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Display of an Inedible Prop as a Signal of Aggression? Adaptive Significance of Leaf-Display by the Turquoise-Browed Motmot, *Eumomota superciliosa*

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Abstract

The incorporation of an inedible object (prop) into a behavioral display is rare among birds. Only four avian taxa have been reported to display with a prop, and in all studied species, prop use has been found to play a role in mate acquisition. However, little is known about the context and adaptive significance of prop use by the motmots. Both male and female motmots perform a leaf-display, whereby a leaf is held horizontally in the tip of the bill for an extended period. I collected observational data on leaf-display by the turquoise-browed motmots (*Eumomota superciliosa*) to investigate the potential role of this display as a mate-choice or agonistic signal. Observations of 61 leaf-displays by 27 individuals indicate that males and females are similarly likely to perform the leaf-display, that the leaf-display is performed throughout the long-breeding season, and that the display is performed by both paired and unpaired birds. These observations suggest that the leaf-display does not play a role in mate-attraction. However, the leaf-display was often performed in association with a chase or fight with a same-sex individual, and the display was sometimes performed in conjunction with an agonistic display at nest sites, suggesting that the leaf-display may function in both sexes as a signal of aggressive intent or as a signal of status.

Introduction

Many avian species perform elaborate behavioral displays when signaling to conspecifics. Elaborate displays are most often performed by males, and are typically performed during pair-formation or agonistic interactions (e.g. mating flight-display by Jackson's widowbird (*Euplectes jacksoni*), Andersson 1992; territorial vocalizations and color signaling by red-winged blackbird (*Agelaius phoeniceus*), Peek 1972). In addition to performing elaborate behavioral, vocal, and morphological displays, a few avian species incorporate inedible objects (props) into their display. The use of a prop has only been recorded in four avian groups, the bowerbirds (Ptilonorhynchidae), the fairy-wrens (Maluridae), the birds-of-paradise

(Paradisaeidae), and the motmots (Momotidae) (for review, see Montgomerie 2006; Scholes 2006).

In all previously described cases of prop use, the display plays a role in mate acquisition. Among bowerbirds, males decorate their courtship bowers with a variety of colored objects, including feathers, leaves, and flowers. Male bowerbirds directly present some of these props to visiting females (Borgia 1986), and the decorations significantly influence mating success (Patricelli et al. 2003). Among birds-of-paradises, males present a leaf to females on their display courts (Scholes 2006). In fairy-wrens, males often carry a flower or fruit in their bills when they court a female on a nearby territory, and the use of a prop is thought to increase mating success (Rowley & Russell 1997). In all of these species, only the males

use props in display, and the displays are performed in contexts clearly associated with mating (Borgia 1986; Rowley & Russell 1997; Doucet & Montgomerie 2003; Rathburn & Montgomerie 2003). The motmots also use a prop in a display, whereby a large leaf is held horizontally in the tip of the bill (leaf-display; Fig. 1.). The motmot's leaf-display is performed by both sexes, and is performed throughout a 6-mo breeding season in contexts not clearly associated with mating (T.M. Murphy, pers. obs.). The leaf-display has been reported in four of the ten species of motmots (*Momotus momota* Skutch 1964; *Barophthengus martii*; Skutch 1971, *E. superciliosa*, *Momotus mexicanus*; T.M. Murphy, pers. obs.), but has not been systematically studied.

In this paper, I present a detailed description of leaf-displays by a color-banded population of colonially breeding turquoise-browed Motmots (*E. superciliosa*) in Yucatan, Mexico. I collected observational data to address: (1) whether the leaf-display was performed more often by one sex, (2) whether the leaf-display was performed more frequently early in the breeding season, when pair formation occurs, compared with later in the season, (3) whether unpaired birds or paired birds were more likely to

perform the display, and (4) whether social interactions (i.e. courting, fighting and chasing) or other displays were associated with the leaf-display. This research provides the first systematic description of the motmot's leaf-display.

Methods

The turquoise-browed motmot is a socially monogamous neotropical bird that often breeds colonially in the Yucatan Peninsula of Mexico. The species nests in tunnels dug into vertical earthen banks in sinkholes and man-made structures, such as freshwater wells and limestone quarries (Orejuela 1977; Scott & Martin 1983; Murphy 2007a). Males and females arrive synchronously on the breeding grounds approx. 3 mo prior to clutch initiation, and both sexes spend similar amounts of time at the breeding colony during the 6-mo breeding season (Murphy 2007b). Motmots breed synchronously (78% of pairs initiate their primary clutch within 6-d, T.M. Murphy, unpubl. data), and fledge a maximum of one brood per year. When early nesting attempts fail, birds often re-nest with the same mate (Murphy 2007b). Unpaired males and females are common, and generally remain throughout the season at the colony where they first settled and do not roam among colonies.

