FUNCTION OF CREST DISPLAYS IN ROYAL FLYCATCHERS (ONYCHORHYNCHUS)¹

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Royal flycatchers (Onychorhynchus coronatus and O. mexicanus) of the neotropics have large, brilliantly colored, fan-shaped crests that are usually concealed but can be erected perpendicularly to the axis of the head in both sexes. Hand-held birds spread their crests and slowly wave their heads from side to side with open bills (Bangs and Barbour 1922, Wetmore 1972, Dick and Mitchell 1979) in a manner convergent with the "snake display" of hole-nesting tits (Sibley 1955). Within the family Tyrannidae (375+ species), both the details of crest elaboration and the head-waving behavior of royal flycatchers appear to be unique. In this paper, I examine hypotheses concerning the adaptive function of crest displays in royal flycatchers and report new field observations, including the simultaneous display of a hand-held pair.

The crest display of hand-held royal flycatchers was aptly described for a Panamanian bird (O. mexicanus) by Wetmore (1972, p. 499), "as I held the bird in my hand it spread the crest widely and threw it far forward, at the same time compressing the nape feathers laterally into a straight sharp edge down the back of the neck. The bird rotated the head from side to side in a swinging motion during which it turned through an arc of 180°. With this the bill was opened widely, and the tongue flicked. . . . "

On 1 July 1977, I mist-netted a male and female O. coronatus together in the forest understory on the alluvial plain of the Río Heath, Department of Madre de Dios, Peru. When removed from the holding bag and held together facing one another, the birds began immediately to perform a synchronous but out-of-phase head-waving display (Fig. 1). After 15-20 sec, the birds were held closer together at a distance of a few centimeters. They locked bills and synchronously rotated their heads back and forth 180°. After several minutes, neither individual could be induced to perform. The display was not accompanied by vocal hissing, which is often produced by hole-nesting birds to discourage predators (Sibley 1955). Bill locking during courtship is unknown in tyrannids (Smith 1966), which suggests that it could have been a mutual attack. However, the birds did not peck at extended fingers or the camera lens.

The crest displays of hand-held royal flycatchers have also been observed in mist-netted birds of both sexes in the Guyanas (Dick and Mitchell 1979), on the Rio Xingu in eastern Brazil (pers. observ.), and in northern Peru and southeastern Paraguay (M. Foster, pers. comm.). Geographic or sexual variation in the behavior, if any, and its ontogeny are unknown. Dick and Mitchell (1979) interpreted this stereotyped behavior as an instance of Batesian mimicry; potential predators are repelled by the snake-like appearance of the bird. Wetmore (1972) suggested that while the crest display may represent a threat function, it might be the result of a "nervous reaction" to being handled or presented otherwise in normal courtship display.

Despite the extensive geographic ranges of royal flycatchers, published observations of crest displays in free-living birds are limited to Skutch's (1960) anecdotes of O. mexicanus in Costa Rica, He observed crest erection several times by preening birds of both sexes, by males during agonistic interspecific encounters, and by males displaying to females building nests or attending eggs. Skutch (1960, p. 525) noted one such display, "the [male's] crest was spread widely while he preened. In the middle of the morning he came with his mate when she returned from an excursion for finding food. Alighting on a vine near the nest, he spread his scarlet diadem to the full and turned his head from side to side so rapidly that the feathers quivered. At the same time, he shook his half-opened wings, fanned out his vellowish tail, and uttered a rapid series of peculiar notes, somewhat like the usual piping call but sharper. This superb display, the only one I have ever seen in many hours of watching Royal Flycatchers, lasted only a few seconds." Skutch (1960) concluded that the principal function of the crest was in courtship displays. Skutch's observation includes two of the principal elements of the crest display of hand-held birds: (1) crest erection; and (2) the side-to-side motion of the head. This suggests that the "snake-like" behavior of hand-held birds may be derived from courtship behavior.

Concealed crown patches occur widely within the Tyrannidae, including genera closely related to *Onychorhynchus* (Traylor 1977). Crown feathers are raised most frequently during intra- and interspecific agonistic encounters. Smith (1966) suggested that the exposed crown feathers of *Tyrannus* spp. mimic the open gape and convey a message of aggression by "doubling" the number of open mouths seen by the signal recipient. Although the elaborate crest of the royal flycatcher might provide a supernormal "gape mimic" during intra- or interspecific interactions, most of which are aerial, there

