

FLEXIBILITY IN NEST-SITE CHOICE AND NESTING SUCCESS OF *TURDUS RUFIVENTRIS* (TURDIDAE) IN A MONTANE FOREST IN NORTHWESTERN ARGENTINA

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ABSTRACT.—We studied the consequences of nest-site choice on nesting success under differing disturbance levels for the Rufous-bellied Thrush (*Turdus rufiventris*). We compared nest-site choice and nest success between a disturbed site and an undisturbed site in a montane subtropical forest in northwestern Argentina. We found no overall difference in daily predation rate (DPR) between the disturbed and undisturbed sites. However, DPR of nests on bromeliads was significantly lower at the microhabitat level than on other types of substrates at the disturbed site. *T. rufiventris* used bromeliads for nesting more often than expected by chance at the disturbed site. DPR did not differ between substrates at the undisturbed site and *T. rufiventris* used all substrates according to their availability. Nests had higher predation at the disturbed site when DPR on non-bromeliad substrates was compared between disturbed and undisturbed sites. Nest fate was independent of nest height. Our results suggest *T. rufiventris*' flexibility in nest-site choice, as reflected by increased use of the safest sites, i.e., bromeliads, in the disturbed site compared to the undisturbed site, may allow this species to survive in an otherwise much riskier habitat. Our results illustrate how microhabitat-scale effects can mediate landscape scale effects. Received 24 October 2009. Accepted 7 April 2010.

Understanding habitat influences on nesting success of birds may be key to their successful conservation, given the sensitivity of this life stage to habitat disturbance (Martin 1992, Easton and Martin 2002). Nest success is influenced by nest-site choice in large part because nest-site characteristics can influence nest predation rates (Martin and Roper 1988, Martin 1993, Holt and Martin 1997, Martin 1998, De Santo et al. 2002, Easton and Martin 2002, Mezquida and Marone 2002, Kellett et al. 2003, Fontaine et al. 2007). Nest predation may be one of the main agents of natural selection influencing evolution of life history traits and nest-site choice (reviewed by Lima 2009, Martin and Briskie 2009). Flexibility in choosing a nest site may allow birds to optimize fitness by exploiting safer substrate types in disturbed conditions, but studies of nesting flexibility and their consequences for nest success are rare.

Nest-site choice, including nesting substrate and nesting height, may be evolutionarily conser-

vative in many species (Martin 1988, Martin and Roper 1988), which may constrain plasticity of choices. Some bird species use the same nest sites in disturbed and undisturbed forest patches, even though this increases predation in disturbed forest patches (Holt and Martin 1997, Easton and Martin 2002). Plastic changes in nest-site selection in response to predation risk have been observed in some species (e.g., Marzluff 1988, Eggers et al. 2006, Peluc et al. 2008). Variation in predation risk is often associated with disturbance of habitats, which also generally reflects differing habitat structure; both differing predation risk and habitat structure could influence nest-site choice (Martin 1992). Few studies have compared nest site choices under differing predation risk or differing habitat structure.

Plasticity of nest-site choice is particularly interesting for tropical and subtropical birds, because they are often thought to have more specialized niches (MacArthur 1972). Consequently, their flexibility of nest-site choice to varying predation risk or habitat structure may be constrained. No study has examined plasticity of nest-site choice by a tropical or subtropical bird. Thus, examination of flexibility of nest-site choice and consequences of that choice on nesting success under differing disturbance levels for tropical or subtropical birds is needed.

Our objective was to test whether nest-site choice and nesting success of the Rufous-bellied Thrush (*Turdus rufiventris*; Turdidae) differed

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between a disturbed site and an undisturbed site in a montane subtropical forest in northwestern Argentina. *Turdus rufiventris* is a common bird that consumes fruits of many species in this environment (Malizia 2001), potentially having an important role in regeneration of native plants. It is widely distributed in central and northern Argentina (Ridgely and Tudor 1989, de la Peña and Rumboll 1998), and is one of the few native forest species that inhabits semi-urban locations (de la Peña and Rumboll 1998, Ferretti et al. 2005). The ability of members of the genus *Turdus*, including *T. rufiventris* (e.g., de la Peña and Rumboll 1998, Ferretti et al. 2005), to live in human-disturbed areas makes them good model species to study how birds adapt to habitat disturbance. Understanding the adaptability of species to disturbance is becoming increasingly important as anthropogenic habitat alterations become increasingly common and intact habitats increasingly rare (Pimm et al. 2001). Examining the effect of habitat characteristics in nest-site choice flexibility and nesting success is important in a threatened but understudied environment such as the subtropics (de la Peña 1979, Mezquida and Marone 2002). We examined nest-site preferences and consequences for nesting success of *T. rufiventris* between undisturbed and disturbed forest sites in northwestern Argentina.

