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CAVITY NESTING IN RAPTORS OF TIKAL NATIONAL PARK AND VICINITY, PETÉN, GUATEMALA

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Resumen. – Nidificación en cavidades por aves rapaces del Parque Nacional Tikal y sus alrededores, Petén, Guatemala. – Examino los resultados de investigaciones recientes sobre aves rapaces que se reproducen en bosques tropicales secos deciduos del Parque Nacional Tikal y sus alrededores, Guatemala. De un total de 26 especies, cuatro especies de Falconidae y tres de Strigiformes nidificaron principalmente en cavidades de árboles. La mayoría de ellas utilizaron cavidades naturales; sólo el Mochuelo Caburé (*Glaucidium brasilianum*) utilizó cavidades excavadas por pájaros carpinteros. Las cavidades apropiadas para la nidificación de las tres especies de búhos parecieron ser abundantes y presumiblemente no limitantes de sus poblaciones. Por el contrario, la evidencia sugirió que las cavidades apropiadas para la nidificación de los halcones eran más especializadas y escasas. Algunas características que contribuyeron a tal rareza incluyeron el tamaño y especie del árbol, el tamaño y la posición del hueco y la naturaleza efímera de los árboles muertos en pie. La pérdida de cavidades-nido es uno de los varios efectos negativos de la destrucción masiva de bosques sobre las poblaciones de aves rapaces de bosque. Incluso la tala selectiva podría tener efectos perjudiciales, en particular para las dos especies de halcones que nidifican en especies arbóreas de valor comercial.

Abstract. – I review recent studies of raptor species that breed in the dry tropical deciduous forests of Tikal National Park, Guatemala. Of 26 breeding species, four species of Falconidae and three species of Strigiformes nested primarily in tree cavities. Most of these used non-excavated cavities; only the Ferruginous Pygmy-Owl (*Glaucidium brasilianum*) used cavities excavated by woodpeckers. Cavities suitable for nesting appeared abundant, and probably did not limit populations of the three owl species. In contrast, evidence suggested that cavities suitable for nesting by falcons were more specialized and rare. Characteristics that contributed to the rarity of such cavities included tree size, tree species, cavity size, position of cavity, and the ephemeral nature of dead snags. Loss of nest cavities is one of many negative effects of deforestation upon populations of forest raptors. Even selective logging may have deleterious effects, particularly for the two species of forest-falcons whose nest cavities occur in commercially valuable tree species. *Accepted 9 January 2004*.

Key words: Cavity-nesting, falcons, Guatemala, owls, raptors, Tikal National Park.

INTRODUCTION

Numerous Neotropical raptors nest in tree cavities. Advantages of cavity nesting include protection from adverse weather conditions, concealment and protection from certain predators (Newton 1979), and the potential for larger broods (Ricklefs 1970, Skutch 1985). Raptors do not excavate cavities, however, and therefore are dependent on naturally-occurring cavities that result from either decay (at the site of a branch or trunk break)

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or those created by primary excavators (woodpeckers and others). Disadvantages of being cavity adopters (Eberhard 2002) include the possibility that optimal nest cavities may be unavailable. Characteristics determining whether a particular cavity is optimal likely include size and placement.

As part of the Maya Project, a comprehensive study of most of the 26 species of Falconiformes and Strigiformes breeding in Tikal National Park in northern Guatemala, I made an *a posteriori* review of cavity nesting as a strategy for raptors in this region. In this paper, I discuss various aspects of cavity nesting in raptors that may have demographic and conservation implications. I compare and contrast the nesting ecology of each of the cavity-nesting raptor species in the area to identify some underlying patterns. To examine these issues further, I will discuss the following questions: Are cavities selected by a given species unique (and potentially rare) or unremarkable (and common)? Does the lack of suitable cavities potentially limit populations of these raptor species?

STUDY AREA

Most of the natural history information described here came from research conducted in Tikal National Park (17°13'N, 89°36'W) in Petén, Guatemala, from similar forest contiguous within the Maya Biosphere Reserve to the east, west, and north, or from human-altered areas to the south of Tikal. The area is classified as tropical semi-deciduous (Pennington & Sarukhan 1968) or subtropical moist forest (Holdridge *et al.* 1971). Tikal National Park encompasses 576 km^2 where the only recent logging has been localized, with selective lumbering of mahogany (*Swietenia macrophylla*) and Spanish cedar (*Cedrela mexicana*). Mean annual rainfall is 1350 mm, and there is a single dry season from February to June. Topography is gently rolling, primarily 200–350 m in elevation. Vegetation is described by Schulze & Whitacre (1999), and a description of the agricultural lands to the south is found in Schulze *et al.* (2000). Methods used to obtain the natural history information discussed here varied among species and are described in the original studies cited in the text.

