Ornitología Colombiana

Artículo

# Nest-site characteristics of Rufous-naped Wrens *(Campylorhynchus rufinucha)* in *Acacia* trees may serve to avoid vertebrate predators

## Características de sitios de los nidos de *Campylorhynchus rufinucha* en árboles de *Acacia* posiblemente sirven para evadir depredación por vertebrados

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### Abstract

The high rate of nest predation in tropical birds results in strong selection pressure. The Rufous-naped Wren *(Campylorhynchus rufinucha)* nests in Bullhorn trees *(Acacia)* in the Mesoamerican dry forest. It has been proposed that bullhorns and their aggressive ants (*Pseudomyrmex* spp.) help to prevent nest predation. I tested the hypothesis that these birds place their nests in particular acacia micro-habitats to avoid predation by vertebrates such as tufted capuchin monkeys *(Cebus capucinus).* I expected to find nests in locations that avoided the foraging behavior preferences of the monkeys. Along 6 km gravel road in Palo Verde National Park, Guanacaste, Costa Rica, I found 52 Rufous-naped Wren nests. The proportion of ant species in acacias with nests did not differ from the background proportion of ant species in acacias without nests, so birds did not prefer to nest in acacias with the most aggressive ant species. *Acacia* trees with wren nests were larger in diameter than control acacias without nests. I found more nests in acacias that were clustered, which consisted of one to five acacias in a 3m radius plot around the acacia with nest. However, the number of acacias with or without nests did not differ in their isolation from other non-acacia trees. Finally, more nests were in unexposed sites within the tree, such as at the base of branches or in the topmost branches, compared with exposed sites such as outer branches. Therefore, the Rufous-naped Wren seemed to place the nest in particular trees and places within them, in sites that may decrease the probability access by a vertebrate such as *C. capucinus* to depredate their eggs and nestlings. Rufous-naped Wren nest site selection may also be influenced by other factors such as mechanical support for the weight of the nest, eggs, nestlings and adults.

Key words: *Acacia collinsii*, *Campylorhynchus rufinucha, Cebus capucinus*, Costa Rica, nest sites, *Pseudomyrmex*.

### Resumen

La alta tasa de depredación en nidos de aves tropical resulta en una fuerte presión de selección. *Campylorhynchus rufinucha* anida en árboles de *Acacia* en bosques secos mesoamericanos. Se ha propuesto que las espinas y las hormigas agresivas (*Pseudomyrmex* spp.) en la planta previenen la depredación de nidos. Evalué la hipótesis de que los nidos de estas aves son puestos en un sustrato y una acacia particular para evitar la depredación por vertebrados como monos carablanca *(Cebus capucinus).* Esperaba que los nidos estuvieran donde evitaran los patrones de forrajeo de estos monos. Al borde de un camino de 6 km de largo dentro del Parque Nacional Palo Verde, Guanacaste, Costa Rica, encontré 52 nidos de *C. rufinucha*. La proporción de especies de hormigas en acacias con nidos no difirió de la proporción de la especie de hormigas en acacias sin nidos, por lo que no prefieren anidar con la especie de hormiga más agresiva. Acacias con nidos tuvieron mayor altura que acacias control sin nido. Encontré más nidos en acacias no aisladas, sino más bien en grupos de dos a cinco acacias en una parcela de 3m de radio. Sin embargo, el número de acacias con o sin nido no difirió con el aislamiento de la planta con respecto a otros árboles no acacias. Finalmente, más nidos estuvieron en sustratos no expuestos del árbol, como la base de las ramas o en las ramas más altas, comparado con sitios expuestos como las ramas exteriores. Por lo tanto, estas aves aparentemente colocan el nido en plantas particulares y sustratos en ellas en los cuales pueden disminuir la probabilidad de que vertebrados como *C. capucinus* accedan al nido y depreden huevos y pichones. Una acacia particular también puede ser seleccionada por *C. rufinucha* para obtener apoyo mecánico para el peso del nido, los huevos, pichones y adultos.

