landscapes. First, tropical nest predators are relatively diverse, including many species of reptiles, mammals, and birds (Ricklefs 1969, Skutch 1985, Roper & Goldstein 1997, Robinson & Robinson 2001, Robinson *et al.* 2005a). This is likely to expose forest edge birds to many potential predators. Second, tropical nest predator populations are likely controlled by higher

trophic level predators that typically disappear from fragmented landscapes. The 'meso-predator release' hypothesis states that nest predator densities in human-generated habitat patches are expected to increase as fragmentation progresses (Soulé *et al.* 1988, Turner 1996, Crooks & Soulé 1999). This mechanism is not restricted to tropical environments, but has attracted attention from tropical ecologists because large cats and other top predators often disappear from fragmented landscapes. A complication is that humans typically hunt in the most accessible forest patches, and the diversity of prey species and intensity of hunting pressure can vary widely (Robinson 1996, Peres 2000, Peres & Lake 2003). Thus, if hunted species are also the major nest predators in a system, humans may replace top carnivores in fragmented landscapes and prevent nest predation from rising dramatically. However, because much tropical avian nest predation appears to be from snakes (Skutch 1985, Robinson & Robinson 2001, Weatherhead & Blouin-Demers 2004, Robinson *et al.* 2005a), which are typically killed only opportunistically by humans, one hypothesis is that a decrease in top predators could lead to an increase in reptilian nest predators. Unfortunately, we generally lack data on snake abundance in tropical forests, and the potential for snakes to control populations of birds remains poorly investigated in tropical regions (but see Wiles *et al.* 2003 for an extreme example).

Brood parasites might also pose a threat to nesting success by tropical birds. For example, the Neotropics contain more species of brood parasites, including cowbirds (*Molothrus* spp.) and some cuckoos (*Tapera naevia*, *Dromococcyx* spp.), than most temperate regions. However, most tropical cowbirds and all three parasitic cuckoos parasitize only a narrow range of hosts (Sick 1993, Payne 1997), in contrast to the generalist brown-headed cowbird (*M. ater*) in North

Received 20 August 2007; revision accepted 13 December 2007.

¹Corresponding author; e-mail: bruce_young@natureserve.org

America (Lowther 1993). The shiny cowbird (*M. bonariensis*), the one Neotropical cowbird with a wide host range and an expanding geographic range, does not yet appear to threaten Neotropical forest birds as much as the brown-headed cowbird threatens forest-based species in North America (Lowther & Post 1999, Stratford & Robinson 2005; but see Woodworth 1997). Although increased brood parasitism is a serious problem in some tropical secondary forest and scrub habitats (Woodworth 1997, 1999), it is not currently a widespread consequence of tropical forest fragmentation on breeding birds in mainland Neotropical forests. A variety of Palearctic cuckoos are brood parasites on forest interior insectivorous birds, but some may also be more sensitive to fragmentation than their hosts, and thus pose little, if any, threat to their host populations in fragmented forest landscapes (Payne 1997, Brooker & Brooker 2003).

We understand how patch size, edge effects, degree of isolation, and other factors associated with forest fragmentation have impacted temperate bird communities (*e.g.*, Robinson *et al.* 1995, Villard *et al.* 1999, Sallabanks *et al.* 2000, Lloyd *et al.* 2005) far better than in the tropics. A persistent barrier to understanding nest predation impacts in tropical landscapes is the difficulty of finding large numbers of sparsely distributed and well-concealed nests, and a consequent reliance on artificial nest studies. However, such studies are likely to be biased because predators and predation rates often differ between artificial and natural nests (Moore & Robinson 2004, Thompson & Burhans 2004, Robinson *et al.* 2005b).

Few studies of fragmentation effects on natural nests exist from tropical forests (Turner 1996, Lahti 2001, Chalfoun *et al.* 2002). In Costa Rica, Lindell and Smith (2003) found that the main effect of fragmentation on forest interior species was a loss of breeding habitat; many forest species simply did not nest in the nonforest plots. However, taking species that nested in both forest and nonforest, nest success rate did not differ between pasture, abandoned coffee plantation, and mature forest (Lindell & Smith 2003). Because their study area was largely forested, it is possible that the nonforested areas were too small and isolated to contain a full suite of nest predators typical of deforested landscapes, but predators were not identified (Lindell & Smith 2003). Insufficient evidence exists to date to evaluate the effects of tropical forest fragmentation on nest success.

The Caribbean lowlands of Costa Rica are appropriate for studying forest fragmentation because the region has undergone intense deforestation over the past 40 yr. Forest habitats remain almost exclusively in private and public reserves (Sánchez-Azofeifa *et al.* 1999, Read *et al.* 2001, Sánchez-Azofeifa *et al.* 2001). La Selva Biological Station is part of a large forested peninsula in a largely agricultural landscape in the northern Caribbean lowlands (Butterfield 1994). La Selva and other smaller forest fragments have lost a significant number of forest-based avian species in the past 30–40 yr (Rangel-Salazar 1995, Matlock *et al.* 2001, Sigel *et al.* 2006, Sigel 2007). The Organization for Tropical Studies successfully protects its La Selva property from poachers, as evidenced by the increases in recent decades in populations of monkeys, medium-sized cursorial mammals including opportunistic nest predators such as white-nosed coati (*Nasua narica*) and collared peccary (*Pecari tajacu*; T.W.

Sherry, pers. obs.). Increases in opportunistic nest predators could be a factor contributing to the declines and disappearances of forest interior bird species from the region's forest fragments.