STRIGIFORMES

Four species of owls were documented at Tikal, including two *Strix* owls, the Mottled Owl (*S. virgata*) and the Black-and-white Owl (*S. nigrolineata*), and two smaller owls, the Guatemalan Screech-Owl (*Otus guatemalae*) and the Ferruginous Pygmy-Owl (*Glaucidium brasilianum*).

Mottled Owls. All Mottled Owl nests were natural cavities in live trees. Most (10 of 13) were in the trunk and were caused by the rotting of a branch. One was formed where the trunk itself had broken, and two were depressions in a main crotch of the tree. Of these three nests that were not side cavities, two were accorded additional protection by the large leaves of climbing vines (*Philodendron* sp.). Nest height was 12.9 ± 3.3 m (n = 13, range = 8.4–17.5 m) above the ground, and nest tree dbh was 64.0 ± 15.7 cm. Cavity depth was 62.3 ± 61.3 cm (n = 13, range = 10–250 cm) and entrance size averaged 17.2 x 32.3 cm (n = 12, range = 8.0 x 16.0 – 30.0 x 40.0; Gerhardt *et al.* 1994).

Several facts suggest that cavities suitable for Mottled Owl nests were numerous in these forests. Of the 13 nests located, nine different tree species were utilized (with *Pimenta dioica* and *Brosimum alicastrum* used four and two times, respectively; Gerhardt *et al.* 1994). Moreover, no nests were reused during the second season of study, even if the nest from the first year was successful. Most telling, however, was the number of seemingly suitable cavities that researchers had to consider in trying to find the one being used. If a female's begging call, heard at night, led to an approximate nest location, a daytime search invariably found several cavities of appropriate height and size within a few meters of the actual nest cavity. Cavities chosen for nesting were unremarkable, though there were undoubtedly some, albeit unquantified limits regarding size and location.

Guatemalan Screech-Owls. Transect surveys indicated that Guatemalan Screech-Owls were even more common at Tikal than Mottled Owls (Gerhardt unpubl.). Information of their nesting ecology was anecdotal; nests were found during the course of other studies. The few nests found were in non-excavated cavities in live trees similar to those used by Mottled Owls. Unlike Mottled Owls, screech-owls also used cavities for diurnal roosting. This implies the need for multiple cavities within a breeding territory. Nonetheless, the types of cavities used for nesting appeared, like those of Mottled Owls, numerous in these forests. The density of screech-owls likewise implies that suitable cavities are common, and may not be limiting the population at this site.

Ferruginous Pygmy-Owls. In and around Tikal, Ferruginous Pygmy-Owls were not found within large tracts of primary forest, but rather near gaps and edges, and in agricultural lands outside the park. The following information about nests comes primarily from studies in south Texas and the same subspecies, *ridgwayi*. Nest cavities were 2–12 m above ground (n = 99; Proudfoot & Johnson 2000), usually between 4 and 6 m (Oberholser 1974, Johnsgard 1988). Twenty-two of 24 Texas cavities were excavated by woodpeckers (Proudfoot & Johnson 2000); various tree species, mostly live, were used. Reuse of nests from one year to the next was apparently common (Weidensaul 1989), but a different cavity was used for second nest attempts within a given year (Proudfoot & Johnson 2000). The number of suitable cavities within a territory may affect breeding success, and cavities near the nest cavity may be used for caching prey and as night roosts by the male (Proudfoot & Johnson 2000).

FALCONIFORMES

Twenty-two species of Falconiformes nested in the forests in and around Tikal (Whitacre in prep.). By family, these consisted of 17 Accipitridae and five Falconidae. All of the accipitrids constructed their own nests of twigs and other materials, and never used tree cavities. The falconids were of three genera, *Falco*, *Micrastur*, and *Herpetotheres.*

Barred Forest-Falcons. The first Barred Forest-Falcon (*M. ruficollis*) nest described (Thorstrom *et al.* 1990) was from Tikal, and subsequent research examined 39 such nests (Thorstrom 2001) representing 70 nesting attempts. All nests were in cavities, with 74% in live trees and 26% in dead trees. Fifteen tree species were used (Thorstrom 2001).

