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Dishonest 'preemptive' pursuit-deterrent signal? Why the turquoise-browed motmot wags its tail before feeding nestlings

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Both sexes of the turquoise-browed motmot, *Eumomota superciliosa*, display their long-racketed tail in an exaggerated side-to-side wag display in two contexts. In the first, the wag display is performed in the presence of predators (predator-elicited wag display), and evidence supports the hypothesis that the signal functions as a pursuit-deterrent signal (Murphy 2006, *Behavioral Ecology*, **17**, 547–553). In the second, the wag display is performed in the apparent absence of predators immediately before feeding nestlings (prefeeding wag display). I tested four hypotheses on the adaptive significance of the prefeeding wag display: (1) a dishonest, preemptive, pursuit-deterrent signal given in case predators are present; (2) a nonfunctional misfire of the predator-elicited wag display; (3) a signal that alerts nestlings to the delivery of food; (4) a sexually selected signal that advertises parental quality to potential mates. There was no support for the hypotheses that the prefeeding wag display was directed to nestlings or potential mates. The wag display was generally performed where nestlings could not detect the signal and the display did not vary with the sex of the displaying bird, the presence of the mate, or the size of the food carried in the signaller's bill. Evidence presented in this paper is most consistent with the hypothesis that the predator-elicited wag display and the prefeeding wag display are performed as a response to the presence or the potential presence of a predator. I discuss the possibility that the prefeeding wag display functions as a dishonest, pursuit-deterrent signal.

Keywords: antipredator behaviour; cheating; dishonesty; *Eumomota superciliosa*; predator–prey communication; pursuit-deterrent signalling; turquoise-browed motmot; unreliable signal

Pursuit-deterrent signals inform predators that they will not profit from continued pursuit or ambush (Woodland et al. 1980). This form of interspecific communication is selectively beneficial for both signaller and receiver because it prevents the sender from wasting time and energy fleeing, and it prevents the predator from investing in a costly pursuit or ambush that is unlikely to result in capture (Zahavi 1977; Hasson 1991). Vocal and visual pursuit-deterrent signals have been reported for a wide variety of taxa (reviewed in: Caro (1995, 2005), including many avian species (Woodland et al. 1980; Alvarez 1993; Cresswell 1994; Spitznagel 1996; Laiolo et al. 2004; Clark 2005; Murphy 2006; Randler 2006).

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Costs associated with pursuit-deterrent signals ensure the reliability of the signal. When pursuit-deterrent signals convey information about the signaller's awareness of the predator (e.g. perception advertisement: Woodland et al. 1980; e.g. erecting of the tail by white-tailed deer, *Odocileus virginianus*: Bildstein 1983), honesty is maintained by the costs incurred by the signaller when it draws attention to itself. The costs of announcing one's location are thought to be substantial because the signaller generally does not have complete information on the location of all nearby predators and unknown predators can catch the signaller unaware (Bergstrom & Lachmann 2001). The cost of drawing attention to oneself should generally prevent signallers from displaying a pursuit-deterrent signal in a context when no predator has been detected.

The turquoise-browed motmot, *Eumomota superciliosa*, wag-displays its long-racketed tail in an exaggerated side-to-side fashion that resembles the regular motion of

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a pendulum. The side-to-side motion is repeated many times during a wag display (Snow 2001; Murphy 2006) and draws attention to the presence of an otherwise hidden bird (Fjeldså & Krabbe 1990; Hilty 2003; Jones 2003). The wag display is performed in two contexts. In the first context, the display is performed by both sexes in the presence of predators, and research on this predator-elicited wag display supports the hypothesis that the signal functions as a pursuit-deterrent signal by communicating awareness of the predator (i.e. perception advertisement; Murphy 2006). In the second context, the wag display is performed by both sexes immediately before delivering food to nestlings, and in this context, it is performed in the apparent absence of predators. This prefeeding wag display is performed only during the short nestling stage of the annual cycle, and is atypical because the majority of wag displays that occur during other times of the year are performed in the presence of predators (Murphy 2006).