I studied motmot leaf-display at two colonies (14 and 39 pairs) between Mar. and Aug. 2002. The two colonies were located approx. 1 km apart, near the Ria Lagartos Biosphere Reserve in Northern Yucatan, Mexico (21°33'N, 88°05'W). I captured motmots in mist nets and color-banded most breeders (98%) and non-breeding floaters (c. 85%). Because the species is sexually monomorphic, all individuals were sexed by laparotomy. There were no noticeable adverse effects of the procedure (see Murphy 2008).

Observations of leaf-display were conducted from permanent blinds located 45–55 m from the colony. Monitoring of multiple focal individuals was facilitated by the simultaneous recording of behavior by two observers with spotting scopes. To minimize human disturbance, observers entered the blind before sunrise while motmots were away from the colony. The presence of observers within the blind had no noticeable effect on motmot behavior (see Murphy 2006, 2007c). Nesting colonies were observed in the mornings for approx. 3 h immediately following sunrise every 2–4 d. Each colony was observed three times over 10–16 d periods throughout the 6-mo breeding season.

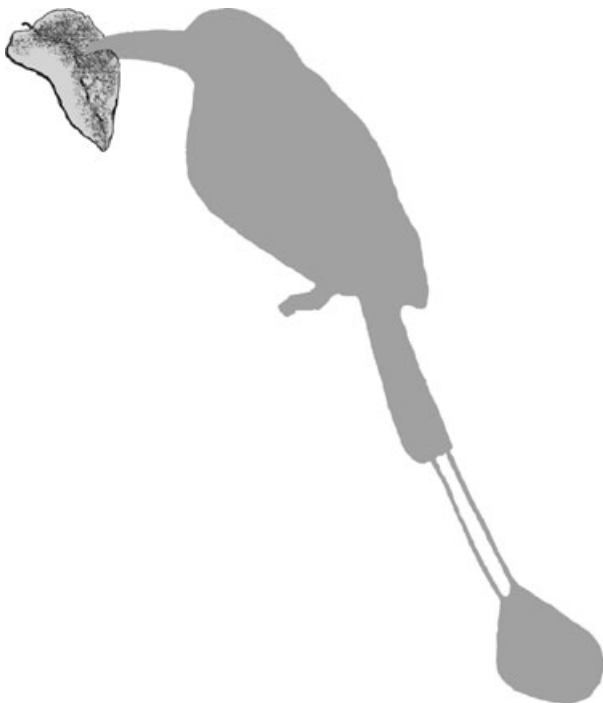


Fig. 1: During a leaf-display, the turquoise-browed motmot holds a large leaf in the tip of its bill.

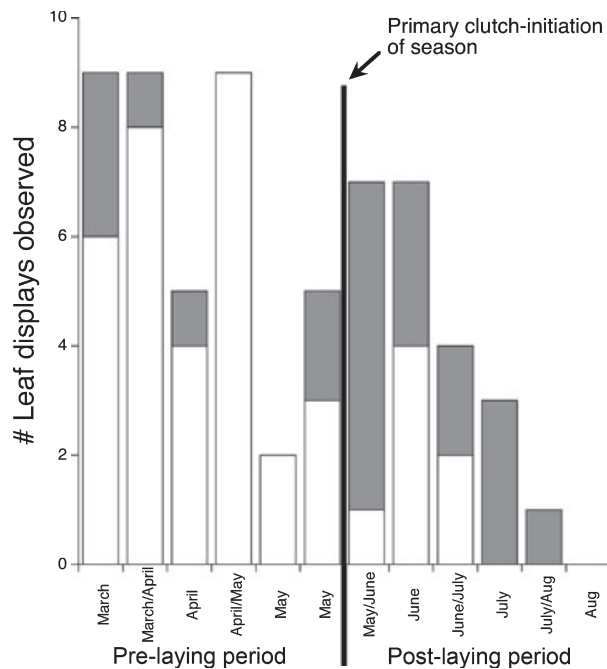


Fig. 2: Seasonal distribution of 61 leaf-displays performed by all motmots (male, female, and unknown-sex) over the 6-mo breeding season in 2002. Observation-blocks along the x-axis are comprised of six 3-h observations (equally divided between two breeding colonies) over 10–16 d. Open bars represent leaf-displays by paired birds, and filled bars represent displays by unpaired birds. The vertical line marks the first clutch of the year, and divides the season into the pre-laying period and the post-laying period.