In this study, we asked how daily nest survivorship and nest success vary among small forest fragments, peninsular La Selva, and the much larger Braulio Carrillo National Park. We predicted lower daily nest survival in all the fragmented sites compared to the two reserve sites (La Selva and Braulio Carrillo). We also predicted that within the fragments proximity to edge would decrease nesting success, based on pronounced edge effects in some temperate zone birds (but see Walters 1998, Lahti 2001), and based on tropical forest edge effects involving the physical environment and diverse organisms (*e.g.*, Laurance *et al.* 2002) that could impact birds directly or indirectly. Across all sites, we asked how nest type influences nesting success, and we predicted that cavity and covered nests would experience higher survival than open cup or ground nests (Martin 1995). Finally, we developed a simple demographic model to explore consequences of fragmentation-caused changes in nesting success.

METHODS

STUDY SITES.—The six study sites consisted of four rain forest fragments, the La Selva Biological Reserve (hereafter 'La Selva'), and Braulio Carrillo National Park (hereafter 'Braulio Carrillo'; Table 1; Fig. 1). All are characterized as tropical wet forest (Holdridge 1967) and consist of old-growth forest with average canopy height of 28–38 m (Lieberman *et al.* 1985). Rainfall at La Selva averages 3692 mm annually, with only a brief drier period typically in January through March (Sanford *et al.* 1994). Precipitation was not measured at Braulio Carrillo, but is likely to be greater due to its higher elevation on the windward side of the Central Volcanic Cordillera (Coen 1983).

The four fragments were isolated from extensive forest during the early to mid 1980s, and are now completely surrounded by banana plantations. All fragments were disturbed more recently to some degree by the extraction of a few large trees. Agricultural workers dug drainage ditches in the Gavilán fragment in preparation for clearing to extend a banana plantation, but then abandoned the effort. The fragments are separated from each other and all other forest remnants by over 2 km. The fragments are separated from La Selva by 4.5–11 km of agricultural lands dominated by banana plantations.

La Selva is located at the tip of an 18 × 4–5 km peninsula of protected forest connected to Braulio Carrillo National Park (> 40,000 ha; Fig. 1). The peninsula also rises steeply in elevation from 100 m asl at the La Selva-Braulio Carrillo boundary to 1000 m asl where it connects to the main body of the park. All La Selva study plots were in old-growth forest located > 500 m from younger forest. The Braulio Carrillo plots were located > 2 km from the nearest disturbed or edge area. Plots in fragments were located centrally within each fragment, although the plot edges in the smallest fragments were as close as 30 m to the fragment

TABLE 1. Characteristics of the six study sites in northeastern Costa Rica.

Character	Braulio Carrillo	La Selva	La Colonia	Hotel	Gavilán	Nogal
Landscape type	Large reserve	Peninsular reserve	Fragment	Fragment	Fragment	Fragment
Extent of old-growth forest (ha)	> 40,000	1000	40	20	10	20
Elevation (m asl)	400	60	20	20	20	20
1997 Plot size (ha), number of plots	–	4, 4	–	–	4, 2	4, 2
1998 Plot size (ha), number of plots	6, 2	6, 2	6, 1	6, 1	4, 2	4, 2

edge. To increase the independence of the samples, the 1998 plots did not overlap the 1997 plots at La Selva. The two fragments studied in both 1997 and 1998 (Gavilán and Nogal) were too small to contain annually nonoverlapping plots. The other three sites (Braulio Carrillo, La Colonia, and Hotel) were sampled only in 1998.

Although all sites are in the same life zone, the Braulio Carrillo site is at a higher elevation (Table 1). Ideally this large reserve site would be at the same elevation as the other sites, but the few other large reserves below 100 m on the Atlantic slope in Costa Rica (*e.g.*, Tortuguero National Park) are substantially smaller, and logistically far more difficult to study. Some bird species typical of higher elevation forest are more common in the Braulio Carrillo plot than at La Selva, but most lowland species also occur at the site used for this study (Stiles *et al.* 1989). Furthermore, bird species similarity observed on our La Selva and Braulio Carrillo plots (Jaccard Index [JI] = 0.40) falls well within the range of similarities between fragmented plot sites at the same elevation (JI = 0.32–0.61).

Most of the potential nest predators we detected occurred at all sites (B. E. Young, unpubl. data). Only top predators and primates requiring large home ranges were missing from the fragments, while one squirrel species occurred only in the fragments. The local brood parasites, bronzed cowbird (*Molothrus aeneus*) and striped cuckoo, generally parasitize birds nesting in more disturbed areas than our forested study sites. The brood parasitic giant cowbird (*M. oryzivorus*) parasitizes only oropendolas (*Psarocolius* spp.), which nest too high to be monitored in the present study.

NEST SEARCHING.—We searched for nests within plots from January to July 1997, and March to June 1998 (see Table 1 for plot sizes). We searched each plot thoroughly twice each week from 0630 h to 1200 h using standard methods (Ralph *et al.* 1993). We also visited all active nests twice weekly to monitor nesting success. To prevent potential nest predators from detecting nests as a result of human activity (*e.g.*, Götmark 1992), we checked nests with single observers from as far away as feasible with binoculars. When possible, we checked nests during our normal nest searching to avoid making special trips to the nest area.

DATA ANALYSES.—We calculated nesting success using the Mayfield (1961, 1975) method, assuming all nests whose contents disappeared before fledging to be lost to predation. The analyses included only those nests whose contents we could observe regularly. We be-

gan counting exposure days for nests when we first saw an egg or chick in the nest. We scored nests that fledged reduced broods as successful because most predators take all eggs or chicks (Ricklefs 1969, Robinson *et al.* 2000). For nests that were abandoned (eggs cold), we included exposure days that preceded abandonment in the analysis as predation-free days, and estimated abandonment date in the same way as predation date. We did not score the abandonment event as a nest loss because of the possibility that our nest visits caused the abandonment.