I tested four nonmutually exclusive hypotheses to address the adaptive significance of the prefeeding wag display. These hypotheses fall into two categories based on the intended receivers of the signal: predators or conspecifics.

Hypotheses

The prefeeding wag display may function as a dishonest, preemptive, pursuit-deterrent signal that is performed regardless of the presence of a predator because there is a chance that an undetected predator is near the nest. As a dishonest signal, the prefeeding wag display would falsely announce that predators have been detected, and the signaller would gain selective benefits if a predator were present and deterred from pursuit or ambush. Alternatively, the prefeeding wag display may represent a nonfunctional misfire of a signal that is functional in other contexts. In other words, the prefeeding wag display may occur because of a misfire of the proximate mechanism that mediates the pursuit-deterrent signal, and it may be given in this prefeeding context because of a lowered response threshold to threatening stimuli while making dangerous deliveries to the nest. If the prefeeding wag display is a misfired signal, then there is no selective benefit associated with performing the wag display in this context.

The prefeeding wag display may instead communicate with conspecifics. The display may be directed to nestlings inside the tunnel nest to alert them that a parent is approaching with food. Alternatively, the display may be a sexually selected signal that draws attention to food exposed in the signaller's bill to advertise parental quality or foraging ability to a current or potential mate.

To test whether the prefeeding wag display has a different function from the predator-elicited wag display (i.e. a function not related to communicating with predators), I investigated whether the prefeeding wag display was directed to conspecific receivers. To address the possibility that the wag display is directed to nestlings, I tested whether the prefeeding wag display was more likely to be performed in front of the tunnel nests where nestlings could detect it. To address the possibility that the prefeeding wag display is a sexually selected signal, I tested whether the wag display was performed more often by males than females. Underlying this test is the assumption that males are more competitive for mates, which has been supported by research showing that male but not female tail length correlates with pairing success, performance and reproductive success (Murphy 2007a). To further address whether the wag display is directed to a current or potential mate, I tested whether the display was performed more often or with greater intensity when the mate was present, or when the signaller carried large food in its bill.

METHODS

General Methods

Both sexes of the turquoise-browed motmot have elongate tails that comprise 60% of the overall length of the bird and terminate in large, racket-shaped tips (Murphy 2007b). The turquoise-browed motmot nests in tunnels (0.4–2.2 m in depth, mean = 1.3 m) built low to the ground in earthen banks. The use of tunnel nests is only for breeding, and motmots do not roost in their nests (except when the female incubates overnight). The species breeds colonially in the Yucatan Peninsula, Mexico. Colony size ranges from 2 to 60 pairs, with colonies of 10–20 pairs being most common (Orejuela 1977; Murphy, in press). The turquoise-browed motmot is socially monogamous and both sexes care for highly dependent altricial chicks (Scott & Martin 1986) (nestling period: $\overline{X} \pm \mathrm{SD} = 32 \pm 2.9$ days, range 27–41, $N = 169$).

I studied the prefeeding wag display in 2002 in the deciduous thorn forest near the Ria Lagartos Biosphere Reserve in northern Yucatan, Mexico (21°33′N, 88°05′W) at four colonies in abandoned limestone quarries (range 7–39 pairs). To facilitate individual identification, approximately 98% of all breeders and 85% of nonbreeding floaters were colour-banded.

Observations on prefeeding wag display were conducted with spotting scopes from permanent blinds 45–55 m from the colony. Monitoring of multiple focal individuals was facilitated by the simultaneous recording of behaviour by two observers with spotting scopes. To minimize human disturbance, observers entered blinds before sunrise while motmots were away from the colony (probably roosting on their off-colony territories). Motmots do not perform the wag display in response to the presence of observers within a blind (Murphy 2007a).

Differences between Predator-elicited and Prefeeding Wag Displays

I tested whether the wag display was performed more often after nestlings hatched by monitoring the wag display behaviour of 10 pairs early in the breeding season before they laid eggs, and again late in the season when the same individuals were caring for nestlings. During both periods, I observed each pair for 2 h on separate days.