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Species-Specific Nest Site Selection by Birds in Ant-Acacia Trees¹

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ABSTRACT

We examined nest site differences among four bird species nesting in acacia (*Acacia collinsi*) trees with ants that may deter nest predators at Palo Verde, Costa Rica. Rufous-naped Wrens (*Campylorhynchus rufinucha*) showed a non-random preference for nesting in trees with unusually active ant colonies. They nested most commonly in trees with the most active ant species (*Pseudomyrmex spinicola* and *P. nigrocinctus*); and, when they nested in trees with a less active species of ant (*P. flavicornis*), these trees usually contained colonies that were more active than the average for their species. Other bird species (Streak-backed Oriole, *Icterus sclateri*; Yellow-olive Flycatcher, *Tolmomyias sulphurens*; Great Kiskadee, *Pitangus sulphuratus*) used trees for nests at random with respect to ant species and consequently these ants were much less active than ants on Rufous-naped Wren nest trees. We found no differences among bird species in tree size, local acacia density, or degree of nest isolation. Nest predation on eggs in artificial nests was higher in acacia than non-acacias due to pecking by Rufous-naped Wrens, suggesting that wrens may be inhibiting other bird species from nesting in the most protected nest sites.

RESUMEN

En Palo Verde, Costa Rica, hemos estudiado los sitios de anidamiento, en arboles de acacia (*Acacia collinsi*), de cuatro especies de aves. En esta especie de acacia viven colonias de hormigas que pueden disuadir a depredadores que atacan nidos. El soterrey matraquero (*Campylorhynchus rufinucha*) anidó en arboles que presentan colonias de hormigas más activas que aquellas que se encuentran en arboles de acacias con nidos de otra especie de ave o de arboles muestreados azarosamente que no presentan nidos de aves. El soterrey matraquero anidó más comunmente en arboles que presentan las colonias más activas de hormigas (*Pseudomyrmex spinicola* y *P. nigrocinctus*). Cuando el soterrey matraquero anidó en arboles con colonias de hormigas poco activas (*P. flavicornis*) siempre lo hizo seleccionando colonias más activas que el promedio. Otras especies de aves (chorcha, *Icterus sclateri*; pecho amarillo, *Tolmomyias sulphurens*; piquiplano azufrado, *Pitangus sulphuratus*) utilizaron para anidar arboles al azar con respecto a la especie de hormiga y consecuentemente estas hormigas fueron menos activas que en los arboles con soterrey matraquero. En nuestro estudio no encontramos diferencias entre las especies de aves en el tamaño del árbol de anidamiento, la densidad local de acacia, o el grado de aislamiento del nido. La depredación de huevos en los nidos artificiales fue mayor en arboles de acacia que en aquellos que no son acacias, debido al picoteo de los soterrey matraqueros. Estos resultados sugirieron que los soterreys pueden estar inhibiendo a otras especies de aves para que aniden en sitios de anidamiento más protegidos.

PREDATION IS COMMONLY A MAJOR agent of nesting mortality, especially in tropical land birds (Snow & Snow 1964; Skutch 1966; Willis 1961, 1974; Ricklefs 1969; Clark & Wilson 1981; but see Oniki 1979). Consequently, individuals should choose nest sites that reduce the risk of predation to young and adults (Martin & Roper 1988).

Swollen thorn ant-acacia trees in the lowland dry forests of the northern Neotropics may provide some protection from predators, which may explain use of these trees by wrens (Troglodytidae), flycatchers (Tyrannidae), orioles (Emberizidae: Icterinae), and antshrikes (Formicariidae; Janzen 1969). Acacia trees provide little foliage for nest concealment, but they have stout thorns and are host to colonies of ants commonly in the genus *Pseudomyrmex* (Janzen 1966, 1967a, b). The thorns and

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the ants' aggressive biting and stinging behavior may deter mammalian and reptilian predators (Janzen 1969). Indeed, bird nesting associations with social insects are well known (*cf.* Hindwood 1959; MacLaren 1950; McCrae & Walsh 1974; Myers 1929, 1935).