We compared daily survival rates in different landscape contexts using CONTRAST (Sauer & Williams 1989), based on

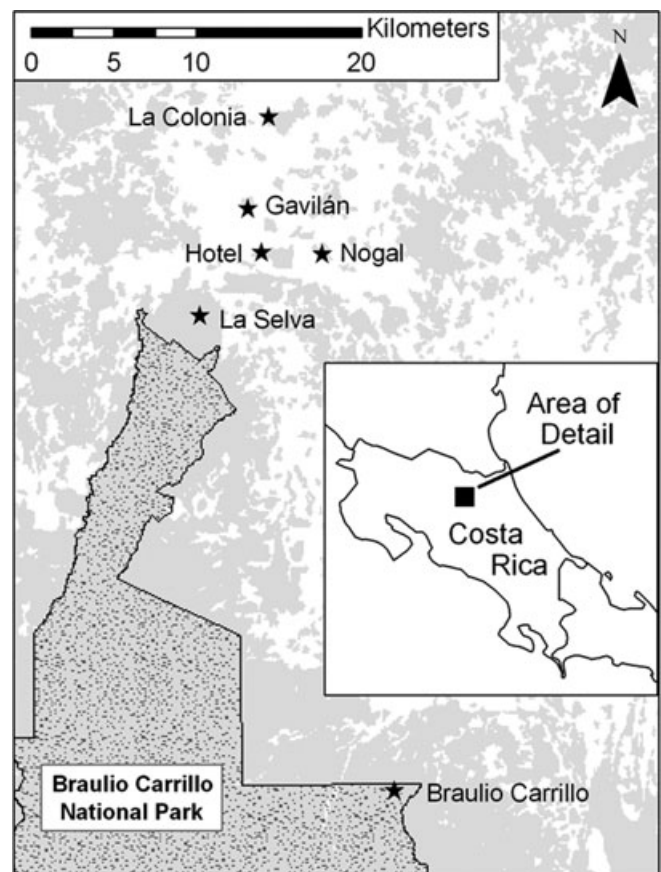


FIGURE 1. Map of Costa Rican study plot locations. Shaded areas represent remaining forest cover according to LANDSAT data collected in 2000.

Chi-squared distributions. To allow estimation of overall nesting success, we assumed that laying, incubation, and nestling stages combined last 30 d, an average for the species with published nesting period information (Skutch 1954, 1960, 1969). An average was necessary in our calculations because we did not have separate daily nesting success data by species. We assumed that daily survival rates do not vary with nesting stage and other possible covariates, admittedly an oversimplification (*e.g.*, Rotella *et al.* 2004); and we also assumed that nesting success from one day to the next is statistically independent. Sample sizes were insufficient to examine variation among nesting stages.

Sample sizes were also insufficient to compare daily survivorship for any single species among the three landscape classes. For example, the species whose nests were found most frequently was *Thamnophilus atrinucha*, with only 14 nests (Table S1). We argue it is reasonable to pool all species here based on the assumption that few nest predators distinguish nests according to species. Rather, nest predators probably make gross distinctions based on nest accessibility and, in the case of snakes, eggs or chicks that are small enough to be consumed. Thus, instead of grouping by species we compared nesting species by ecological factors more likely to be meaningful to nest predators: (1) all species; (2) species that construct open-cup nests; (3) hummingbirds (all of which in this study attached their open-cup nests to the tips of palm leaflets or *Heliconia* spp. leaves); and (4) species or genera that were common to two or more landscape classes. To test the hypothesis that enclosed and cavity nests are safer from predation than open nests, we compared the daily survivorship of all cavity (including burrow) and enclosed (including domed, retort-shaped, or pyriform) nests versus open-cup nests, again using CONTRAST.

To determine whether nesting success increased with distance from forest edge we categorized nests *a priori* as edge (< 75 m), intermediate (76–125 m), or interior (> 125 m), and then compared daily survivorship using CONTRAST. These categories are arbitrary, but correspond to changes in microclimate and increased presence of nonforest species at ≤ 75 m from edges, and to decreases in invertebrate abundance and canopy height at up to 125 m from edges (Laurance *et al.* 2002). We performed this analysis only on nests found in fragments because all study plots at La Selva and Braulio Carrillo were > 500 m from edges. All data are presented as mean \pm 1 SE.

DEMOGRAPHIC MODEL.—We explored the practical effect of fragmentation-caused differences in nesting success using a simple demographic model parameterized for the spotted antbird (*Hylophylax naevioides*; Table 2, largely from Styrsky 2003), one of the rain forest understory species included in the present study. Our female-based model assumes that birds begin reproducing when they are 1-yr old, that the population is spatially discrete (corresponding to isolation in a forest fragment), that reproduction takes place during one breeding season per year, and that age does not influence reproductive success or survivorship. The closed form of the model is

$$\lambda = s_a + i(c/2)ns_j,$$

TABLE 2. Spotted Antbird life-history measures used to parameterize the demographic model.

Life-history measure	Term in model	Value (\pm 95% CI)	Source
Adult survivorship ¹	s_a	0.75 (0.066)	Styrsky 2003
Clutch size	c	2 ²	Robinson <i>et al.</i> 1999
Number of nests initiated per year	i	4	Styrsky 2003
Annual survivorship from fledging to age 1 yr	s_j	0.24 (0.06)	Scaled from tropical population of <i>Troglodytes aedon</i> , Young 1996 ³

¹Adult male and female survivorship are not significantly different (Styrsky 2003).

²The model assumes one egg per clutch yields a female offspring, *i.e.*, balanced sex ratio.