Palabras clave: *Acacia collinsii,* anidación, *Campylorhynchus rufinucha, Cebus capucinus,* Costa Rica, *Pseudomyrmex.*

## Introduction

In the tropics, predation on eggs and nestlings in bird nests is high, accounting for up to 69% of nest failures (Ricklefts 1969, Ahumada 2001). Birds in these environments are expected to have strategies that reduce predation to maximize reproductive success. Some of these strategies include nesting in concealed places, cryptic nest sites (Martin & Roper 1988, Holway 1991), associating with other noxious organisms (such as wasps) that could function in nest defense (Dejean & Fotso 1996), or nesting inside tree cavities (Li & Martin 1991, Sandoval & Barrantes 2009). Nest site selection is an important component to produce a successful nest.

One association between birds and noxious organisms are species that nest in *Acacia* spp. trees (Mimosaceae) inhabited by aggressive ant colonies of *Pseudomyrmex* and *Crematogaster* (Formicidae) in Neotropical environments (Janzen 1969). Among those birds are *Campylorhynchus rufinucha, Cyphorhinus phaeocephalus,Tolmomyas sulphurescens*, *Uropsila leucogastra* and *Icterus pustulatus*, which may obtain protection against predators due to the ants' presence (Gilardi & von Kugelgen 1991, Joyce 1993, Robinson *et al.* 2000). Previous workers have hypothesized that the sharp spines in the bullhorn and the active ants protect and dissuade predators from foraging in those trees and attacking the nests (Young *et al.* 1990, Flaspohler & Laska 1994).

The Rufous-naped Wren, *Campylorhynchus rufinucha* (Trolgodytidae) is an abundant territorial bird in Mesoamerican dry forests. It ranges from central México to northwestern Costa Rica (Stiles & Skutch 1989) and in recent years it has expanded its distribution towards the southeast of Costa Rica, becoming abundant in traditionally wetter (and more urbanized) sites in central Costa Rica (Sandoval 2004). Its nests are very conspicuous and globular, built with plant twigs and fibers (Stiles & Skutch 1989). During the breeding season, from April through August (Stiles & Skutch 1989, Bradley & Mennill 2009), this species may build an additional nest (Wiley 1983). The females lay eggs and incubate them in the newly built nests and the male sleeps in the old one, perhaps to dissuade predators (Flashoper & Laska 1994).

The nest success of the Rufous-naped Wren in acacia trees is higher near wasp *(Polybia rejecta)* nests (Joyce 1993), apparently because nest-defending wasps deter vertebrate predators (such as snakes, coatis or monkeys) from attacking both wasps' and birds' nests. Also, the aggressiveness of the ant colonies inhabiting the acacia could prevent nest predation (Young *et al.* 1990, Cuervo 2001). Young *et al.* (1990) suggested that acacia trees near other non-acacia tree species are more accessible to predators, and placing the nest in an area with a high density of acacia may help protect the nest.

Tufted capuchin monkeys *(Cebus capucinus)* prey upon nests in acacia by pulling the acacia branch from a branch in a nearby tree (Joyce 1993). Certain aspects and preferences of the foraging behavior and food sources of these monkeys are known. In the Mesoamerican dry forest they consume fruits of 42 plant species (including *Acacia* fruits) and insects, including adults and larvae of the acacia ants, with the consequent destruction of the tree branches (Freese 1976, 1977, Gilbert *et al.* 1990). Also, *C. capucinus* monkeys were recorded having one successful prey capture event every 15 hours of observation, preying mostly on vertebrates such as coatis, squirrels, bats, lizards and eggs, nestlings and adult birds in Santa Rosa National Park in northwestern Costa Rica (Fedigan 1990). Finally, a recent study showed that *C. capucinus* more commonly foraged in acacias greater than 30 mm diameter at breast height (DBH) (Young *et al.* 2008). The monkeys were seen foraging in trees where the nearest tree was not an acacia, and avoided foraging in trees inhabited by mutualistic ants (Young *et al.* 2008).

It is unknown whether the nesting preferences of Rufous-naped Wrens reflect the foraging pattern of its predators in a way that minimizes predation, especially from tufted capuchin monkeys, which have been seen depredating Rufous-naped Wren nests (Joyce 1993). Since data on where this predator prefers to forage are available (Young *et al.* 2008) and given that capuchin monkeys prey on bird nests, I expected that wrens would place their nests in sites that appeared to be less accessible to these monkeys. Previously it has not been reported whether these birds choose to nest in isolated acacia trees, or in unexposed parts of those trees.