Effectiveness of predator deterrence by acacia tree nest sites may vary with several factors. **TREE SIZE**—bigger trees may have larger ant colonies that provide greater deterrence to predators. **ANT SPECIES**—obligate acacia ants vary in their aggressiveness (Janzen 1969, 1975) and more aggressive species may provide a greater deterrence to predators. **COLONY ACTIVITY**—the abundance of active ants may vary over a colony's lifetime; trees with fewer active ants may deter predators less than more active colonies. **TREE ACCESSIBILITY**—acacia trees with crowns near non-acacia trees may be more accessible to predators than isolated acacias. **ACACIA TREE DENSITY**—areas of high acacia density may also make nest trees more inaccessible to predators.

In this study we compared these five factors for acacia trees used by birds for nesting versus acacia trees not used for nesting. Also, we tested the assumption that acacias provide more protection to nests than other trees by comparing predation rates on artificial nests placed in acacia versus non-acacia trees. The results of this experiment shed light on a mechanism by which one species may be influencing nest site selection in other acacia-nesting species.

METHODS

We conducted this study 16–21 July 1988 in the Refugio Nacional de Fauna Silvestre Dr. Rafael Lucas Rodriguez Caballero at Palo Verde, Guanacaste Province, Costa Rica (10°20'N, 85°15'W; described by Slud 1980). We searched for acacia (*Acacia collinsi*) trees with recently built bird nests throughout the refuge. Some of these nests could have been used as dormitory nests (Skutch 1960, Wiley 1983).

At each nest tree we recorded the following information. We determined the bird species that built the nest. We measured tree dbh. We identified occupant ant species to three categories: *Pseudomyrmex spinicola* group, including *P. spinicola* (*P. ferruginea* in Janzen 1983) and *P. nigrocinctus*, two aggressive red-colored ants indistinguishable to us in the field; *P. flavicornis* (*P. belti* in Janzen 1983), an aggressive black ant; and non-stinging ants, including *P. nigropilosa* (*cf.* Janzen 1975), *Zacryptocerus maculatus*, and *Crematogaster ampla*.

We measured ant colony activity in response to controlled disturbances. We counted the number of times in 30 sec that ants crossed an imaginary line halfway around the tree's circumference at two-thirds tree height. We made the first count upon arrival at the tree, rapped sharply on the tree 5 times with a rock, and immediately took 2 sequential 30 sec counts. For comparison with the first count, we averaged these latter two counts. This activity measure is an index of the rate at which a nest predator would encounter ants on the tree. We assume the likelihood of a predator climbing an acacia is inversely proportional to its encounter rate of stinging and biting ants.

We scored nest accessibility. Accessible nests were those located less than 5 m from a non-acacia tree over 10 cm dbh from which a primate, the most agile nest predator at the study site, could jump. Note that this is but a partial measure of accessibility, since nests inaccessible to primates were still unprotected from bird and bat predation.

We measured local acacia tree density, defined as the number of 3 m or taller acacias within a 3 m radius of the nest tree. We looked for nesting associations with wasps which have been described for acacia-nesting birds (Slud 1964).

To characterize the average acacia tree available for nesting in our study area, we examined the nearest 3.0 m or taller acacia to 25 points 50 m apart along the length of the reserve entrance road in our study area. At each of these randomly sampled trees, we measured dbh, identified resident ant species, and measured ant activity as for the nest trees. Some of these trees contained nests; we consequently defined a subsample of these randomly sampled trees without nests as "no-nest trees" for comparisons of trees with nests to those without.

To test the assumption of greater security of nests in acacia versus other trees, we measured predation on artificial nests in acacia and non-acacia trees. We placed 100 wicker nest baskets, each with two quail (*Coturnix coturnix*) eggs, in ten paired clumps of five nests each along the reserve entrance road. A pair consisted of one clump of five nests 1–3 m apart set 1 m high in acacia trees and a similar clump 20–30 m away in non-acacia trees. Treatment pairs were located 50 m apart along the road. The nests were then checked 5 days later for egg loss; nests with ≥ 1 egg lost or damaged were scored as predation losses. Although our open nests did not perfectly mimic the covered nests built by most acacia-nesting birds, we used them only as an index of how predators would respond to real nests.

TABLE 1. Characteristics of nest and randomly sampled acacia trees at Palo Verde, Costa Rica.