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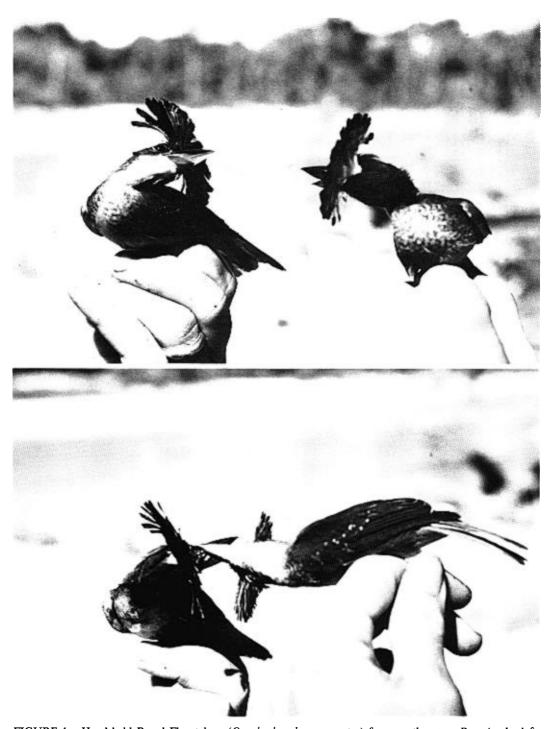


FIGURE 1. Hand-held Royal Flycatchers (Onychorhynchus coronatus) from southeastern Peru (male, left; female, right) performing simultaneous crest display and head-waving behavior. Mouth lining of both sexes is bright yellowish-orange. Ground color of crest is red in males and orange or yellowish-orange in females.

is scant evidence that its primary function is as a badge of aggression.

S. Hilty and M. B. Robbins (Hilty, in litt.) observed an intraspecific crest display by males of *O. mexicanus* in Chiapas, Mexico, in June 1975: "Both birds held their crests fully erect as they snapped and scuffled for perhaps 45 s. Without knowing the context of the aggression, it seemed to be birds contesting a territorial boundary . . . there was some head tilting as the birds lunged at each other repeatedly." Hilty (in litt.) also reported that both males and females will readily investigate playbacks of tape-recorded calls, but do not raise their crests when responding.

Female royal flycatchers incubate eggs in an enclosed niche, which is entered through a vertical slit, in a loosely constructed hanging nest (Skutch 1960). Males do not incubate eggs or feed the young but continue to defend the nesting territory throughout the nesting period. Skutch reported that the partially spread crest of a female could be seen gleaming in the shadows in the back of the open niche, which seemed to diminish the value of the otherwise cryptic coloration of the sitting bird. The brilliant crest of the incubating female, in combination with the open gape, may be especially effective in startling or momentarily deterring avian and mammalian predators that discover the nest. Although crests (red or orange with dark terminal band) exhibit "coral snake" colors, they do not appear to be snake mimics (e.g., multiple bands). The small nest cup would seem to prevent exaggerated side-to-side movement of the head and crest and there is no evidence that royal flycatchers ever perform a crest display in defense of the nest.

Roosting habits of the male royal flycatchers are unknown. However, if Skutch is correct about sexual roles during incubation, then it seems unlikely that males, or females away from the nest, could become cornered by predators in a confined space during the day when the crest could have a "startle effect" on predators with color vision. In the absence of evidence that royal flycatchers are unpalatable or dangerous to potential predators, it seems unlikely that the crest functions as an aposematic signal.

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In summary, the scant data suggest that crest displays are performed during at least two circumstances in freeliving birds: (1) courtship display; and (2) intra- and interspecific aggression. Crests of both sexes (crest length of sexes is nearly identical) may play an important role in courtship, and ultimately, it would appear that sexual selection is the agent responsible for their elaboration. Because the brilliant crests are concealable, moderate increases in feather length through sexual selection may not be subject to selection from predators with color vision (i.e., birds). Interpretation of crest displays in hand-held birds is uncertain, but they may represent a ritualized behavior induced by the shock of being mist-netted and hand-held rather than an antipredator defense. Likewise, the data do not corroborate the hypotheses that crest displays are aposematic warning signals or snake mimics.

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DAYTIME FEEDING BY LEACH'S STORM-PETREL ON A MIDWATER FISH IN THE EASTERN TROPICAL PACIFIC¹

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Key words: Leach's Storm-Petrel; vertical migrators; Vinciguerria lucetia; seabird foraging; nocturnal feeding.

Information on the diet of Leach's Storm-Petrel (Oceanodroma leucorhoa) has been obtained almost exclusively from breeding colonies where crustaceans (mainly euphausiids, but with amphipods and coppods locally important) and fish (mainly myctophids) make up the bulk of the diet (Linton 1978, Watanuki 1985, Vermeer and Devito 1988). Almost nothing is known about this species' foraging habits in the tropical

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