The greater presence of bullhorns in unexposed sites of the plant would make the nests less reachable, perhaps more protected, and could dissuade predator attacks, especially because ants patrol and respond to intruders more quickly on the base of the tree trunk than on the leaves (Amador-Vargas 2008).

I investigated the hypothesis that the Rufous-naped Wren nests in certain acacias and substrates within them that are less accessible to predators to decrease the possibility of nest predation. I expected to find: (1) more nests in acacia trees containing colonies of *P. spinicola*, the ant species which is reported to be most aggressive (Young *et al.* 1990, Cuervo 2001). This prediction was constructed under the assumption that predators are deterred by the ants and higher aggression reduces predation on a given acacia; (2) nests placed at lower heights than the preferred foraging height of capuchin monkeys; (3) more nests in acacias that had other acacias around it, which may prevent a predator from reaching the nest from a non-acacia; (4) more nests in acacia trees in which the foliage was isolated from other non-acacia trees, where monkeys could not reach the eggs or nestlings from surrounding vegetation; finally (5) more nests in unexposed parts of the acacia tree.

## Materials and Methods

I conducted this study in Palo Verde National Park, Guanacaste, Costa Rica (10°20' N, 85°21' W; elevation 15 m), from 11 to 13 February 2009. The site is a seasonal tropical dry forest, which was mostly cattle fields left to natural regeneration since 1972, when the area was protected. I walked an approximately 6 km transect along a major gravel road through the forest, searching for nests within 15 m on either side of the road. At the study site *Acacia collinsii* and *A. cornigera* are very common, and their average (± one standard deviation) DBH is 3.53 ± 1.69 cm; range: 0.60 – 9.10; n=183 trees (S. Amador-Vargas, unpubl. data). For every nest found I recorded the species of the acacia tree holding it, and the ant species inhabiting the acacia tree. I used data from Hernández-Montero *et al.* (2009) together with my own data to estimate the proportion of each ant species in the study site. I measured each tree's DBH as an estimation of its height, because acacia height and DBH are positively correlated (r = 0.79; S. Amador -Vargas unpubl.data, Tewari & Gadow 1999). I also took a picture of the tree with nest and I estimated each nest's height within the tree using Image Tool (Wilcox *et al.* 2002). I counted the number of acacia trees with a DBH greater than 10 mm within a 3m radius of the tree with the nest.

To compare the nest height with a control acacia, I randomly selected one acacia without a nest in the plot as control, and measured its DBH. I used that acacia as control because it had the same isolation and microhabitat conditions as the one with nest.

Also, I determined how accessible the acacias were to potential predators by scoring whether the foliage was isolated or not from other non-acacia trees. A tree was defined as isolated if it had a minimum distance of 30 cm in every direction from any other trees or shrubs. Finally, I scored the location of the nest in the acacia, mostly based on the quantity of branches (and their density) and spiny bullhorns containing aggressive ants, as well as on the accessibility to the nest, all of which may deter predators from attacking the nest. I defined exposed nests as those surrounded by few branches and bullhorns: (a) nest located in the basal part of the trunk where there were neither branches nor thorns, (b) in the outer branch tips, or (c) between branches in the tree's canopy periphery. Unexposed nests were those surrounded by more branches and bullhorns: (d) located within the branching of the major trunks, (e) between the trunk and the secondary branches, or (f) between two secondary branches.

I used chi-square tests to analyze if the Rufous-naped Wren nests in acacias with *P. spinicola* differed in comparison to the nests in acacias inhabited by other ant species, corrected by the proportion of each ant species in the area. With a paired t-test I compared if the acacias with nests had a larger DBH than neighboring trees without nests.

Also, I used a chi-square test to compare the abundance of the acacias with nests and controls according to whether the acacias were isolated or not, and a chi-square with a Yates correction to compare the number of nests in exposed versus unexposed substrates. Finally, I tested the relationship between nest height and acacia height with a simple linear correlation.