Trees	N	dbh (\pm SD) (cm)	<i>P. spinicola</i> group	<i>P. flavicornis</i>	Non-stinging/ none
With <i>C. rufinucha</i> nests	41	5.65 \pm 1.6	24 ^a	11	6
With <i>I. sclateri</i> nests	13	6.99 \pm 2.0	3 ^b	7	3
With <i>T. sulphurescens</i> nests	8	5.18 \pm 2.5	2 ^c	5	1
With <i>P. sulphuratus</i> nests	3	7.07 \pm 1.2	1 ^d	2	0
Randomly sampled	25	6.09 \pm 1.6	9	10	6

^a *C. rufinucha* nested in trees with *P. spinicola* group ants significantly more often than expected from the frequency of *P. spinicola* group ants in randomly sampled trees ($\chi^2 = 8.7$, $df = 2$, $P < 0.05$).

^b *I. sclateri* showed no preference for any ant category ($\chi^2 = 1.4$, $df = 2$, NS).

^c *T. sulphurescens* showed no preference for any ant category ($\chi^2 = 1.9$, $df = 2$, NS).

^d Sample size too small for analysis.

Since dbh was normally distributed, we used *t*-tests and ANOVA for among-species comparisons. We used non-parametric Mann-Whitney, Kruskal-Wallis, and Spearman rank-correlation tests for comparisons of ant activity data. For assessing bird species preference for a particular ant species category, we used Chi-square tests comparing the distribution of nest trees among ant categories with that expected from the frequency of the ant categories in randomly sampled trees. To evaluate the hypothesis that acacia nests suffer less predation, we used a one-tailed Wilcoxon Matched Pairs test comparing pairs of nest clumps.

RESULTS

We found 65 nests built by four bird species (Table 1): Rufous-naped Wren (*Campylorhynchus rufinucha*), Yellow-olive Flycatcher (*Tolmomyias sulphurescens*), Great Kiskadee (*Pitangus sulphuratus*), and Streak-backed Oriole (*Icterus sclateri*). We also found one Banded Wren (*Thryothorus pleurostictus*) nest and one unidentified nest, but these are not included in the analysis. We are confident that we

missed no nest in an acacia tree due to the ease of finding nests in the sparse foliage.

There were no differences in dbh of nest trees among bird species and the no-nest trees (ANOVA, $F_{3,80} = 2.30$, NS).

Rufous-naped Wrens nested in trees with *P. spinicola* group colonies twice as often as expected by the frequency of these colonies in the randomly sampled trees (Table 1). The nest trees of the other three bird species did not differ from randomly sampled trees in representation of host ant species (Table 1).

P. spinicola group and *P. flavicornis* ant colonies were more common and showed more activity after disturbances than the non-stinging ants (Table 2). *P. spinicola* group colonies were more active than *P. flavicornis* both before and after the controlled disturbances (Table 2). *P. flavicornis* colonies inhabited larger trees than *P. spinicola* group colonies (Table 2), but ant activity was not correlated with tree dbh (Spearman rank-correlation; *P. flavicornis*, before: $r = 0.22$, after: $r = -0.05$; *P. spinicola* group, before: $r = 0.05$, after: $r = -0.25$, all NS).

Ant activity before disturbance was greater in

TABLE 2. Host tree size and activities of colonies of different ant species before and after artificial disturbances to their host trees.

Ant species category	N	Tree dbh (\pm SD)	Line crosses	
			Before dist. (\pm SD)	After dist. (\pm SD)
<i>P. spinicola</i>	34	5.5 \pm 1.4	8.4 \pm 9.4 ^a	24.5 \pm 20.2 ^b
<i>P. flavicornis</i>	30	6.8 \pm 1.8 ^c	3.9 \pm 6.9	13.5 \pm 15.0
Non-stinging	6	5.6 \pm 1.4	7.2 \pm 8.4	7.8 \pm 9.0

^a *P. spinicola* group colonies were significantly more active than *P. flavicornis* colonies before disturbance (Mann-Whitney two-tailed $Z = 2.63$, $P < 0.01$).

^b *P. spinicola* group colonies were significantly more active than *P. flavicornis* colonies after disturbance (Mann-Whitney two-tailed $Z = 2.57$, $P < 0.01$).

