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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).

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.

I quantified the number of 1-min intervals in which a wag display was observed during the first 20 min that the male and female were present at the colony.

Prefeeding Wag Display

I operationally defined a prefeeding wag display as a wag display performed by a parent motmot with food in its bill when no predator was observed in the vicinity. To establish that it was unlikely that a predator was in the vicinity, I visually scanned the colony area for predators and monitored the behaviour of other motmots at the colony. Because most motmots at a colony perform a wag display when a predator is present (Murphy 2006), the behaviour of nonfocal individuals was a reliable indicator of whether a predator was present and visible to motmots.

Descriptive data on prefeeding wag display were collected from 38 pairs. Alternative hypothesis were based on detailed behavioural observations of 14–15 pairs. Pairs were observed for 2 h at a time, and each pair was observed on a separate day.

Alert nestlings to food delivery

To test whether the nestlings are the likely receivers of the signal, I monitored where prefeeding wag displays were performed in relation to the entrance of the tunnel nest. I considered only feeding events that were preceded by a wag display, and calculated for each individual, the percentage of feeding events in front of the colony face where they could be detected by nestlings.

Advertise parental quality or foraging ability to a current or potential mate

To test whether the wag display functions as a sexually selected signal, I monitored whether males were more likely to perform the prefeeding wag display by comparing the percentage of feedings that were preceded by a wag display for each sex. I also tested whether males performed the wag display with greater intensity than females (total number of side-to-side movements of the tail before delivering food to nestlings).

To test whether the current mate is the likely receiver of the signal, I monitored whether individuals returning to the nest with food were more likely to perform the wag display, or perform the display with greater intensity, when their mate was present than when their mate was absent. For each individual, I compared the percentage of feeding events that were preceded by a wag display, or the mean intensity of the wag display in these two social contexts.

To test whether a potential mate is the likely receiver of the signal, I tested whether food size was related to whether a motmot performed the wag display. I compared mean food size when feeding events were and were not preceded by a wag display by the same individual. Motmots carry food (generally an insect) exposed in the bill, and a single item is carried per delivery. I measured food length and width by comparing the food item to the length and width of the bill. With these values, I calculated the volume of a rectangular prism ($L \times W^2$) that approximated the volume of the food. There is little variation in bill size (Murphy 2007a), and thus bill size served as a reliable reference with which to measure food. I also tested whether the wag display was performed with greater intensity when individuals returned to the nest with a large food item by correlating food size to the intensity of the wag display for one randomly selected feeding event for each individual.

Statistical Analyses

Nonparametric statistics (Kruskal–Wallis, Wilcoxon matched-pairs signed-ranks, Spearman rank correlation) were used to analyse data. All statistical analyses were two tailed, and rejection level was set at $P > 0.05$. Descriptive statistics are listed as mean ± SE. Statistical analyses were conducted using JMP software (SAS Institute, Cary, North Carolina, U.S.A., 1989–2007).

RESULTS

Differences between Predator-elicited and Prefeeding Wag Displays

Individuals performed the wag display significantly more often when they were caring for nestlings than earlier in the season before eggs were laid (Wilcoxon matched-pairs signed-ranks test: 10 males: $T = 1.5$, $N = 8$, $P = 0.016$; 10 females: $T = 0.0$, $N = 7$, $P = 0.016$; Fig. 1). Predators were detected by the observer in 100% (3/3) of the cases where the wag display was performed before eggs were laid, but in only 8% (4/48) of the cases where the wag display was performed after nestlings hatched.

Prefeeding Wag Display

Description

Before delivering food to nestlings, motmots generally perched within 30 m of the nest, but sometimes flew

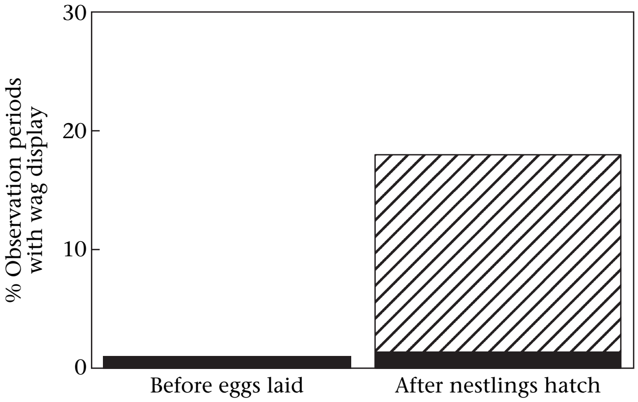

Figure 1. Percentage of observation periods during which the wag display was performed by turquoise-browed motmots early in the season before eggs were laid and after nestlings hatched. ■: occasions when the wag display was performed in the presence of a predator (predator-elicited wag display); ▨: occasions when the wag display was performed in the absence of an apparent predator by a parent with food in its bill (prefeeding wag display).

directly into the tunnel nest without first landing (proportion of feeding events where motmot perched before delivery: males: 0.76 ± 0.04, $N = 37$; females: 0.72 ± 0.04, $N = 38$). When a motmot perched before feeding, about one-third of the feedings were preceded by a wag display (males: 0.30 ± 0.05; females: 0.30 ± 0.06). When all feedings were considered, including when the bird first perched and when the bird flew directly into the nest, the prefeeding wag display was performed before approximately one-fourth of feedings (males 0.25 ± 0.04, $N = 37$; females: 0.24 ± 0.05, $N = 38$).