## Results

I found 51 *C. rufinucha* nests in *A. collinsii* and one nest in *A. cornigera*. The *A. cornigera* acacia with a nest was inhabited by the ant *P. flavicornis*. The acacias that contained a nest had on average (± one standard deviation) 1.96 (± 1.75) acacia trees within a 3 m radius. Sixteen acacia trees with nests had no acacias within the 3 m radius plot. Forty-one acacias with nests were inhabited by *P. spinicola*, seven by *Crematogaster* sp., three by *P. flavicornis* and one by *P. nigrocinctus*. The proportion of trees with wren nests according to the ant species that inhabited it was not different from the background abundance of ants in acacias ($\chi^2$=4.91, df=3; p=0.18, Fig.1). I found that 36 % of the nests were at the edge of the road. Also, six nests were on branches with closed wasp nests (likely Polistinae).

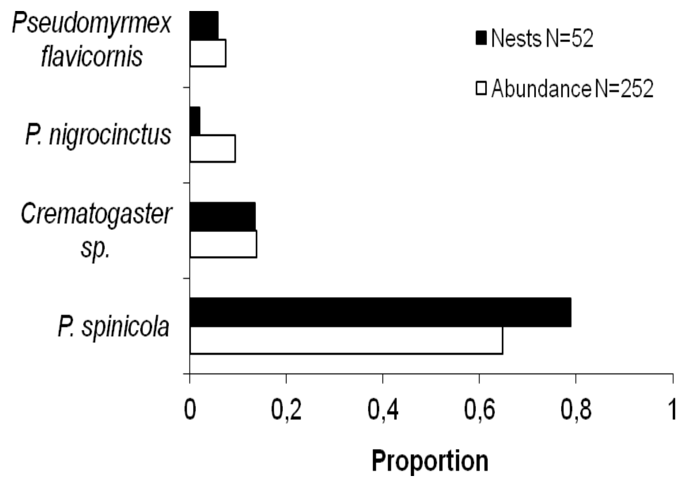


Figure 1. Proportion of 52 Rufous-naped Wren *(Campylorhynchus rufinucha)* nests in *Acacia* spp. trees and the abundance of the ant species (*Pseudomyrmex* spp. or *Crematogaster* sp.) inhabiting them. Palo Verde National Park, Guanacaste, Costa Rica, 11 to 13 February 2009. df=3; p=0.18.

Acacia trees with nests (DBH = 48.0 ± 15.0 mm) were larger than controls without nests (DBH = 39.0 ± 15.0 mm) (t=3.07, df=51, p=0.03). Nests were at 4.5 ± 1.5 m from the ground, and nest height was strongly and positively correlated with the acacia's height (r=0.88, t=12.90, df=50, p<0,001). Nests were on average (± one SD) 77 ± 11 % of the acacia's height (range: 41– 95%). I found more nests in acacias surrounded by acacias than in acacias isolated from other acacias ($\chi^2$=81.38, df=5, p<0.001). Also, most acacias with nests were not isolated, 70% (36) had from one to five other acacias in the surrounding 3 m radius plot. I found that the isolation of the acacias did not affect the probability that it had a nest in it ($\chi^2$=0.88, df=1, p=0.35, Fig. 2). Finally, I found more nests in unexposed parts of the acacia (surrounded by more branches and bullhorns) than in exposed parts ($\chi^2$=19.69, df=1, p<0.001, Table 1, Fig. 3).

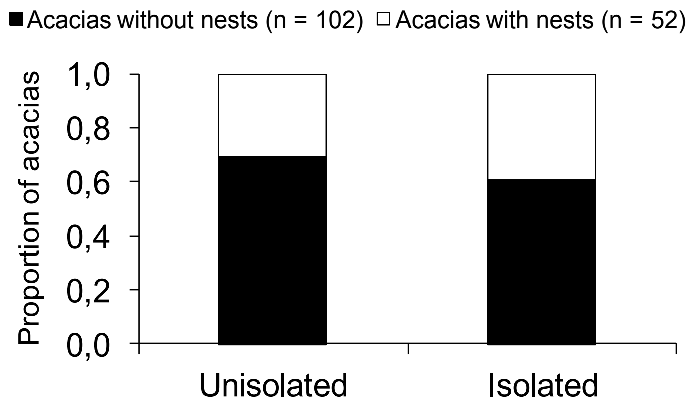


Figure 2. Proportion of *Acacia* spp. trees with Rufous-naped Wren *(Campylorhynchus rufinucha)* nests (N=52) and trees without nests (N=102) relative to the isolation of the entire tree in Palo Verde National Park, Guanacaste, Costa Rica, 11 to 13 February 2009. $\chi^2$=0.88, df=1, p=0.35.