³Assumes higher fledgling survivorship proportional to the higher adult survivorship of spotted antbirds, *i.e.*, $s_j(\text{antbird}) = s_j(\text{wren}) \times s_a(\text{antbird})/s_a(\text{wren})$.

where λ is the population multiplication rate, s_a is adult survivorship, i is the number of clutches initiated per year, c is clutch size (dividing by 2 assumes an equal sex ratio), n is nesting success, and s_j is juvenile survivorship, *i.e.*, from fledging to entry into the breeding population the following year. Setting λ equal to 1 and solving for n yields the minimum nesting success needed to stabilize the female population.

RESULTS

NESTING SUCCESS.—During the 2 yr of study we monitored 130 nests of 43 species on all plots (Table S1). The majority of nests were found during the dry season (February–mid May). We found most of the nests early in the nesting cycle, either in construction (12%) or incubation (73%) stages. We detected no annual differences in daily survivorship in either La Selva or the fragments (using CONTRAST), thus we present results of data pooled across years from these sites (other sites were only sampled in one year). Overall, nesting success was poor. For the entire study, all nests pooled, daily survivorship probability was 0.954 ± 0.005 , yielding a nesting success of 24.4 percent (0.954^{30} , *i.e.*, the product of average daily survival rate for all 30 d of the standard nest-exposure period). Predation was responsible for 91 percent of all failed nests. The remaining nests failed due to either branch or treefalls, or flooding, the sole causes of abandonment observed here. No abandonment was attributable to human disturbance. Additionally, no nests were parasitized by either cowbirds or cuckoos.

Daily survivorship, based on pooled nests for all species, was significantly higher at Braulio Carrillo than either La Selva or the isolated small fragments (Table 3). Estimated nesting success was 2.5 times higher at Braulio Carrillo than elsewhere. The pattern for open-cup nests parallels that found overall nest success was at least

TABLE 3. Nesting success of birds in three landscape classes in northern Costa Rica. Nesting success is calculated assuming a 30-day nesting period (i.e., daily survival probability raised to the power of 30; see Methods). Differences in nesting success are tested with χ^2 .

Comparison	Landscape class									χ^2 (df)	<i>P</i>
	Braulio Carrillo			La Selva			Fragments				
	<i>N</i>	Daily survival probability (SE)	Nesting success	<i>N</i>	Daily survival probability (SE)	Nesting success	<i>N</i>	Daily survival probability (SE)	Nesting success		
All nests	25	0.977 (0.008)	0.501	47	0.948 (0.009)	0.200	58	0.948 (0.008)	0.202	8.6 (2)	0.01
Open cup nests	14	0.973 (0.012)	0.437	34	0.932 (0.013)	0.125	42	0.951 (0.009)	0.222	5.3 (2)	0.07
Hummingbirds	—	—	—	16	0.949 (0.016)	0.206	27	0.962 (0.010)	0.310	0.49 (1)	0.48
Species/genera in common to > 1 landscape class	15	0.975 (0.011)	0.466	40	0.945 (0.011)	0.182	40	0.946 (0.010)	0.192	4.9 (2)	0.08

twice as high at Braulio Carrillo than elsewhere, but this was not statistically significant ($P = 0.07$). We found no hummingbird nests at Braulio Carrillo, and daily survivorship of hummingbird nests did not differ in the two other landscape classes. Finally, a comparison of only those species or genera for which we found nests in more than one of the three landscape classes showed a nonsignificant trend for daily survivorship to be greater at Braulio Carrillo than either La Selva or the fragments.

NEST TYPE.—Nest type did not appear to influence daily survivorship in this study. Daily survivorship of cavity (0.970 ± 0.011 ; $N = 14$), enclosed (0.958 ± 0.013 ; $N = 21$), and open cup (0.950 ± 0.006 ; $N = 95$) nests from all the sites pooled did not differ significantly ($\chi^2 = 2.70$, $df = 2$, $P = 0.26$).

DISTANCE FROM EDGE.—The distance of a nest from a fragment edge also did not influence daily survivorship. Daily survivorship of edge (0.929 ± 0.064 ; $N = 19$), intermediate (0.961 ± 0.056 ; $N = 24$), and interior (0.950 ± 0.069 ; $N = 15$) nests did not differ significantly ($\chi^2 = 0.14$, $df = 2$, $P = 0.93$).

DEMOGRAPHIC MODEL.—Using demographic parameters for the Spotted Antbird (Styrsky 2003; Table 2), one of the best-known species at our study site demographically, we estimate that an average of 0.266 (95% CI: 0.156–0.454) nesting success is necessary for a stable population. Populations in which females require more than one year to mature, those with fewer nesting attempts per season, and those with lower adult survivorship (e.g., in fragments) would require even higher nesting success to persist. Nesting success at both La Selva and the fragments was lower than 0.22 for all comparisons (except hummingbirds occurring in fragments), whereas the measures of success for nests in Braulio Carrillo were all greater than 0.43.

DISCUSSION

This study is among the first tropical studies to demonstrate an influence of forest fragmentation on overall avian nesting success using real nests, although pooled across species. Birds inhabiting small forested fragments had less than half the nesting success of birds nesting in the large forest reserve (Braulio Carrillo). A 1000-ha old-growth forest at La Selva, although connected by a corridor to a much larger protected area, did not afford any higher nesting success to forest interior birds than small 40-ha fragments. Thus, La Selva behaved as a forest fragment in terms of nesting success. Within fragments, distance from fragment edge in small fragments did not appear to influence nesting success.