^c *P. flavicornis* colonies inhabited significantly larger trees than *P. spinicola* group colonies (two-tailed *t*-test, $t = 3.26$, $P < 0.01$).

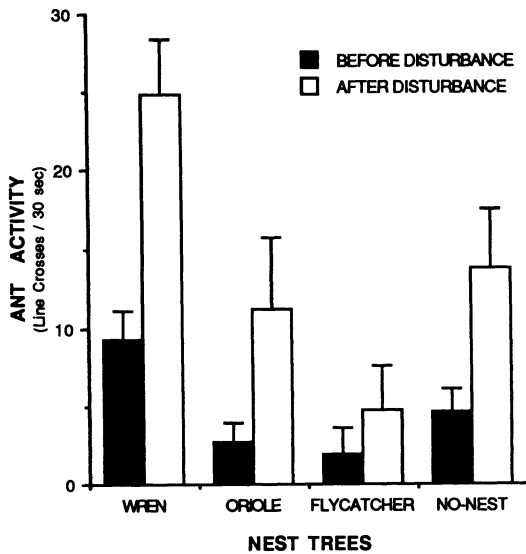


FIGURE 1. Ant activity (mean ± SE) on nest and non-nest acacia trees before and after experimental disturbances.

trees with wren nests than in trees with other nests or in no-nest trees because of the wrens' preference for trees with *P. spinicola* group ants (Fig. 1, Kruskal-Wallis $H = 9.24, P < 0.05$). Following disturbance, ants were again more active on wren nest trees than either of the other bird species or the no-nest trees (Fig. 1, $H = 11.43, P < 0.01$). Activity of *P. spinicola* group colonies did not differ before ($H = 1.30, NS$) or after ($H = 1.33, NS$) disturbance among wren, non-wren (grouped due to infrequency of occurrence in *P. spinicola* group trees), and no-nest trees (Fig. 2a). Activity of *P. flavicornis* did not differ among wren, oriole, flycatcher, and no-nest trees before disturbance ($H = 4.75, NS$, Fig. 2b). After disturbance, though, *P. flavicornis* were much more active on wren nest trees than they were on the other three classes of trees ($H = 12.07, P < 0.01$; Fig. 2b).

Nest trees were rarely isolated from non-acacia trees, and the four species of birds did not differ in choice of patch with respect to density of acacia trees around the nest (Kruskal-Wallis, $H = 3.34, NS$). We also found no wasp nest in any acacia tree, perhaps because annual dry season fires sweep through the xeric forest where acacias are abundant. Wasp nests were located in the more mesic, less fire damaged, upland forest of Palo Verde where acacia trees were uncommon.

In the artificial nest experiment, 36.0 percent of 50 nests in acacias and 18.4 percent of 49 nests