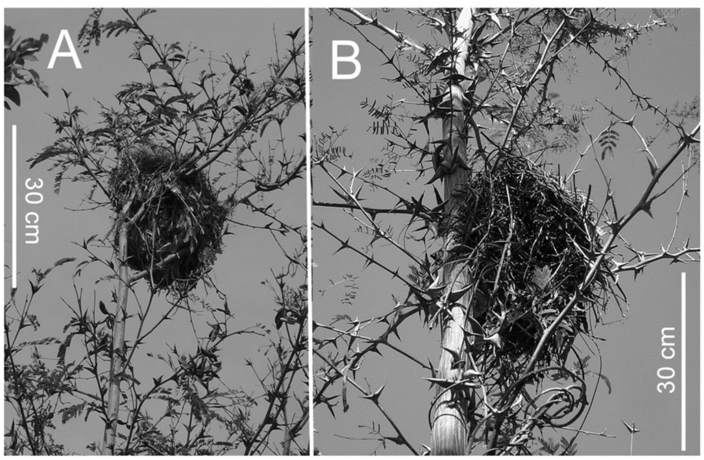


Figure 3. Two nests of the Rufous-naped Wren *(Campylorhynchus rufinucha)* found in Palo Verde National Park, Guanacaste, Costa Rica, 11 to 13 February 2009, differing in the surrounding density of branches and bullhorns (which contain aggressive ants), that therefore may differ in their accessibility and vulnerability to predation. (A) An unexposed nest in the top branching; (B) a lower, exposed nest against the trunk (see also Table 1).

## Discussion

Rufous-naped Wren nests were in larger acacias with non-isolated foliage and the nests were located in unexposed substrates within the trees.

Therefore, I found partial support for my hypothesis that these birds place their nests in order to avoid predation. However, wrens did not show a preference for a particular species of acacia ant, since the proportion of nests in acacias with particular ant species reflected the proportion of ant species in acacias without wren nests. This result does not corroborate the results of Flaspohler & Laska (1994) and Cuervo (2001), who found that these birds place their nests in acacias with the most aggressive ant species (*P. spinicola)* twice as often as expected by chance in another Rufous-naped Wren population in Costa Rica. However, in the Palo Verde population ant aggressiveness was not a factor for nest site selection. One possible explanation for this pattern is each ant species has a wide range of aggressiveness.

Table 1. Number of Rufous-naped Wren *(Campylorhynchus rufinucha)* nests in *Acacia* spp. trees, as a function of substrate exposure (relative to the density of branches and bullhorns containing aggressive ants, as well as the accessibility to the nest, all of which may deter predator to attack the nest), in Palo Verde National Park, Guanacaste, Costa Rica. 11 to 13 February 2009.

| Exposure | Substrate | Number of nests |
|---|---|---|
| Exposed | In/against the trunk | 3 |
| | Branches near the edge | 4 |
| | Within branches | 3 |
| Unexposed | Between trunk and branches | 14 |
| | Major trunk branches | 13 |
| | Top branching | 15 |

Contrary to my prediction, acacia trees with nests were larger than the minimum 30 mm DBH limit in which *C. capucinus* forage, as reported by Young *et al.* (2008). Therefore, acacia trees in which the birds placed their nests could be accessible to the monkeys. However, it is also possible that an acacia lower than 30 mm in DBH could not hold a nest, since the trunk and its branches maybe thinner than required to provide the mechanical support needed by the nest containing eggs, nestlings and adults. This is supported by the observation that nest height correlated with acacia height, suggesting that birds place their nest within some proportional range that might be better to sustain their nests.