What is the practical effect of the differences in nesting success we observed on population trends in this landscape? Although the differences seem to be substantial, the low nesting success might not be severe enough to prevent population persistence. For example, many tropical birds survive better as adults than temperate counterparts (Johnston *et al.* 1997, Ricklefs 1997, Peach *et al.* 2001, but see Karr *et al.* 1990, Sandercock *et al.* 2000), and tropical birds also appear to reneest more readily following failure (Sieving & Karr 1997). Our demographic model represents a first, approximate attempt to calculate for tropical rain forest species the minimum nesting success necessary for breeding adults to replace themselves. Our model is simplistic, e.g., by ignoring age-specific nesting success and survival, and by parameterizing it for only one forest interior species. Nonetheless, the model supports the contention that observed differences in nesting success potentially explain why populations of some species have declined in tropical forest fragments: The nesting success we have documented at La Selva and in nearby fragments appears to be sufficiently low (< 0.19) to fail to maintain populations, particularly in La Selva open-cup nests (Table 3). If fragments also experience either reduced adult survival, juvenile survival, clutch size, or number of reneesting attempts, all of which seem plausible, then even greater nesting success would be necessary to maintain the populations.

The finding of relatively high nest predation rates in the smallest fragments and at La Selva suggests that the relevant nest predators responded to aspects of the landscape such as forest patch area and isolation. Further interpretation of our results requires identifying and quantifying the nest predators, and doing so at a landscape scale. The only satisfactorily unbiased way to identify predators at real nests is with cameras, which are expensive and logistically challenging at any scale (Moore & Robinson 2004, Robinson *et al.* 2005a, b). Larger sample sizes of nests are also clearly desirable, both to parameterize demographic models and to examine species and nest-type differences in susceptibility to nest predators. For example, we likely lacked the statistical power to detect expected effects of nest type, which have been documented in other tropical studies (*e.g.*, Robinson *et al.* 2000).

The lack of a detectable edge effect *per se* on nest success further suggests a landscape scale effect of nest predation. Moreover, this apparent lack of an edge effect suggests that whatever animals contributed to nest depredation in the region may not be edge-associated species, in contrast to many temperate forest fragmentation studies, but instead appear to be species that become disproportionately abundant or effective at finding nests *throughout* forest fragments, not just at forest edges. This interpretation is consistent with other tropical studies that have documented imbalanced trophic relationships throughout forest islands (*e.g.*, Terborgh *et al.* 2001, Feeley 2003, Feeley & Terborgh 2006), although those studies involved true islands created by dam construction. We did not explicitly test for an edge effect in the Braulio Carrillo and La Selva sites due to the location of these study sites well within large forests. It is possible that our classification of 'edge' (in terms of distance) is too narrow, or that a different set of distance criteria for categorizing nests would better test for an edge effect. Although we may have failed to detect an edge effect due to small sample sizes, the very existence of a landscape effect (reduced nest success overall in our smallest fragments) indicates that very large sample sizes would be necessary to detect any edge effect, *i.e.*, to detect further reductions in nesting success near the site exteriors. Further study of potential edge effect in large forests is needed to understand the relative importance of edge versus landscape-scale effects. In a south-temperate landscape in Chile, the evidence for an edge effect on nest success depended on the edge context: edges of fragments were actually safer from nest predation than fragment interiors, but there was no apparent edge effect in large, control plots (De Santo *et al.* 2002). All of these issues further justify the need to identify nest predators, and to continue evaluating the likelihood that nest predators benefit from forest edge.

Perhaps one of the most disturbing results of this study is that La Selva behaves as a much smaller fragment with respect to nest predation. La Selva is one of the larger (1600 ha of old and second growth) Neotropical reserves, and one that is often considered a 'control' site in studies of forest fragmentation (*e.g.*, Blake & Loiselle 2001, 2002; Matlock *et al.* 2001; Bell & Donnelly 2006). La Selva also behaves as a much smaller fragment in terms of avian diversity and community composition (Sigel *et al.* 2006, Sigel 2007). This suggests that La Selva's avian diversity is currently limited by abnormally high rates of nest predation combined perhaps with limited

immigration from the Braulio Carrillo corridor or any other potential source areas in the region. Thus, some of the most pressing research needs in fragmented tropical landscapes such as La Selva are the identification of nest predators and quantification of dispersal ability in different sized corridors, and across different kinds of non old-growth forest matrices.

ACKNOWLEDGMENTS

We thank the many landowners who allowed access to properties in their care: M. Madrid and C. Vega at Chiquita Brands Company, R. Rios at the Rainforest Aerial Tram in Braulio Carrillo, M. Amalia Sotela at Hotel Gavilán Lodge, J. Corea at La Colonia, and R. Matlock at La Selva. For invaluable logistic and field help we thank R. Alvarado, R. Chester, M. Denton, A. Downs, Y. Hernández, A. Illes, L. Castillo, J. Lacayo, and especially field leader J. Zook. Funding for this research came from the Chiquita Brands Company, the George Storrer Foundation, the British Embassy in Costa Rica, the Tinker Foundation via the Roger Thayer Stone Center for Latin American Studies (Tulane University), the Society of Sigma Xi, and Organization for Tropical Studies Fellowship (to B.J.S.), and A. W. Mellon Research Exploration Award in Tropical Biology via the Organization for Tropical Studies (to T.W.S. and B.J.S.). S.W. was supported by a Louisiana Board of Regents Fellowship during the preparation of this manuscript. P. Stouffer and two anonymous reviewers provided important insights that improved this manuscript.

SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online at: www.blackwell-synergy.com/loi/btp

TABLE S1. *Type, sample size, and daily survivorship for 130 avian nests found in the six study sites in northeastern Costa Rica.*

LITERATURE CITED

- BELL, K. E., AND M. A. DONNELLY. 2006. Influence of forest fragmentation on community structure of frogs and lizards in northeastern Costa Rica. *Conserv. Biol.* 20: 1750–1760.
- BIERREGAARD, R. O., JR., AND P. C. STOUFFER. 1997. Understory birds and dynamic habitat mosaics in Amazonian Rainforests. *In* W. F. Laurance, and R. O. Bierregaard (Eds.). *Tropical forest remnants: Ecology, management, and conservation of fragmented communities*, pp. 138–155. University of Chicago Press, Chicago, Illinois.
- BIERREGAARD, R. O., JR., C. GASCON, T. E. LOVEJOY, AND R. MESQUITA (EDS.). 2001. *Lessons from Amazonia: The ecology and conservation of a fragmented forest*. Yale University Press, New Haven, Connecticut.
- BLAKE, J. G., AND B. A. LOISELLE. 2001. Bird assemblages in second-growth and old-growth forests, Costa Rica: Perspectives from mist nets and point counts. *Auk* 118: 304–326.
- BLAKE, J. G., AND B. A. LOISELLE. 2002. Manakins (Pipridae) in second-growth and old-growth forests: Patterns of habitat use, movements and survival. *Auk* 119: 132–148.
- BRAWN, J. D., S. K. ROBINSON, D. F. STOTZ, AND W. D. ROBINSON. 1998. Research needs for the conservation of Neotropical birds. *In*

- J. M. Marzluff and R. Sallabanks (Eds.). Avian conservation: Research and management, pp. 323–335. Island Press, Washington, DC.
- BROOKER, M., AND L. BROOKER. 2003. Brood parasitism by Horsfield's Bronze-Cuckoo in a fragmented agricultural landscape in Western Australia. *Emu* 103: 357–361.
- BUTTERFIELD, R. P. 1994. The regional context: Land colonization and conservation in Sarapiquí. In L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (Eds.). *La Selva: Ecology and natural history of a Neotropical rain forest*, pp. 299–306. University of Chicago Press, Chicago, Illinois.
- CHALFOUN, A. D., F. R. THOMPSON, III, AND M. J. RATNASWAMY. 2002. Nest predators and fragmentation: A review and meta-analysis. *Conserv. Biol.* 16: 306–318.
- COEN, E. 1983. Climate. In D. H. Janzen (Ed.). *Costa Rican natural history*, pp. 35–46. University of Chicago Press, Chicago, Illinois.
- CROOKS, K. R., AND M. E. SOULÉ. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400: 563–566.
- DE SANTO, T. L., M. F. WILLSON, K. E. SIEVING, AND J. J. ARMESTO. 2002. Nesting biology of tapaculos (Rhynocryptidae) in fragmented south-temperate Rainforests of Chile. *Condor* 104: 482–495.
- FEELEY, K. 2003. Analysis of avian communities in Lake Guri, Venezuela, using multiple assembly rule models. *Oecologia* 137: 104–113.
- FEELEY, K. J., AND J. W. TERBORGH. 2006. Habitat fragmentation and effects of herbivore (Howler Monkey) abundances on bird species richness. *Ecology* 87: 144–150.
- FERRAZ, G., G. J. RUSSELL, P. C. STOUFFER, R. O. BIERREGAARD, JR., S. L. PIMM, AND T. E. LOVEJOY. 2003. Rates of species loss from Amazonian forest fragments. *Proc. Natl. Acad. Sci. USA* 100: 14069–14073.
- FERRAZ, G., J. D. NICHOLS, J. E. HINES, P. C. STOUFFER, R. O. BIERREGAARD, JR., AND T. E. LOVEJOY. 2007. A large-scale deforestation experiment: Effects of patch area and isolation on Amazon birds. *Science* 315: 238–241.
- GOTMARK, F. 1992. The effects of investigator disturbance on nesting birds. In D. M. Power (Ed.). *Current Ornithology* Vol. 9, pp. 63–104. Plenum Press, New York, New York.
- HOLDRIDGE, L. R. 1967. *Life zone ecology*. Tropical Science Center, San José, Costa Rica.
- JOHNSTON, J. P., W. J. PEACH, R. D. GREGORY, AND S. A. WHITE. 1997. Survival rates of tropical and temperate passerines: A Trinidadian perspective. *Am. Nat.* 150: 771–789.
- KARR, J. R., J. D. NICHOLS, M. K. KLIMKIEWICZ, AND J. D. BRAWN. 1990. Survival rates of birds of tropical and temperate forests: Will the dogma survive? *Am. Nat.* 136: 277–291.
- LAHTI, D. C. 2001. The “edge effect on nest predation” hypothesis after twenty years. *Biol. Conserv.* 99: 365–374.
- LAMPILA, P., M. MÖNKKÖNEN, AND A. DESROCHERS. 2005. Demographic responses by birds to forest fragmentation. *Conserv. Biol.* 19: 1537–1546.
- LAURANCE, W. F., T. E. LOVEJOY, H. L. VASCONCELOS, E. M. BRUNA, R. K. DIDHAM, P. C. STOUFFER, C. GASCON, R. O. BIERREGAARD, JR., S. G. LAURENCE, AND E. SAMPAIO. 2002. Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conserv. Biol.* 16: 605–618.