Upon observing a leaf-display, I recorded the identity and sex of the bird, whether the displaying bird was paired or unpaired, the age of the bird based on feather wear (Murphy 2005), and whether the display occurred in the pre-laying period (before the first clutch was initiated for the season) or post-laying period of the breeding season. I recorded social interactions (i.e. courting, fighting, or chasing) and other displays that were performed during the leaf-display, or that immediately followed the display. When possible, I also recorded social interactions that preceded the leaf-display, although this was not always possible because we generally did not start following an individual until after we detected the display.

Non-parametric statistics was used because data were not normally distributed. All probabilities are two-tailed and rejection level was $p > 0.05$. Descriptive data are based on all observed leaf-displays ($n = 61$); however, in some analyses, I used data from the first recorded leaf-display of each individual to avoid pseudoreplication ($n = 27$).

Results

The leaf-display was only occasionally observed. Over the 6-mo breeding season, I observed only 61 leaf-displays performed by 27 individuals. Both males and females were observed performing the leaf-display (sexual distribution among displaying individuals: 12 males, 10 females, five unknown sex; Binomial test: $Z = 0.43$, $p = 0.67$, $n = 22$; sexual distribution among all observed displays: 27 displays by males, 25 displays by females, nine display by birds of unknown sex; $Z = 0.28$, $p = 0.78$, $n = 52$). While holding a leaf, a motmot would typically sit still on the vertical colony-face or on a nearby perch. The leaf was generally held horizontally in the tip of the bill by the displaying bird, and was held for many minutes, occasionally for long periods (c. 60 min). In most cases (78%), the leaf was yellow or brown, but occasionally it was green [color of displayed leaf: 17 yellow, four brown, six green; percent of leaves displayed that were yellow or brown by males = 83% (10/12), by females 80% (8/10)]. Birds either picked up a leaf from the ground or plucked one from a tree, and birds were often seen plucking a yellow or brown leaf from a tree that was mainly covered with green leaves.

The leaf-display was performed throughout the long-breeding season, although it was performed more often in the pre-laying period (observed displays: pre-laying period = 39, post-laying period = 22) (Fig. 2). Out of the 27 individuals observed performing the leaf-display, 19 were paired (11 males, eight females), and eight were unpaired (one male, two females, five unknown sex). During the pre-laying period, paired and unpaired birds performed the leaf-display with similar frequency to their ratio in the population (pre-laying period ratio of unpaired to paired was approx. 25:75%): four unpaired birds performed 18% (7/39) of all observed leaf-displays. Furthermore, unpaired birds represented 19% (4/21) of all birds observed performing the leaf-display in the pre-laying period (Fig. 2). During post-laying period, when fewer birds were unpaired (post-laying period ratio of unpaired to paired was approx. 15:85%), the proportion of unpaired birds performing the leaf-display was much greater than their proportion in the population: eight unpaired birds performed 68% (15/22) of all observed leaf-displays, and unpaired birds comprised more than half (62%, 8/13) of all birds observed performing the display (Fig. 2).

The displaying individual was often involved in a chase or fight immediately before, during, or after

the period when the leaf was held in its bill [41% (11/27) of cases of leaf-display were associated with chases or fights]. There was not a significant difference in the sex of the displaying bird involved in an agonistic interaction (male = 7, female = 4; Binomial test: $Z = -0.90$, $p = 0.37$, $n = 11$). Most of the chases or fights that were associated with a leaf-display were between same-sex individuals: when both birds involved in a chase or fight were identified, the sex of the leaf-displaying bird was the same as the sex of opponent in 86% (6/7) of cases.

Although a displaying bird generally sat still while holding a leaf, there were two behavioral displays that occasionally accompanied the leaf-display. In the first, a leaf-displaying bird would fly to the entrance of a nesting tunnel and perform the agonistic scoot-display, which involves moving rapidly in and out of the entrance to the nesting tunnel in a piston-like fashion. The scoot-display is a commonly observed agonistic display that is performed by a paired bird while defending its nest, or by an unpaired floater while attempting to usurp a nest (unpubl. data). Although the scoot-display was generally performed without a leaf in the displaying bird's bill, the leaf-display was performed in conjunction with the agonistic scoot-display in seven cases (four males and three females). In the second display, the bird would repeatedly whack the leaf onto a substrate by quickly flinging its bill downward in a similar manner used to kill and pulverize captured prey. Whacking of the leaf was observed in five individuals (two males, one female and two unknown sex).

