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Cavity Nesting by Great Kiskadees (*Pitangus sulphuratus*): Adaptation or Expression of Ancestral Behavior?

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Beginning with the work of von Ihering (1904), the nature of the nest has been used for formulating systematic hypotheses within the family Tyrannidae. Here, I provide several records of cavity nesting by Great Kiskadees (*Pitangus sulphuratus*). I then discuss nest location (exposed vs. concealed) and nest structure (cup-shaped vs. domed) of *Tyrannus* relatives (12 genera and ca. 33 species) as they relate to the systematics of the group, and suggest that cavity nesting is a primitive trait in certain branches of the Tyrannidae.

Great Kiskadees usually build large globular or domed nests on high, exposed sites atop isolated trees (von Ihering 1904; Haverschmidt 1968, 1974; pers. obs.). The nests contain a lateral entrance and are firmly attached to the forks of branches (Euler 1900, Sick 1985). On 18 September 1989, I located a Great Kiskadee nest in a cavity (hereafter "niche") 7.84 m above the ground in the front wall of the Imaculada Conceição Church in Piracicaba, southeastern Brazil. The nest faced a public square that contained many trees. It was in a corner of the building and partly protected by a large vertical column. Internal dimensions of the niche were: width, 13 cm; height, 47 cm; and horizontal depth, 25 cm. The globular nest occupied the entire width of the niche, although a small space occurred above the nest. The entrance hole was at the front of the nest. I observed two adults feeding at least two nestlings at the nest entrance, and the ground below the nest was littered with insect fragments and pellets. The nest was inactive on 25 September, but by 8 October a pair of House Sparrows (*Passer domesticus*) occupied the nest and subsequently nested successfully. The remains of the kiskadee nest were visible on the church wall five years after I discovered the nest.

On 7 December 1993, I found another nest, nearly identical to the nest described above, in a niche 10.54 m above the ground in a side wall of the same church. This nest also was partly protected by a vertical column. Old pellets typical of those produced by Great Kiskadees were on the ground beneath the nest. Judging by the appearance of the nest and pellets, I am confident that the nest was constructed by Great Kiskadees. On 27 November 1995, I found a third kiskadee nest in this same niche, but saw no kiskadees (the 1993 nest had been removed by maintenance workers in 1994).

The literature contains several reports of Great Kiskadees nesting in niches, including inside domed nests of other birds (Zuberbhuler 1971, Belton 1985) and in an old woodpecker hole (Haverschmidt 1974). In addition, Great Kiskadees may build open-cup nests in concealed sites (e.g. beneath palm leaves [Smith 1962, Sick 1985] or among dense foliage over water [J. W. Fitzpatrick pers. comm.]) or build an open nest that gradually is covered during the first part of incubation (Traylor and Fitzpatrick 1982). Therefore, nest structure is not especially rigid in this species, perhaps suggesting an evolutionary pathway from open nests to globular nests.

The Lesser Kiskadee (*Philohydor lictor*) formerly was placed in *Pitangus*. It builds a cup nest (Smith 1962, Willis 1962, Haverschmidt 1968) so unlike that of the Great Kiskadee that Haverschmidt (1957) wondered whether the two species really were congeners. Owing to differences in nest structure and syringeal traits, Lanyon (1984) placed *lictor* into the newly created genus *Philohydor*. Several other close relatives of Great Kiskadees occasionally place their nests inside cavities, including Eastern Kingbirds (*Tyrannus tyrannus*; Brewster 1937, Bent 1942), Western Kingbirds (*T. verticalis*; Munro 1919, Bent 1942), and Social Flycatchers (*Myiozetetes similis*; Traylor and Fitzpatrick 1982). In addition, obligate or facultative cavity nesters are found in the tyrannid genera *Pyrrhomyias, Sayornis, Xolmis, Fluvicola, Colonia, Machetornis, Attila, Casiornis, Rhytipterna, Sirystes, Myiarchus, Deltarhynchus, Ramphotrigon, Conopias, Myiodynastes,* and *Tityra* (Euler 1900, von Ihering 1904, Tyler *in* Bent 1942, Haverschmidt 1957, Skutch 1960, Traylor and Fitzpatrick 1982, Lanyon and Fitzpatrick 1983, Parker 1984, Lanyon 1985, Sick 1985, Hilty and Brown 1986, Tostain 1989). As summarized here, *Pitangus* can be added to this list.

Lanyon (1985) suggested that cavity-nesting behavior in several tyrannid subfamilies is attributable to convergent or parallel evolution. Among the obligate cavity nesters, *Conopias* and *Myiodynastes* are the closest relatives of *Pitangus*. The *Tyrannus*/*Pitangus* assemblage comprises 12 genera and 33 species (Traylor 1977, Traylor and Fitzpatrick 1982, Lanyon 1984): *Tyrannus* (13 species), *Empidonomus* (1), *Griseotyrannus* (1), *Tyrannopsis* (1), *Megarhynchus* (1), *Conopias* (3), *Myiodynastes* (5), *Myiozetetes* (4), *Legatus* (1), *Philohydor* (1), *Pitangus* (1), and *Phelpsia* (1). I hypothesize that cavity nesting is a primitive character in certain branches

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of the Tyrannidae. Members of some assemblages (notably the *Tyrannus* relatives) maintain the behavior, whereas others within the same assemblage have evolved toward building exposed, open nests or even domed nests.