- LIEBERMAN, D., M. LIEBERMAN, G. HARTSHORN, AND R. PERALTA. 1985. Growth rates and age-size relationships of tropical wet forests in Costa Rica. *J. Trop. Ecol.* 1: 97–109.
- LINDELL, C., AND M. SMITH. 2003. Nesting bird species in sun coffee, pasture, and understory forest in southern Costa Rica. *Biodivers. Conserv.* 12: 423–440.
- LINDELL, C. A., S. K. RIFFELL, S. A. KAISER, A. L. BATTIN, M. L. SMITH, AND T. D. SISK. 2007. Edge responses of tropical and temperate birds. *Wilson J. Ornithol.* 119: 205–220.
- LLOYD, P., T. E. MARTIN, R. L. REDMOND, U. LANGNER, AND M. M. HART. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. *Ecol. App.* 15: 1504–1514.
- LOWTHER, P. 1993. Brown-headed Cowbird (*Molothrus ater*). In A. Poole, and F. Gill (Eds.). *The birds of North America*, No. 47. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, DC.
- LOWTHER, P., AND W. POST. 1999. Shiny Cowbird (*Molothrus bonariensis*). In A. Poole, and F. Gill (Eds.). *The birds of North America*, No. 399. The Birds of North America, Inc., Philadelphia, Pennsylvania.
- MARTIN, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.* 65: 101–127.
- MATLOCK, R. B., JR., D. ROGERS, P. J. EDWARDS, AND S. G. MARTIN. 2001. Avian communities in forest fragments and reforestation areas associated with banana plantations in Costa Rica. *Agric., Ecosyst. Environ.* 181: 1–17.
- MAYFIELD, H. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73: 255–261.
- MAYFIELD, H. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87: 456–466.
- MOORE, R. P., AND W. D. ROBINSON. 2004. Artificial bird nests, external validity, and bias in ecological field studies. *Ecology* 85: 1562–1567.
- PAYNE, R. B. 1997. Family Cuculidae (Cuckoos). In J. Del Hoyo, A. Elliott, and J. Sargatal (Eds.). *Handbook of the birds of the world*, Vol. 4, pp. 508–610. Lynx Edicions, Barcelona, Spain.
- PEACH, W. J., D. B. HANMER, AND T. B. OATLEY. 2001. Do southern African songbirds live longer than their European counterparts? *Oikos* 93: 235–249.
- PERES, C. A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conserv. Biol.* 14: 240–253.
- PERES, C. A., AND I. R. LAKE. 2003. Extent of nontimber resource extraction in tropical forests: Accessibility to game vertebrates by hunters in the Amazon basin. *Conserv. Biol.* 17: 521–535.
- RALPH, C. J., G. R. GEUPEL, P. PYLE, T. E. MARTIN, AND D. F. DESANTE. 1993. *Handbook of field methods for monitoring landbirds*. General Technical Report PSW-GTR-144. Pacific Southwest Research Station, Forest Service, US Department of Agriculture, Albany, California.
- RANGEL-SALAZAR, J. L. 1995. *Diversidad de aves de sotobosque asociadas a plantaciones de banano en Costa Rica*. MSc Dissertation, Universidad Nacional de Costa Rica, San José, Costa Rica.
- READ, J. M., J. S. DENSLow, AND S. M. GUZMAN. 2001. Documenting land-cover history of a humid tropical environment in northeastern Costa Rica using time-series remotely sensed data. In A. C. Millington, S. J. Walsh, and P. E. Osborne (Eds.). *GIS and remote sensing applications in biogeography and ecology*, pp. 69–89. Kluwer, Boston, Massachusetts.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* 9: 1–48.
- RICKLEFS, R. E. 1997. Comparative demography of New World populations of thrushes (*Turdus* spp.). *Ecol. Monogr.* 67: 23–43.
- ROBINSON, J. G. 1996. Hunting wildlife in forest patches: An ephemeral resource. In J. Schelhas, and R. Greenberg (Eds.). *Forest patches in tropical landscapes*, pp. 111–130. Island Press, Washington, DC.
- ROBINSON, S. K., F. R. THOMPSON, III, T. M. DONOVAN, D. R. WHITEHEAD, AND J. FAABORG. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267: 1987–1990.
- ROBINSON, W. D., T. R. ROBINSON, S. K. ROBINSON, AND J. D. BRAWN. 2000. Nesting success of understory forest birds in central Panama. *J. Avian Biol.* 31: 151–164.
- ROBINSON, W. D., AND T. R. ROBINSON. 2001. Observations of predation events at bird nests in central Panama. *J. Field Ornithol.* 72: 43–48.
- ROBINSON, W. D., G. ROMPRÉ, AND T. R. ROBINSON. 2005a. Videography of Panama bird nests shows snakes are principal predators. *Ornithologia Neotropical* 16: 187–195.
- ROBINSON, W. D., J. N. STYRSKY, AND J. D. BRAWN. 2005b. Are artificial bird nests effective surrogates for estimating predation on real bird nests? A test with tropical birds. *Auk* 122: 843–852.
- ROPER, J. J., AND R. R. GOLDSTEIN. 1997. A test of the Skutch hypothesis: Does activity at nests increase nest predation risk? *J. Avian Biol.* 28: 111–116.