METHODS

The study was conducted between October 1997 and January 1998 at El Rey National Park (hereafter El Rey; 24° 42' S, 64° 38' W) in Salta Province, and at Sierra de San Javier Biological Park (hereafter San Javier; 24° 47' S, 65° 22' W) in Tucumán Province. Both sites are in northwestern Argentina and are part of the Yungas ecosystem represented by a subtropical montane forest (Brown 1995, Brown et al. 2001). An old cattle farm, El Rey was declared a national park in 1948 and has been preserved intact with no human activity since then. It encompasses 44,162 ha, is 200 km from the nearest city, and no significant logging has been conducted in the area; it represents the undisturbed site. The canopy is dominated by *Cinnamomum porphyrium* (Lauraceae), *Blepharocalix salicifolius* (Myrtaceae), *Cedrella lilloi*, and *C. angustifolia* (Meliaceae). A second stratum is comprised of species typically <20 m high, including *Allophylus edulis* (Sapindaceae), *Zanthoxylum coco* (Rutaceae), and *Prunus tucumanensis* (Rosaceae)

(Blake and Rouges 1997). San Javier was created by the National University of Tucumán in 1973 and covers 14,100 ha; it is 15 km west of the city of San Miguel de Tucumán and 2 km northwest of the city of Yerba Buena. The area has been subject to different land uses including selective logging focused on the most valuable timber species (*Cedrella lilloi*) affecting a large proportion of the sierra, modern agriculture (sugar cane, citrus, horticulture, floriculture), and expanding urbanization (Grau et al. 2008). Trekking and biking trails cross the San Javier site. The secondary forest where we sampled occurs near agricultural and urban sectors (Grau et al. 1997, Aragón and Morales 2003), and represents our disturbed site. Common canopy species at San Javier are *Parapiptadenia exelsa* (Fabaceae), *Cinnamomum porphyrium* (Lauraceae), *Juglans australis* (Juglandaceae), and *Myrsine laetevirens* (Myrsinaceae) while the subcanopy is dominated by *Piper tucumanum* (Piperaceae), *Allophylus edulis* (Sapindaceae), and *Psychotria cartagenensis* (Rubiaceae) (Grau et al. in press). The native pioneers *Heliocarpus popayanensis* (Malvaceae), *Tecoma stans* (Bignoniaceae), *Solanum riparium* (Solanaceae), and exotic colonizers including *Morus* spp. (Moraceae), *Ligustrum lucidum* (Oleaceae), and *Citrus* spp. (Rutaceae) (Grau and Aragón 2000) are also common at San Javier. Bromeliads are one of the main groups represented among the abundant epiphytes both at San Javier and at El Rey (Blake and Rouges 1997).

We located nests following Martin and Geupel (1993). This method involves detecting and following birds carrying food or nesting material to the nest, or following female calls. Nest searching was done daily from 0630 to 1245 hrs from October to December. Nests were checked every 2–4 days to record nest stage (e.g., building, incubating, nestlings), number of eggs or nestlings when nests were accessible, nesting substrate, and nest height (Martin and Geupel 1993). The nest was considered failed or fledged if, after three checks, no bird activity was recorded at the nest (the last check had to be at least 30 min), depending on the stage recorded at the last active visit. We were unable to assign the cause of failure of many nests due to inaccessibility, but fledging was confirmed whenever possible by looking for parents with food or fledglings near the nest shortly after the assumed fledge date. We calculated nest success following Mayfield (1961) using the approach outlined by Hensler and

Nichols (1981). We compared daily predation rates between sites and between substrates using a Chi-square test based on program CONTRAST (Hines and Sauer 1989).

The two most common substrates used at San Javier, bromeliads and *Psychotria cartagenensis*, seemed to differ substantially in mean height, and the differences in daily predation rate found between the substrates could be attributed to substrate height and not to type of substrate *per se*. Thus, we tested whether the difference in substrate height was statistically significant using a Mann-Whitney *U*-test, and whether predation was independent of substrate height in San Javier using a Chi-square test.