Discussion

Both male and female turquoise-browed motmots occasionally perform a leaf-display at the breeding colony, whereby a colored leaf, generally yellow or brown, is held horizontally in the tip of the bill and held for an extended period. Based on behavioral observations of the social contexts during which the display is performed, two lines of evidence support the possibility that the leaf-display may function as a signal of aggressive intent or as a signal of status. First, the leaf-display is often performed in association with a chase or fight, often with a same-sex individual. Second, the leaf-display is occasionally performed in conjunction with a commonly observed agonistic display (scoot-display), which is performed at the entrance of nesting tunnels by territory owners defending their nest, or by unpaired floaters attempting to usurp a nest.

Behavioral observations indicate that the baseline level of agonistic interactions is low at breeding colonies, and that on average, males and females are involved in less than one agonistic interaction per hour during both the pre- and post-laying periods (unpubl. data). Because agonistic interactions are infrequent, it seems likely that the observed link between agonistic interactions and the similarly infrequent leaf-display is meaningful. Even though chases and fights are associated with less than half of the observed leaf-displays, the co-occurrence of these uncommon behaviors suggests that the leaf-display is causally related to agonistic interactions and that the display may function during resource defense.

The lack of association between the leaf-display and agonistic interactions in the remaining 60% of cases may reflect that the display has multiple signaling functions, or that the display is only performed in response to certain types of agonistic interactions. However, the absence of a strong link between the leaf-display and agonistic interactions may arise if the display successfully deters an opponent from further interactions, and thus prevent the signaler from escalating to a fight or chase. Alternatively, interacting birds may react by increasing non-overt defensive behaviors, such as territorial or mate defense, which would not have been detected with our observation methods. Furthermore, the link between agonistic interactions and the leaf-display may be significantly higher than our estimate because we only began observing birds after detecting a leaf-display, and so it is likely that we missed many relevant interactions that preceded leaf-displays.

The leaf-display does not appear to function as a mate-choice signal because paired birds perform the display throughout the long-breeding season, and unpaired birds do not perform the display more often than paired birds during the pre-laying period when most pair formation occurs. Furthermore, both males and females perform the leaf-display, and the sexes perform the display with similar frequency, which suggests that the signaling function of the display is similar for the sexes (there is no evidence for mutual sexual selection in this species (Murphy 2007b, 2008), so females are not predicted to solicit mates).

It is interesting that both unpaired and paired birds perform the display with similar frequency (based on their relative proportions in the population) during the pre-laying period of the breeding season, yet unpaired birds perform the leaf-display

more often than paired birds during the post-laying period. This pattern may arise because competition for nest sites is most extreme during the pre-laying period. In contrast, during the post-laying period, paired birds invest significant time into breeding and less time into nest defense, whereas most unpaired birds continue to spend much time attempting to usurp pre-constructed nest sites (unpubl. data).

The disproportionate use of yellow or brown leaves suggests that motmots might prefer these colors and that leaf coloration may be an important component of the signal. Future research should investigate a potential color preference, possibly by presenting different colored objects near the nests that could be used as props. It is noteworthy that motmots do not line their nest with leaves or vegetative material, or use vegetative material in any other fashion, and so the origins of the display are enigmatic.

Three other species of motmots have been observed performing the leaf-display, and unlike the turquoise-browed motmot, none of these species are colonial breeders. In the blue-crowned motmot (*M. momota*), Skutch (1964) observed three birds displaying in a group; one had green guava leaf, the other picked up a small stick, and the third picked up a fragment of bark or dead leaf. Skutch (1971) also observed the rufous motmot (*B. martii*) performing leaf-displays while in a large group. He observed 13 birds in one tree, and noted that one individual held something green in its bill that he thought was a fragment of a leaf. In the russet-crowned motmot (*M. mexicanus*), I have repeatedly observed leaf-display of yellow or green leaves by multiple individuals while congregating in large groups (two to nine individuals). The reasons why these groups form are not clear, but behavioral observations suggest that the groups of *M. mexicanus* are composed of pairs from neighboring territories (unpubl. data), and that the leaf-display may function in these congregations in territorial defense. Moreover, simulated conspecific intrusion into territories of *M. mexicanus* has been found to elicit leaf-display, further suggesting that the leaf-display plays a role in territorial defense (unpubl. data).

The use of props in display represents a unique method of signaling that has been reported in only a few avian taxa. In all previously reported cases, a prop is used exclusively by males during mate acquisition (for review, see Montgomerie 2006). In contrast, the motmot's leaf-display is performed by both males and females in contexts apparently unrelated to courtship. Behavioral observations suggest a

link between agonistic interactions and the leaf-display, and may indicate that the display functions as a signal of aggressive intent or as a signal of status. Future research on this enigmatic display should utilize a manipulative approach, possibly with simulated territorial intrusion, to test if individuals forced to defend resources are more likely to perform the display. Continued research into the adaptive significance of this unique display will further elucidate how selection can favor novel methods for intraspecific communication.

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