In several ways, cavities used for nesting by Barred Forest-Falcons were unique, and likely uncommon. All were in large trees (dbh = 94.8 ± 40.5 cm, n= 39) that comprised only 5% of the trees on 50 sample plots (Thorstrom 2001). Nest tree size likely influenced cavity size, which was also large (depth = 80.9 ± 58.8 cm, n = 39); nest height was 17.4 ± 4.2 m (n = 39). Most (66/70) nest attempts were in non-excavated cavities, the remaining four in cavities excavated by large woodpeckers. Barred Forest-Falcons showed a significant selectivity for one tree species, *Cedrela mexicana* (Thorstrom 2001). Moreover, there was a significant difference in nesting success between live trees, where most nests were successful, and dead trees, where most nest attempts resulted in failure (Thorstrom

2001). Nest predation was believed to be the major factor in productivity (Thorstrom *et al.* 2000a). Barred Forest-Falcons competed (successfully) for nest sites with Keel-billed Toucans (*Ramphastos sulfuratus*) and Mealy Parrots (*Amazona farinosa*). Reuse of the same nest was the norm, except following failures, after which pairs generally used a different site the following year. Thorstrom (1993) concluded that nest sites are a limiting resource for Barred Forest-Falcons.

Collared Forest-Falcons. The second nest described for Collared Forest-Falcons (*M. semitorquatus*) was from Tikal (Thorstrom *et al.* 1990), and subsequent research found and analyzed six nests representing nine nesting attempts (Thorstrom *et al.* 2000b, Thorstrom 2001).

Nest cavities were unique and likely limited (Thorstrom 2001). All were non-excavated cavities in large (dbh = 167.0 ± 91.1 cm, n = 6) live trees. Nest height was 19.9 ± 3.1 m, and cavity depth was 47.4 ± 34.4 cm. Three cavities had two entrances (all others had one each), and the main entrance averaged 55.9 x 38.9 cm. Collared Forest-Falcons showed selectivity for *Cedrela mexicana* as nest trees. In one case of apparent nest-site competition, a pair of Collared Forest-Falcons laid eggs (albeit later than at other nests) after the egg of a pair of Black Vultures (*Coragyps atratus*) was removed from the nest cavity. Pairs of these forest-falcons tended to use the same cavity even after a failed nest attempt – the only instance of their switching to a new nest site followed a successful nesting.

Laughing Falcons. Laughing Falcons (*Herpetotheres cacchinans*) were found both within the park and in the agricultural lands to the south (Parker 1997, Parker & Guzmán in prep.). Thirteen nest sites (representing 23 breeding attempts) were found, eight within the park and five outside. All nests were in non-excavated cavities or depressions, and many had epiphytes associated with them. Four of the eight nests within the park were in dead trees; the remaining nine nests were in live trees (Parker 1997, Parker & Guzmán in prep.).

Laughing Falcon nest cavities were unique, and potential nest sites uncommon and limited because of their distinctive placement. For example, all nests were in large (mean dbh = 304.4 cm), tall, lone or emergent trees (Parker 1997). Moreover, the nest cavities themselves were above the adjacent canopy (averaging 20.9 m above ground and 4.3 m above the canopy; Parker 1997). This characteristic makes such sites quite rare, particularly within the primary forest. In support of this is the fact that pairs reused nest sites year after year even when the previous year's attempted nesting resulted in failure by predation. In one case, a nest tree fell down between breeding seasons. The pair of this territory, though using the same area for hunting both years, moved to a new nest site 1.6 km distant following the loss of the first nest tree (Parker 1997, Parker & Guzmán in prep.).