We measured substrate availability based on the observed substrates used by *T. rufiventris* to examine if nests were randomly placed. We followed the quarter method (Matteucci and Colma 1982), modified to include bromeliad availability. We established two 200 m-long transects at random in the study area. The starting point of the transect was at the end of a random number of steps chosen by a person not familiar with the study site. A second random number indicated the orientation of the transect as measured by a compass. We established four quadrants every 10 m along each of these transects. We projected an imaginary line 17-m high (the maximum nest height recorded during this study) from the center point, and recorded the plant species closest to the imaginary line in each quadrant. We recorded when a bromeliad was the closest substrate, but not the substrate supporting the bromeliad. Only plants with >1.5 cm diameter at breast height (dbh) were recorded because no nest was found on plants with a smaller dbh. At least 160 plants were counted along each transect. We analyzed these data using a Z-test for comparing two proportions (Zar 1999) to examine if nest site was chosen according to plant availability.

RESULTS

We found 44 nests of Rufous-bellied Thrushes on 12 different substrates (Fig. 1A) at San Javier of which only 27 had at least one egg laid. Only those 27 nests were used to calculate nest success. All 44 nests at San Javier were included in the substrate use analyses. Sixty-five nests with at least one egg laid were found at El Rey on 19 different substrates (Table 1). These nests were used for estimating nest success and substrate use.

Nests at San Javier were most common on

Psychotria carthagenensis and bromeliads. However, bromeliads were used in higher proportion than expected according to their availability at San Javier while the other substrates (including *P. carthagenensis*) were used in lower proportion than expected ($Z = 10.8$, $df = 2$, $P < 0.0001$; Table 2). Substrates at El Rey were used as expected by their availability ($Z = 0.66$, $df = 2$, $P = 0.26$; Table 2).

Overall daily predation rate (DPR \pm SE) at San Javier (0.0684 ± 0.0095 , $n = 27$, exposure days = 248.5) did not differ from El Rey (0.0592 ± 0.0089 , $n = 65$, exposure days = 709; $X^2 = 0.669$, $df = 1$, $P = 0.414$). Nest success on *P. carthagenensis*, the most common understory shrub at San Javier, was not different from success on all substrates other than bromeliads ($X^2 = 0.5$, $df = 1$, $P = 0.48$) and substrates were combined for further analysis. Nests on bromeliads at San Javier were more successful (DPR = 0.0308 ± 0.0175 nests/day, $n = 7$, exposure days = 97.5) than nests on other substrates (DPR = 0.1126 ± 0.0257 nests/day, $n = 20$, exposure days = 151) ($X^2 = 6.92$, $df = 1$, $P = 0.0085$). Success of nests on bromeliads at El Rey (DPR = 0.0522 ± 0.0207 nests/day, $n = 9$, exposure days = 115) was not significantly different from success on other substrates (DPR = 0.0606 ± 0.0098 , $n = 56$, exposure days = 594) ($X^2 = 0.17$, $df = 1$, $P = 0.68$). We believe that lack of difference between substrates in DPR at El Rey was not affected by low sample size given the significant difference found for San Javier, where sample size was even smaller. Bromeliads were used more often at San Javier than at El Rey, and the high nest success on bromeliads may increase overall nest success at San Javier. Thus, we compared nest success between San Javier and El Rey without considering nests on bromeliads. Non-bromeliad nests experienced higher daily predation rates at San Javier than at El Rey ($X^2 = 4.076$; $df = 1$; $P = 0.044$).

Nests built on *P. carthagenensis* at San Javier were significantly lower ($\bar{x} = 2.1$ m) than those on bromeliads ($\bar{x} = 8.9$ m) (Mann-Whitney *U* = 10, $P = 0.0004$). However, nest success was independent of nest height ($X^2 = 0.50$, $df = 5$, $P = 0.48$). Nests occurred between 1 and 17 m above ground with a bimodal distribution (Fig. 1A). Most nests were between 1 and 2 m above the ground with a second peak of nests at 10 m. The two most common substrates mostly explained the distribution of nests at different heights (Fig. 1B).