Motmots that performed the wag display before delivering food to nestlings were never observed performing the display after delivering food to nestlings ($N = 75$ individuals), even though the bird often returned to the same perch where it originally performed the display and remained there for many minutes.

Alert nestlings to food delivery

Prefeeding wag displays were performed significantly more often behind or above the colony face than in front of the colony where they could be detected by nestlings (mean ± SE percentage of wag displays in front of colony face: males: 9 ± 3%; Kruskal–Wallis test: $\chi^2_1 = 23.0$, $N = 15$, $P < 0.0001$; females: 15 ± 4%; $\chi^2_1 = 21.8$, $N = 15$, $P < 0.0001$).

Advertise parental quality or foraging ability to a current or potential mate

There was no significant sexual difference in the percentage of all feedings that were preceded by a wag display (Kruskal–Wallis test: $\chi^2_1 = 0.32$, $N = 75$, $P = 0.57$; Fig. 2). The mean ± SE intensity of the prefeeding wag display (number of left–right movements of the tail before delivering food to the nest) did not differ significantly between the sexes (males: 7.2 ± 1.3, $N = 15$; females: 6.7 ± 1.3, $N = 15$; Kruskal–Wallis test: $\chi^2_1 = 0.18$, $N = 30$, $P = 0.68$).

The presence of an individual's mate was not significantly related to the mean ± SE percentage of feeding events that were preceded by a wag display (14 males: mate present = 0.23 ± 0.05; mate absent = 0.30 ± 0.08; Wilcoxon matched-pairs signed-ranks test: $T = 31.5$, $N = 12$, $P = 0.57$; 14 females: mate present = 0.27 ± 0.07; mate absent = 0.19 ± 0.07; $T = 45.5$, $N = 14$, $P = 0.67$). The presence of an individual's mate was not significantly related to the mean ± SE intensity of wag displays (14 males: mate present = 7.3 ± 2.4; mate absent = 7.4 ± 1.3; $T = 34.0$, $N = 13$, $P = 0.45$; 14 females: mate present = 7.6 ± 1.7; mate absent = 6.1 ± 1.4; $T = 28.5$, $N = 12$, $P = 0.42$).

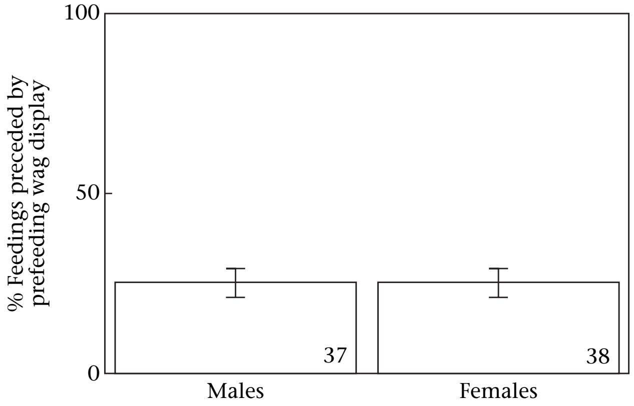

Figure 2. Mean ± SE percentage of feedings to nestlings that were preceded by a prefeeding wag display by adult male and female motmots. Sample sizes are shown in each bar.

There was no significant relationship between the mean ± SE size of the food item delivered to the nest and whether the motmot performed the wag display (15 males: feeding event preceded by wag display, food size = 1713.0 ± 461.0 mm^3; feeding event without wag display = 1679.5 ± 424.3 mm^3; Wilcoxon matched-pairs signed-ranks test: $T = 57.0$, $N = 15$, $P = 0.89$; 15 females: feeding event preceded by wag display, food size = 1350.4 ± 220.5 mm^3; feeding event without wag display = 2015.7 ± 520.5 mm^3; $T = 45.0$, $N = 15$, $P = 0.42$). There was no significant relationship between the size of food delivered to the nest and the intensity of wag displays (Spearman rank correlation: males: $r_S = -0.33$, $N = 15$, $P = 0.23$; females: $r_S = -0.03$, $N = 15$, $P = 0.90$).

DISCUSSION

The wag display of the turquoise-browed motmot is performed in two contexts. In the first, the display is performed in the presence of predators (predator-elicited wag display), and evidence from previous research supports a pursuit-deterrent function to the display (Murphy 2006). In the second, the display is performed in the apparent absence of predators immediately before delivering food to nestlings (prefeeding wag display). This display is performed when a parent motmot returns from a foraging trip to feed its nestlings and the display is typically repeated until the bird delivers the food to the nest. However, the prefeeding wag display is not performed after a parent delivers food to the nest, even though the parent often returns to the same perch from which it originally performed the wag display.

In an attempt to identify whether the prefeeding wag display is performed for similar reasons to those underlying the predator-elicited wag display (i.e. whether both contexts of the wag display are related to the presence or potential presence of a predator), or whether the prefeeding wag display has a separate communicative function, I tested whether two categories of conspecifics are likely receivers of the signal.