- ROTELLA, J. J., S. J. DINSMORE, AND T. L. SHAFFER. 2004. Modeling nest-survival data: A comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodivers. Conserv.* 27: 187–205.
- SALLABANKS, R., J. R. WALTERS, AND J. A. COLLAZO. 2000. Breeding bird abundance in bottomland hardwood forests: Habitat, edge and patch size effects. *Condor* 102: 748–758.
- SÁNCHEZ-AZOFEIFA, A., C. QUESADA-MATEO, P. GONZALEZ-QUESADA, S. DAYANANDAN, AND K. S. BAWA. 1999. Protected areas and conservation of biodiversity in the tropics. *Conserv. Biol.* 13: 407–411.
- SÁNCHEZ-AZOFEIFA, G. A., R. C. HARRISS, AND D. L. SKOLE. 2001. Deforestation in Costa Rica: A quantitative analysis using remote sensing imagery. *Biotropica* 33: 378–384.
- SANDERCOCK, B. K., S. R. BEISSINGER, S. H. TOLESON, R. R. MELLAND, AND C. R. HUGHES. 2000. Survival rates of a Neotropical parrot: Implications for latitudinal comparisons of avian demography. *Ecology* 81: 1351–1370.
- SANFORD, R. L., JR., P. PAABY, J. C. LUVALL, AND E. PHILLIPS. 1994. Climate, geomorphology, and aquatic ecosystems. In L. A. McDade, K. S. Bawa, H. A. Hespeneheide, and G. S. Hartshorn (Eds.). *La Selva: Ecology and natural history of a Neotropical rain forest*, pp. 19–43. University of Chicago Press, Chicago, Illinois.
- SAUER, J. R., AND B. K. WILLIAMS. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. *J. Wildl. Manage.* 53: 137–142.
- SICK, H. 1993. *Birds in Brazil*. Princeton University Press, Princeton, New Jersey.
- SIEVING, K. E., AND J. R. KARR. 1997. Avian extinction and persistence mechanisms in lowland Panama. In W. F. Laurance, and R. O. Bierregaard, Jr. (Eds.). *Tropical forest remnants: Ecology, management, and conservation of fragmented communities*, pp. 156–170. University of Chicago Press, Chicago, Illinois.
- SIGEL, B. J., T. W. SHERRY, AND B. E. YOUNG. 2006. Avian community response to lowland tropical Rainforest isolation: 40 years of change at La Selva Biological Station, Costa Rica. *Conserv. Biol.* 20: 111–121.
- SIGEL, B. J. 2007. The susceptibility of tropical forest bird communities to forest fragmentation. PhD Dissertation, Tulane University, New Orleans, Louisiana.
- SKUTCH, A. F. 1954. Life histories of Central American birds. *Pacific Coast Avifauna* 31.
- SKUTCH, A. F. 1960. Life histories of Central American birds II. *Pacific Coast Avifauna* 34.
- SKUTCH, A. F. 1969. Life histories of Central American birds III. *Pacific Coast Avifauna* 35.
- SKUTCH, A. F. 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. *Ornithol. Monogr.* 36: 575–594.
- SODHI, N. S., L. H. LIOW, AND F. A. BAZZAZ. 2004. Avian extinctions from tropical and subtropical forests. *Annu. Rev. Ecol. Evol. Syst.* 35: 323–345.
- SOULÉ, M. E., D. T. BOLGER, A. C. ALBERTS, J. WRIGHT, M. SORICE, AND S. HILL. 1988. Reconstructed dynamics of rapid extinctions on chaparral-requiring birds in urban habitat islands. *Conserv. Biol.* 2: 75–92.
- STILES, F. G., A. F. SKUTCH, AND D. GARDNER. 1989. *A guide to the birds of Costa Rica*. Cornell University Press, Ithaca, New York.
- STOUFFER, P. C., R. O. BIERREGAARD, C. STRONG, AND T. E. LOVEJOY. 2006. Long-term landscape change and bird abundance in Amazonian rainforest fragments. *Conserv. Biol.* 20: 1212–1223.
- STRATFORD, J. A., AND P. C. STOUFFER. 1999. Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. *Conserv. Biol.* 13: 1416–1423.
- STRATFORD, J. A., AND W. D. ROBINSON. 2005. Gulliver travels to the fragmented tropics: Geographic variations in mechanisms of avian extinction. *Front. Ecol. Environ.* 3: 85–92.
- STYRSKY, J. N. 2003. Life history evolution and population dynamics of a Neotropical forest bird (*Hylophylax naevioides*). PhD Dissertation, University of Illinois at Urbana-Champaign, Illinois.
- TERBORGH, J., L. LOPEZ, N. V. PERCY, M. RAO, G. SHAHABUDDIN, G. ORIHUELA, M. RIVEROS, R. ASCANIO, G. H. ADLER, T. D. LAMBERT, AND L. BALBAS. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294: 1923–1926.
- THIOLLAY, J.-M. 1997. Disturbance, selective logging and bird diversity: A Neotropical forest study. *Biodivers. Conserv.* 6: 1155–1173.
- THOMPSON, F. R., III, AND D. E. BURHANS. 2004. Differences in predators of artificial and real songbird nests: Evidence of bias in artificial nest studies. *Conserv. Biol.* 18: 373–380.
- TURNER, I. M. 1996. Species loss in fragments of tropical rainforest: A review of the evidence. *J. Appl. Ecol.* 33: 200–209.
- VILLARD, M., M. K. TRZCINSKI, AND G. MERRIAM. 1999. Fragmentation effects on forest birds: Relative influence of woodland cover and configuration on landscape occupancy. *Conserv. Biol.* 13: 774–783.
- WALTERS, J. R. 1998. The ecological basis of avian sensitivity to habitat fragmentation. In J. M. Marzluff, and R. Sallabanks. (Eds.). *Avian conservation: Research and management*, pp. 181–192. Island Press, Washington, DC.
- WEATHERHEAD, P. J., AND G. BLOUIN-DEMERS. 2004. Understanding avian nest predation: Why ornithologists should study snakes. *J. Avian Biol.* 35: 185–190.
- WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66: 1211–1214.
- WILCOVE, D. S., C. H. MCLELLAN, AND A. P. DOBSON. 1986. Habitat fragmentation in the temperate zone. In M. E. Soulé (Ed.). *Conservation biology*, pp. 237–256. Sinauer Associates, Inc. Sunderland, Massachusetts.
- WILES, G. J., J. BART, R. E. BECK JR., AND C. F. AGUON. 2003. Impacts of the brown tree snake: Patterns of decline and species persistence in Guam's avifauna. *Conserv. Biol.* 17: 1350–1360.
- WOODWORTH, B. L. 1997. Brood parasitism, nest predation, and season-long reproductive success of a tropical island endemic. *Condor* 99: 605–621.
- WOODWORTH, B. L. 1999. Modeling population dynamics of a songbird exposed to parasitism and predation and evaluating management options. *Conserv. Biol.* 13: 67–76.
- YOUNG, B. E. 1996. An experimental analysis of small clutch sizes in tropical House Wrens. *Ecology* 77: 472–488.