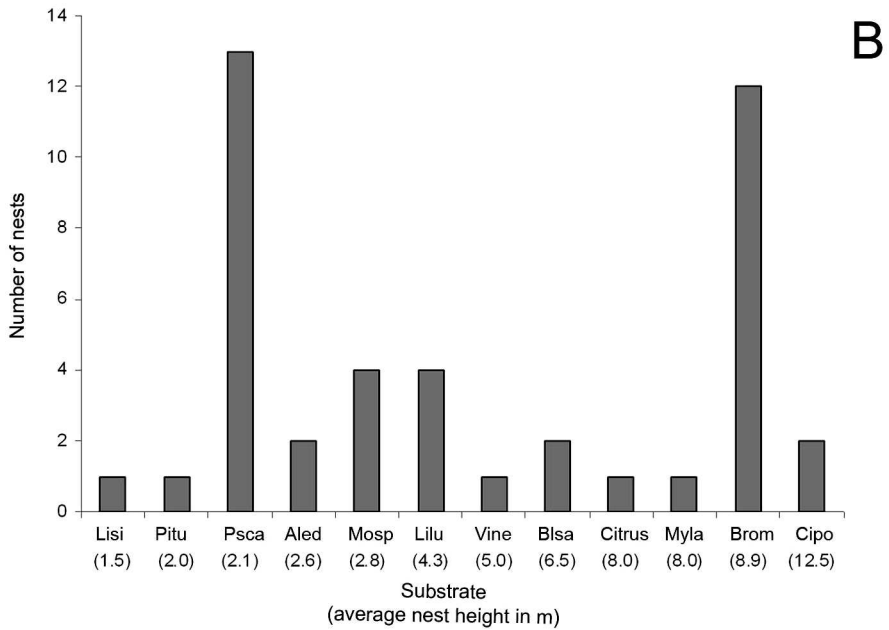
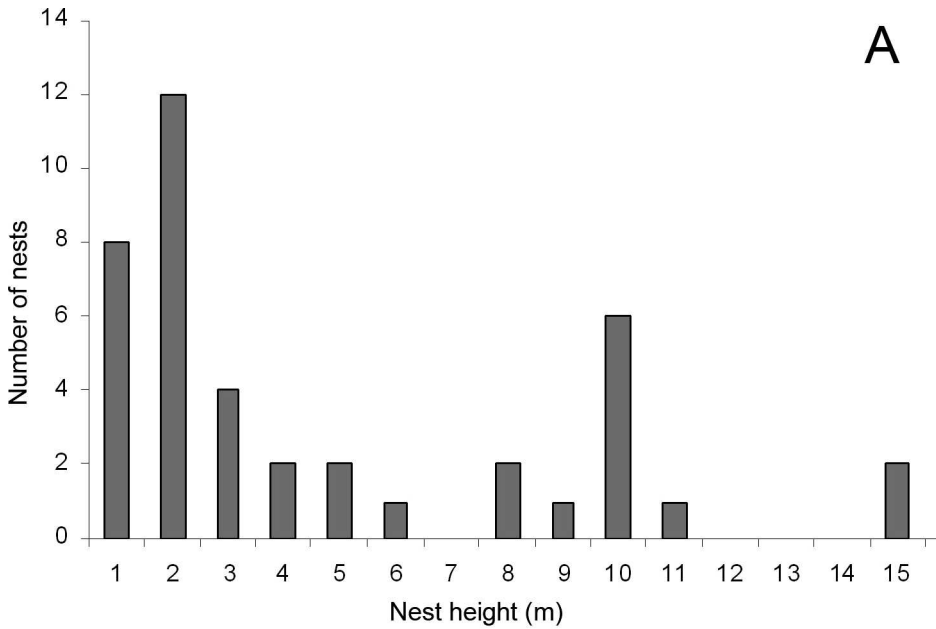


FIG. 1. (A) Distribution of *Turdus rufiventris* nest heights. (B) Number of *Turdus rufiventris* nests found per substrate species ($n = 42$). Numbers in parentheses show mean height at which nests were built on each substrate. Lisi: *Ligustrum sinense*; Pitu: *Piper tucumanum*; Psca: *Psychotria carthagenensis*; Aled: *Allophylus edulis*; Mosp: *Morus* spp., Lilu: *Ligustrum lucidum*; Vine: unidentified vine; Blsa: *Blepharocalyx salicifolius*; Citrus: *Citrus* spp.; Myla: *Myrsine laetevirens*; Brom: bromeliads; Cipo: *Cinnamomum porphyrium*.

TABLE 1. Substrates used by *Turdus rufiventris* at El Rey National Park, Salta, Argentina.

Substrate species	# Nests	Family
<i>Acacia aroma</i>	3	Fabaceae
<i>A. visco</i>	1	Fabaceae
<i>Allophylus edulis</i>	21	Sapindaceae
<i>Celtis spinosa</i>	1	Celtidaceae
<i>Condalia buxifolia</i>	3	Rhamnaceae
<i>Enterolobium contortisiliquum</i>	1	Fabaceae
<i>Eugenia uniflora</i>	1	Myrtaceae
<i>Gleditsia amorphoides</i>	2	Fabaceae
<i>Nectandra pichurim</i>	1	Lauraceae
<i>Pogonopus tubulosus</i>	1	Rubiaceae
<i>Sambucus peruviana</i>	2	Adoxaceae
<i>Scutia buxifolia</i>	5	Rhamnaceae
<i>Sideroxylon obtusifolium</i>	1	Sapotaceae
<i>Urera caracasana</i>	2	Urticaceae
<i>Vassobia breviflora</i>	1	Solanaceae
<i>Xylosma pubescens</i>	1	Salicaceae
Unidentified bromeliad	9	Bromeliaceae
Unidentified fern	1	
Unidentified moss	2	
Unidentified Myrtaceae	2	Myrtaceae
Unidentified vine	4	
Total	65	