Cavity nesting must have appeared early in the *Tyrannus* group, being a primitive character because cavity nesters need only build a simple cup within an existing site. The evolutionary shift from secondary cavity nesting to building a domed nest would maintain the advantages of cavities (i.e. concealment from predators and protection from wind and rain) while obviating the need to acquire and defend a scarce resource that is exploited by many species of animals (Collias and Collias 1984). Indeed, the aggressive habits of tyrannines might be related to building and maintaining nests in exposed situations, as suggested by von Ihering (1904). The fact that several species that normally build a globular nest occasionally revert to nesting in cavities (i.e. *Myiozetetes* and *Pitangus*) suggests that domed nests evolved as substitutes for cavities. In addition, the Piratic Flycatcher (*Legatus leucophaius*) is a nest parasite of species that use closed nests (Skutch 1960, Sick 1985), which may be a sign that it evolved from a line that built closed nests or used cavity nests.

Facultative or obligate cavity nesting occurs in several branches of the phylogenetic tree proposed by Lanyon (1984) for the Tyranninae. The genetic background for cavity nesting may be present but unexpressed in some tyrannid groups, and expressed occasionally in other species that normally build open-cup or domed nests. I hypothesize the latter to apply for Great Kiskadees and Social Flycatchers. Under this evolutionary scenario, facultative cavity nesting would be an expression of ancestral behavior.

I propose the Latin term "arbocavicola" ("arbocavicolous" in English) as a technical and more concise substitute for "tree-cavity nesting," "tree-hole nesting," or "tree-cavity using" animals, following the rules for scientific neologisms in Brown (1985). The complete neologism would be "arbocavinidicola," pertaining to the use of a tree cavity for nesting. General neologisms would be "cavicola," for use of any cavities, and "cavinidicola," for use of any cavities for nesting.

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Interbreeding of a Tricolored Heron and a Snowy Egret in South Dakota

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Reports of interbreeding among herons are uncommon and include a Little Blue Heron (*Egretta caerulea*) and a Cattle Egret (*Bubulcus ibis*) in California (Bailey et al. 1989), a Little Blue Heron and a Snowy Egret (*E. thula*) in Florida (Sprunt 1954), and a Little Blue Heron and a Tricolored Heron (*E. tricolor*) in Arizona (Phillips et al. 1964). In addition, a possible hybrid between a Snowy Egret and a Tricolored Heron was photographed in Florida in 1960 (Dickerman and Parkes 1968). In this paper, we report interbreeding between a Tricolored Heron and a Snowy Egret. To our knowledge, this hybrid combination has not been reported previously.

Tricolored Herons and Snowy Egrets occur sympatrically along the Atlantic coast from New York to South America, and along the Pacific coast from Mexico to Peru (Hancock and Elliott 1978). Tricolored Herons rarely nest inland as far north as South Dakota (Schmidt 1979, Skadsen 1986), whereas Snowy Egrets have been locally common breeders in eastern South Dakota since at least the early 1980s (South Dakota Ornithologists' Union 1991).

On 23 June 1995, we observed a Tricolored Heron in a mixed-species heronry in Brown County, South Dakota (45°40′N, 98°05′W). This observation was only the fifth record of a Tricolored Heron in South Dakota (South Dakota Ornithologists' Union 1991). The heronry was in a flooded, 5-ha stand of dead Russian olive (*Elaeagnus angustifolia*) trees. Extensive flooding in 1993 and 1994 had increased the available aquatic habitat and probably contributed to the establishment of the heronry. Nesting species included Cattle Egrets, Great Egrets (*Ardea alba*), Snowy Egrets, Little Blue Herons, and Black-crowned Night-Herons (*Nycticorax nycticorax*). About 1,200 pairs of herons (mostly Cattle Egrets) nested in the heronry in 1994 (Peterson 1995), and about 5,950 pairs (95% Cattle Egrets) nested there in 1995 (Naugle unpubl. data).

On 30 June 1995, we marked a nest site after observing the Tricolored Heron perched on the rim of a nest bowl. This nest contained four light-bluish eggs and was constructed of Russian olive branches about 30 cm above the water. On 2 July, a Snowy Egret was incubating the remaining two eggs in the marked nest, which also contained two nestlings. While we were observing the incubating Snowy Egret, a Tricolored Heron landed near the nest. Subsequently, we observed a "nest relief ceremony," in which the Tricolored Heron and the Snowy Egret raised their head plumes and began bill-nibbling and vocalizing (see Rodgers 1977). Following the nest relief ceremony, the Tricolored Heron settled on the nest and incubated the eggs.

All four eggs had hatched by 6 July. During that visit we photographed and recorded a nest relief ceremony on standard 1.25-cm VHS tape. The Snowy Egret fed the chicks regurgitated food. The Tricolored Heron also fed the chicks in the absence of the Snowy Egret. On 1 August, photographs were taken of the four juveniles (which were in the late branching stage of development) at the nest site (VIREO accession batch V06/24/001-005; Academy of Natural Sciences, Philadelphia). Their plumage and soft-part colors were unlike those typical of juvenile Snowy Egrets or Tricolored Herons (McVaugh 1972, 1975). Their heads were marked with a gray-brown crown that extended down the nape of the neck and graded to a slate gray on the back and wings (see Fig. 1). The sides of the neck and breast varied among individuals from slate gray to pale rufous. All juveniles were white on the head and undersides of the neck and body. Their irides were yellow, and their bills were black above and dark orange below, grading to black distally. The legs were yellow-green proximally and posteriorly, grading to dark on the distal anterior surface. There was no brownish-red color on the primary or secondary coverts or on the sides of the neck or breast, as would be typical of juvenile Tricolored Herons.