I found no support for the hypothesis that the prefeeding wag display functions to communicate with conspecifics. Nestlings are unlikely receivers because the display was generally performed above and behind the nesting colony where nestlings would be unable to detect the signal from inside their tunnel nest. Furthermore, I found no support for the hypothesis that the prefeeding wag display is a sexually selected signal that communicates parental quality or foraging ability because males did not perform the display with greater probability or intensity than females. In addition, the mate is an unlikely receiver because the probability of performing the display and the intensity of the display did not vary with the presence or absence of the mate or with the size of the food carried in the bill of the displaying bird.

Although the turquoise-browed motmot often breeds colonially in the Yucatan Peninsula, the prefeeding wag display is also performed by noncolonial motmots (Wagner 1950; Skutch 1971; T. G. Murphy, personal observation of *Momotus mexicanus* and *E. superciliosa*), whose widely dispersed nests are likely to prevent communication between (nonmate) conspecifics. Thus, it is unlikely that the prefeeding wag display is directed to categories of conspecifics that were not tested in this study.

The results are most consistent with the hypothesis that the prefeeding wag display and the predator-elicited wag display are performed for similar reasons. Previous work supports the hypothesis that the wag display, when performed in the presence of a predator, functions as a pursuit-deterrent signal (Murphy 2006). To test the function of the predator-elicited wag display, I experimentally presented predators to motmots and observed when natural predators were at nesting colonies. The predator-elicited wag display was frequently performed when the signaller was alone and not within signalling distance of conspecifics (i.e. was performed in the presence of only the predator), and the probability and intensity of the display did not vary with the presence of mate or other conspecifics. This evidence supports the hypothesis that the signal is not directed at conspecifics, but is instead directed to the predator and communicates awareness to deter pursuit or ambush (Murphy 2006). Because ambush predators rely on being hidden or undetected while hunting, the motmot's pursuit-deterrent signal would dissuade such predators from attempting ambush (e.g. artiodactyls: Caro et al. 2004; great gerbil, *Rhombomys opiums*: Randall et al. 2000; kangaroo rats, *Dipodomys*: Randall & Boltas King 2001; sciurids: Clark 2005); Diana monkeys, *Cercopithecus diana*: Zuberbühler et al. 1997).

Because the wag display is most often linked to the presence of predators (Murphy 2006), the prefeeding wag display may also be linked to risks of predation. During the nesting period, when the prefeeding wag display is performed, the risks of adult predation are probably elevated. Motmots are rather large, slow-flying birds, and so are susceptible to ambush predators while making repeated localized movements to their tunnel nest. Many predators lie in wait where they anticipate their prey to occur, and motmot nests are placed near the ground, so adult motmots are susceptible to both terrestrial and aerial ambush predators. In addition, motmots nest in a long tunnel, so adults are visually isolated from the outside world when inside, and thus can be taken by surprise when leaving the nest. The observation that motmots only perform the prefeeding wag display before, but not after, they travel to the nest is consistent with an increased risk of predation while travelling to and from the nest.

There are two antipredation hypotheses that may account for the performance of the prefeeding wag display. The display may be a misfired signal, which arises as a byproduct of a lowered threshold to threatening stimuli during a period of high risk. Performance of the predator-elicited wag display is probably mediated by proximate mechanisms that evaluate the risk of predation and trigger the performance of the wag display when risks exceed a certain level. The threshold at which a motmot responds to threatening stimuli might be lowered when predation pressure is high, such as during the nestling stage. Thus, the prefeeding wag display could represent a nonfunctional use of a display that is selectively beneficial in another context (i.e. when predators are present). Although this nonfunctional hypothesis is plausible, it requires that few or no selective benefits are associated with the prefeeding wag display. However, because the wag display is thought to confer antipredation benefits when performed in the presence of predators (Murphy 2006), it seems likely that the prefeeding wag display may also confer antipredation benefits during the nestling stage. Thus, it is possible that the prefeeding wag display is currently maintained by selection.

If the prefeeding wag display successfully deters predators, then the display would best be categorized as a dishonest, preemptive, pursuit-deterrent signal (also see Spitznagel 1996; Randler 2006). The prefeeding wag display may function similarly to the predator-elicited wag display, but in this context, the signal would dishonestly announce that a predator has been detected. Because predation's impact on fitness is extreme, motmots would gain a substantial selective advantage if this dishonest pursuit-deterrent signal were successful at dissuading attack. Such dishonest signalling could be maintained by selection in this system because the wag display is generally given in an honest context (i.e. when a predator has been detected) during the rest of the year, and predators would generally benefit by abandoning pursuit or ambush when they detect the display.

Further study is required to test the possibility that the prefeeding wag display is a dishonest signal that effectively deters pursuit or ambush by predators near the nest. Future research on this system should address the prediction that predators would be deterred upon detecting the prefeeding wag display. Future work on predator-elicited signalling in all systems should consider the hypothesis that dishonest, preemptive, pursuit-deterrent signals may occur in instances when animals are especially vulnerable to predation.

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