DISCUSSION

The high variability of substrate type and nest height used by Rufous-bellied Thrushes is contrary to that expected if nesting was conserved within a species (Knight and Fitzner 1985; Dhindsa et al. 1988; Martin 1988, 1993; but see Forstmeier and Weiss 2004, Eggers et al. 2006, Peluc et al. 2008). This species nested on at least 12 substrate types, including understory shrubs, bromeliad epiphytes, canopy trees, and exotic as well as native species. *Turdus rufiventris* also placed nests at a wide range of heights from 1.5 to 17 m.

Rufous-bellied Thrushes did not seem to specialize on one substrate type, but were selective of nesting substrate, particularly at the site where microhabitat selectivity was associated with potential fitness benefits. *Turdus rufiventris* favored bromeliads, the substrate associated with highest nest success at San Javier, in accordance with the expectation that birds should maximize nest success (Martin 1998). In contrast, this species was not selective with respect to substrate at El Rey, where predation rates did not differ between nest sites.

Our results on nest-site choice and nest success in relation to disturbance differed depending on the scale at which we analyzed our data. Our results at a large scale did not support the hypothesis that anthropogenic disturbance increases the threat of nest predation (i.e., overall DPR was similar for San Javier vs. El Rey) (Holt and Martin 1997, De Santo et al. 2002, Easton and Martin 2002, Kellett et al. 2003). However, when examined at the microhabitat scale, we found that predation rate was much higher at the disturbed than at the undisturbed site. The higher predation rate at the disturbed site on non-bromeliad nest sites suggests predation rates were higher in the disturbed habitat but birds compensated through nest-site choice. These results confirm the importance of examining ecological patterns at multiple scales (Holling 1992, Levin 1992); if we had ignored microhabitat scale mechanisms, large scale disturbance effects would have been misinterpreted.

What makes bromeliads a safer nesting site at San Javier, and why is this not the case at El Rey? We showed that substrate height is not the determining factor; thus, bromeliads must be influencing other aspects of nest-site structure that affect predation risk. We believe bromeliad

TABLE 2. Nest success and number of nests of *Turdus rufiventris* (Turdidae) on bromeliads and other substrates, and substrate availability at El Rey National Park, Salta, and Sierra de San Javier Biological Park, Tucumán, Argentina.

	El Rey National Park	Sierra de San Javier Biological Park
Overall DPR	0.0592 ± 0.0089	0.0684 ± 0.0095
DPR on bromeliads	0.0522 ± 0.0207	0.0308 ± 0.0175
DPR on other substrates	0.0606 ± 0.0098	0.1126 ± 0.0257
Number of nests on bromeliads (% of total nests)	9 (14%)	7 (26%)
Number of nests on other substrates (% of total nests)	56 (86%)	20 (74%)
Substrate availability		
Bromeliads (%)	7	3
Others (%)	93	97

structure may make nests less visible and less vulnerable to predation by white-eared opossums (*Didelphis albiventris*) and black rats (*Rattus rattus*), which are common around houses in disturbed areas, but not to predation by House Wrens (*Troglodytes aedon*), Plush-crested Jays (*Cyanocorax chrysops*), and brown capuchin monkeys (*Cebus apella*), common nest predators in the undisturbed site (Auer et al. 2007). In addition, the relevant structural feature may be one that only influences predation risk in disturbed areas. Predator communities most likely differ between disturbed and undisturbed sites (Auer et al. 2007; J. P. Jayat, pers. comm.); thus, the relevant structural feature must be one that conceals nests from predators that occur in disturbed sites, either exclusively or at least in higher numbers.

Our results suggest a potential mechanism by which birds could adapt to the negative effects of human disturbance on nest predation risk. *Turdus rufiventris* apparently adjusts its nest-site choices to compensate for elevated predation risk in disturbed habitats. Additional studies of other species that compare both microhabitat choices and microhabitat-predation relationships in disturbed versus undisturbed areas are necessary to establish the generality of this mechanism. Studies of a range of species that vary in adaptability to human disturbance would be particularly helpful. Our ability to make general conclusions from this study is somewhat limited given the inclusion of only one disturbed site and one undisturbed site. Additional studies incorporating more replication would be valuable.

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