More nests were in acacias with foliage not isolated from other non-acacia trees, contrary to my prediction. This means that the acacia (and its nest) could be more accessible to predators. Perhaps nesting in a vegetation-isolated acacia might expose eggs and nestlings to desiccation from increased exposure to direct sunlight, as suggested by Young *et al*. (1990). Also, one-third of acacias with nests were at the edge of the road, where they had greater isolation due to the vegetation-cleared road and probably greater sunlight exposure throughout the day. The habitat in which I conducted my study was hot (25-30º C), dry (rainless from December to May) and windy (wind speed ranges 3.0 – 5.8 m/s) (meteorological data: Organization for Tropical Studies website database). Therefore, avoiding egg desiccation could be a trade-off with predation avoidance. High temperatures and wind affected the nest-site selection and behavior of the Cactus Wren (*C. brunneicapillus)* in a North American desert (Ricklefs & Hainsworth 1968, Facemire *et al*. 1990). On the other hand, as expected, acacias with nests were more frequently surrounded by other (one to five) acacias. Finally, I found more nests in unexposed substrates within the acacia. Placing a nest in acacias surrounded by other acacias and with greater vegetation density (Seeley *et al*. 1982) could make the nest less accessible to predators. Also, the acacia density increases the number of sharp bullhorns and ant stings (Amador-Vargas 2008), and that may discourage predators such as the tufted capuchin monkeys from reaching the birds' eggs or nestlings, favoring the vertebrate predation avoidance benefit of nest-site selection.

This study was carried out in February, when the Rufous-naped Wrens are not breeding (Stiles & Skutch 1989). However, I do not expect that this affects my results greatly because presumably the majority of nests I observed were used to incubate during the past breeding season. In the breeding season, starting in April, these birds may build a second nest in which females lay eggs and incubate (Wiley 1983), and/or refurbish nests from pasts breeding seasons in which males roost (Wiley 1983). Therefore, the Rufous-naped Wrens make their nest site selection decisions (such as tree and specific substrate) during the breeding season, because that is the time of the year were egg and nestling predation pressure is present.

Predation intensity by tufted capuchin monkeys is unknown, as well as for other supposed vertebrate predators. In the study site I would expect boas, coatis, squirrels, jays and other birds to be potential vertebrate predators of nests of Rufous-naped Wrens, and presumably the nest-site selection of these birds is driven by the combined pressure of all predators. However, since the foraging behavior and microhabitat preferences of these animals are unknown, it is unclear how they may shape nest-site selection. The foraging patterns of the tufted capuchin monkeys are recently described (Young *et al*. 2008), but the effect on bird nesting success is poorly known, and the few available data come from anecdotal and sporadic observations of *C. capuchinus* (Fedigan 1990, Olmos 1990, Joyce 1993). Because predation is high in other species and environments (Ricklefs 1969, Møller 1989), it is expected to exert strong selective forces on avian nesting behavior. For example, two species of Troglodytidae in Colombia suffered 66% nest failure, 53% apparently due to predators (Ahumada 2001). In the Song Wren (*C. phaeocephalus)*, nest failure varied from 46 to 63% across several populations and over multiple years in Panamá, with predation being one of the main causes (Robinson *et al.* 2000). In *C. phaeocephalus* 78% of the nests were placed in *A. melanoceras*, but those nests were preyed on at equal rates as nests in trees undefended by ants (Robinson *et al*. 2000). Further research on predator pressure, as well as on the avoidance of microclimatic conditions (temperature, sun exposure and wind), will provide insight into nest site selection in the Rufous-naped Wren, especially how that selection is related to breeding success. Any of those possible factors that may affect nest site selection (ant aggressiveness, acacia isolation, temperature and wind avoidance, etc.) could be experimentally tested in order to convincingly establish its influence, as was convincingly done by Joyce (1993) with the wasp nest associations.

## Acknowledgments

I thank F. Joyce, A. Farji-Brener, F. Chinchilla, and A. Amézquita for their advice in the design and analysis of this project. S. Amador helped me in the field and to identify ants and acacias. F. Joyce, T. R. Defler, C. J. Clark, L. Sandoval, J. Chaves and F. G. Stiles made useful comments on an early version of this manuscript. C. J. Clark also kindly provided a useful revision of the English throughout the manuscript. The Organization for Tropical Studies, the Universidad de Costa Rica and the Ministerio de Ciencia y Tecnología de Costa Rica provided logistic and financial support.

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*Recibido:* 01 de marzo de 2012. *Aceptado:* 20 de abril de 2013.