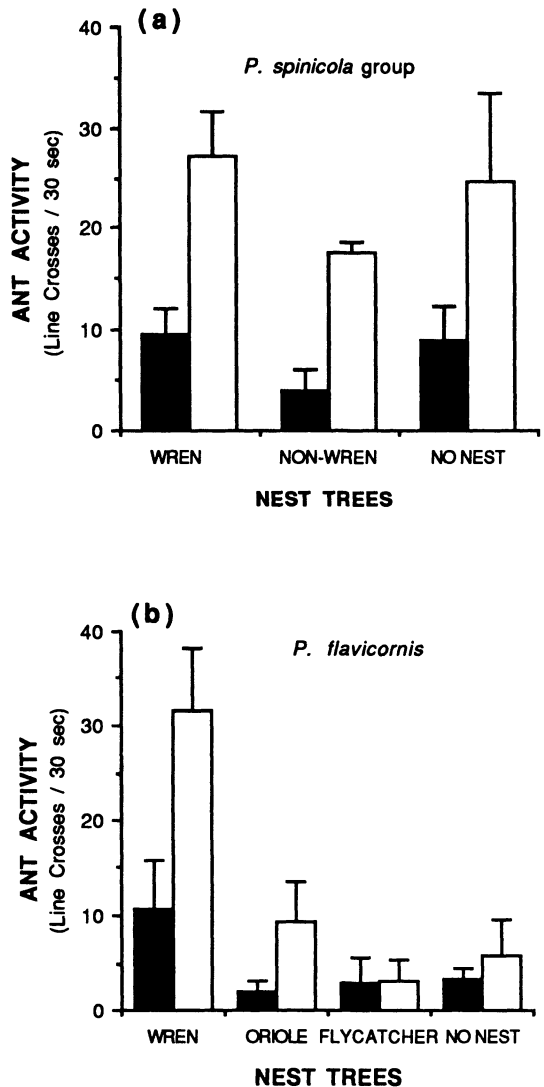


FIGURE 2. (a) *Pseudomyrmex spinicola* group (see text) activity on Rufous-naped Wren nest trees, non-wren (Streak-backed Oriole and Yellow-olive Flycatcher) nest trees, and no-nest trees before and after experimental disturbances; (b) *P. flavicornis* activity on Rufous-naped Wren nest trees, Streak-backed Oriole nest trees, Yellow-olive Flycatcher nest trees, and no-nest trees before and after disturbances.

(one nest was not counted since we could not relocate it) in non-acacias were attacked by predators. The greater nest loss in the acacia trees was marginally significant (Wilcoxon $t = 1.439, P = 0.085$), but in the opposite direction expected. However, in 72 percent of the acacia nests and 44 percent of the non-acacia nests lost to predation, the eggs had

single puncture holes and the yolk remained inside the shell.

DISCUSSION

Janzen (1969, 1975) identified 13 ant species occupying acacia trees and noted that these species varied in their aggressiveness. Our measures of ant activity, a component of aggression, support this contention for the acacia ants at Palo Verde, Costa Rica; *P. spinicola* group colonies were more active than other species we encountered (Table 2). Janzen (1969) did not consider that differences in ant aggressiveness may influence choice of trees by nesting birds. Yet, our results suggest such effects. Rufous-naped Wrens preferred trees with more ant activity. This nest site selection occurred in two ways. First, Rufous-naped Wrens chose trees with *P. spinicola* group colonies out of proportion to their frequency in randomly sampled trees (Table 1). They also selected among colonies, nesting in trees with *P. flavicornis* colonies that were more active in response to tree disturbances than randomly sampled *P. flavicornis* colonies (Fig. 2b). In contrast, the other three bird species did not appear to prefer active ants; they used trees for nesting randomly with respect to ant species. Moreover, ant activity in these nest trees did not differ from no-nest trees and was lower than for trees chosen by Rufous-naped Wrens. In fact, flycatchers seemed to choose nest trees with less active ants than in no-nest trees (Fig. 2b).

Presumably, more active ants provide greater protection from predators, so that Rufous-naped Wrens are choosing trees that minimize predation risk. Why do the other bird species not show similar preferences? One explanation is that they may be less tolerant of aggressive ants either as nestlings or as adults. This hypothesis is weakened, however, by our finding that some individuals of each bird species built nests in trees with *P. spinicola* group ants. Alternatively, the wrens may inhibit other birds from using the best nest sites by destroying their

eggs. The peck holes in eggs in artificial nests matched the bill size of the Rufous-naped Wren; a congeneric wren (*C. brunneicapillus*) punctured eggs in artificial nests in another study (Simons 1988), and other wren species are well known for this behavior (*cf.* Picman 1977). More nests were lost to such pecking in acacia trees than in non-acacia trees, even though both groups of trees were in the same areas. Such egg destruction by wrens may select against other bird species nesting in acacias with aggressive ants or even nesting in acacias at all. This behavior by the wrens may reduce local interspecific competition for food (Picman 1977) or reduce local nest density and the associated chance of attracting nest predators (Martin 1988a, b). Clearly, more work is needed to examine such alternatives.

Few nests built by any species were isolated from non-acacia trees, at least by our definition of isolation. Nests in acacias less than 5 m from other trees may still be out of reach of some primate and most snake nest predators. A disadvantage to nesting in a completely isolated acacia could be that the nest would receive too much solar radiation or insufficient protection from torrential rains common during the nesting season.

Of course, it would be valuable to correlate natural nest predation with occupant ant colony vigor. The results of this study suggest that orioles, flycatchers, and kiskadees nesting in acacias would suffer more nest predation than wrens, and that the probability of predation on the wren nests would be accounted for in part by ant activity level.

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