Bat Falcons. The small sample of focal Bat Falcon (*Falco rufigularis*) nests at Tikal was atypical, since two of four nests were in artificial structures in the form of Maya temples. One was a cavity in a termite nest, believed excavated by trogons, whereas the fourth was a more typical cavity in a dead tree (Parker 1997). A larger sample of nests comes from similar forests in the nearby states of Chiapas, Campeche, and Tabasco in southern Mexico (Whitacre *et al.* in prep.). Of 20 nest cavities documented, 15 were in dead trees, three were in live trees, one was in a cliff pot-hole, and one was on the petiole of a palm frond. Size and shape of cavities varied considerably, but all were apparently non-excavated. Nest height averaged 13 m (range = 6–20 m, n = 15), which was relatively high (the forests there being somewhat shorter than those at Tikal). All were in open situations, either above the canopy in an emergent tree or in a tree isolated from others. Members of this species spend little or no time within the forest canopy, but perch and hunt in the open and at or above the canopy (Parker 1997, Whitacre *et al.* in prep.).

Although their occasional occurrence in man-made structures, caves, and palm petioles attest to some adaptability in placement of eggs, optimal nests sites for Bat Falcons are likely uncommon. Cavities are apparently unsuitable unless positioned above the canopy or in open situations such as tree-fall gaps. Most are at considerable height in dead trees, and such sites are undoubtedly ephemeral. Moreover, relative to the other cavity-nesting raptors discussed herein, Bat Falcons may face greater levels of competition for such nest sites. They were observed attacking or heckling several species of non-prey birds that likely were potential competitors for nest sites, including Green Parakeet (*Aratinga holochora*), White-fronted Parrot (*Amazona albifrons*), Red-lored Parrot (*A. autumnalis*), Yellow-headed Parrot (*A. ochrocephala*), Lineated Woodpecker (*Dryocopus lineatus*), Acorn Woodpecker (*Melanerpes formicivorus*), Golden-fronted Woodpecker (*Centurus aurifrons*), and Collared Aracari (*Pteroglossus torquatus*), the latter of which is also a potential nest predator (Whitacre *et al.* in prep.).

DISCUSSION

Each of the species that utilized tree cavities for nesting belonged to one of two groups – the owls and the falcons – that do not construct their own nests. Of the four owls and five falcons that bred in these forests, most (three owls and four falcons) nested primarily in tree cavities. Black-and-White Owls laid their single-egg clutches on bare epiphytes rather than in cavities (Gerhardt *et al.* 1994), and Orange-breasted Falcons (*F. deiroleucus*) used large cliffs for their nest sites (Baker *et al.* 2000).

Within habitat that provided for all of their other needs, tree cavities suitable for nesting appeared to be common for each of the three smaller owl species. Such was the case whether the chosen cavities were non-excavated (Mottled Owls and Guatemalan Screech-Owls) or excavated by other birds (Ferruginous Pygmy-Owls). By contrast, optimal nest cavities were deemed uncommon and special for each of the four cavity-nesting falcons.

So what attributes of selected cavities contributed to their being common or rare?

Characteristics of cavities used by falcons that contributed to their rarity were thought to include tree size (all four species), tree species (at least the two forest-falcons), cavity size (all four, though perhaps less so for Bat Falcons), position (see below), and the ephemeral nature of dead trees (Bat Falcons). I believe that a more concise explanation subsumes all of these attributes into one, that being cavity position.

The common cavities used by each of the owls were in trees that were part of the understory (i.e., not part of the canopy). By contrast, cavities used by forest-falcons were within the overstory (canopy-forming) trees, while lone or emergent trees were used by Bat Falcons and Laughing Falcons. This requirement, rather than height per se, may limit the potential nest trees, in terms of species and size, to the point of being unique and rare.

The cavity-nesting raptor species discussed here are primarily forest species and therefore at risk to deforestation. Ferruginous Pygmy-Owls inhabit openings, but require forest fragments for nest cavities, perches, and cover. Mottled Owls (and perhaps Guatemalan Screech-Owls) can be found in areas where logging and agriculture have occurred; they nonetheless require intact forest fragments for nesting, and exist in such areas in lower numbers than in the primary forest. Although Laughing Falcons appeared to be more numerous in the agricultural lands south of the park than within, a larger percentage of those outside the park did not nest in a given year (Parker 1997). These apparent relationships need further study, but are of special interest to this particular discussion.

Even localized selective logging may have a deleterious effect upon cavity resources (as shown for Thai forests; Pattanavibool & Edge 1996) needed by these falcons. Both forest-falcon species, in particular, selected large Spanish cedars as nest trees. This is foremost among commercially valuable trees and a species that has historically been logged in these forests. Given the apparent rarity of optimal nest trees for the four falcon species discussed, any further loss of such trees may adversely affect their reproductive opportunities.

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