# The wag-display of the blue-crowned motmot (*Momotus momota*) as a predator-directed signal

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## ABSTRACT

This study addresses whether the tail wagging displayed in the family Momotidae serves as a signal directed towards predators to deter pursuit, as supported by previous research on the turquoise-browed motmot (*Eumomota superciliosa*). The blue-crowned motmot (*Momotus momota*) demonstrates several characteristics: territoriality, high site fidelity, impaired flight performance, and sedentary habits that could make the bird more vulnerable to prey-stalking and ambushing predators. Like other motmots, the blue-crowned motmot performs an exaggerated tail-wagging motion when presented with a potential predator. I studied the different reactions elicited by four treatments to examine if tail wagging was directed towards a predator that had been visually located by the displaying motmot. I presented either an avian predator or non-predator model or played back an avian call from a predator or a non-predator to motmots, and observed behaviors. Motmots were significantly more likely to wag-display ($p = 0.0009$) upon seeing an ambush predator model (a perched bird of prey), more likely to not interrupt normal behavior like foraging when presented with a non-predatory control call, and subjects never approached either of the predator stimulus trials. Despite the more disturbed study site and niche differences between the blue-crowned motmot and the turquoise-browed motmot, my results in *M. momota* are consistent with, and corroborate, previous research on the latter species, suggesting that motmots may use the wag-display as a pursuit-deterrent signal to advertise awareness of the predator. In the blue-crowned motmot, because the visual signal of the wag-

display draws attention to the bird, it is presumably more advantageous to signal to a predator that has been sighted rather than to a predator of uncertain location. Additionally, I observed captive motmots and noted an alternate tail display that was associated with more aggressive behavior.

## INTRODUCTION

Pursuit- or ambush-deterrent communication (hereafter referred to as predation-deterrent signaling because not all signals are given during a chase context) is a form of interspecific signaling directed from the prey to the predator. By signaling to a predator, the prey advertises that it is aware of the presence of the predator and is prepared to escape (Caro 1995, Hasson 1991). Although some signals, which may be as simple as tail flicking or pumping (Carder and Ritchison 2009, Woodland *et al.* 1980), are less energetically expensive than fleeing, predator directed displays may convey information about the ability of the individual's physical condition and escape capability to the predator, which could advertise the unprofitability of pursuit and deter attack (Baker & Parker 1979, Woodland *et al.* 1980, Hasson 1991, Caro 1995, Leal 1999, Carder and Ritchison 2009).

Predation-deterrent signals are simple and conspicuous even from a distance (Hasson 1991), so that escape is still possible and predators have sufficient time to give up approaching the prey (Jones *et al.* 2009, Caro 1995, Carder and Ritchison 2009). These signals draw attention to the signaler (Woodland *et al.* 1980) and are stereotypic movements performed year-round throughout the population in order to educate predators (Baker & Parker 1979). Because predators prefer to attack less vigilant animals (Krause and Godin 1996), just being observed may be sufficient to discourage attack from stalking or ambush predators (Caro 2005). Animals with impaired escape performance, such as those busy feeding (Krause and Godin 1996), those that are slower moving due to size (Jones *et al.* 2009), or those that remain in place while potential for discovery increases (Martin *et al.* 2009), are vulnerable to ambush predators. If advertising vigilance or awareness discourages an attack, potential prey that signal to predators can reduce their chance of fatal predation as well as avoid an energetically expensive and time consuming escape response (Baker & Parker 1979, Woodland *et al.* 1980, Hasson 1991, Carder and Ritchison 2009). Attending to predation-deterrent signaling is advantageous for the predator as well: predators, such as raptors, may have low hunting success (Rudebeck 1951), and if prey advertise their vigilance and readiness to escape or physical ability to escape attack, the predator can learn to avoid expending energy on unprofitable pursuits (Cresswell 1994, Young 1971). Thus predators should benefit from responding to signals that advertise vigilance and readiness to flee in the event of pursuit to reduce the chance of a failed attack.

I studied tail wagging as a predation deterrent signal in blue-crowned motmots (*Momotus momota lessonii*) in Monteverde, Costa Rica, to examine if previous suggestions to this effect in another species (see below) may apply to other members of the motmot family. Since the wag display is characteristic to all motmots (Skutch 1971, Stiles and Skutch 1989), it is important to understand the similarities and differences in life history traits across species as well as the evolutionary history of the family. Therefore, I reviewed the literature pertaining to the taxonomy and general morphology, habitat, conservation status, trophic interactions, breeding, and behavior of the family Momotidae. This review covers characteristics that would make motmots vulnerable to stalking or ambush predators, thus placing my study on predation deterrent signaling into context. Furthermore, by synthesizing the current understanding of the family, new directions of study can be developed.

Past research (Murphy 2006) involving the turquoise-browed motmot (*Eumomota superciliosa*) suggested that exaggerated tail wagging may function as a signal directed at predators that have been sighted from a distance great enough to allow the motmot to escape. Murphy (2006) observed wagging in his study species in the absence of kin, a mate, or other conspecifics, but only occasionally and under certain circumstances in the absence of predators (Murphy 2007a). Murphy (2006) also observed that certain potential predators such as cats, foxes, perched birds of prey, and humans elicited wagging the most consistently. Because *E. superciliosa* begins, and continues to wag-display, when predators are present and ceases when the predator departs, Murphy (2006) concluded that tail wagging advertises that *E. superciliosa* detected the predator, and thus tail wagging would likely discourage the continuation of stalking and ambush attempts.

Both *E. superciliosa* and *M. momota* belong to the family Momotidae. However, *E. superciliosa* prefers semi-arid habitats such as scrubby woodlands, whereas, where their habitats overlap, *M. momota* is found in taller, moist forest (Orejuela 1980). Both species are socially monogamous, tunnel-nesting birds that can tolerate human disturbances (Murphy 2006, Skutch 1947, Skutch 1964). Unlike *E. superciliosa*, which will nest colonially and can reach high population densities (Orejuela 1980, Murphy 2006), the blue-crowned motmot is more territorial. Murphy (2006) ruled out signaling to conspecifics as a function of tail wagging in the more social *E. superciliosa*; thus my study focused on whether a predator had to be sighted to elicit wagging from a blue-crowned motmot.

To test if *M. momota* also directs wag displays towards predators to advertise vigilance and deter predation, I presented two predator stimuli, one visual model and one call playback, and two corresponding and non-threatening control stimuli. If *M. momota* wags its tail as a signal directed towards ambush predators that have been sighted, then I would expect to find tail wagging directed towards the visual predator model. I would not expect to see wagging in response to a non-predator control visual nor in response to auditory cues. Because larger birds may have impaired escape performance or not be as maneuverable as smaller birds (Jones *et al.* 2009, Carder and Ritchison 2009), it seems unlikely that *M. momota* would falsely signal awareness of a predator's location in response to predatory auditory cues because the tail wagging increases the likelihood of drawing attention to the previously cryptic bird from undetected predators. I found that *M. momota* wags its tail significantly more in response to a predatory bird model and to show that motmots are less likely to interrupt their regular behavior when confronted with control stimuli.

Following my study on tail wagging as a predation deterrent signal, I observed a population of blue-crowned motmots at the Denver Zoo. On several occasions during these sessions, I saw a tail display unlike the typical and apparently predator directed wag display. As in the typical wag-display, the displaying motmot's tail moved through an arc. However, in this atypical display, the displaying motmot held the tail up and fanned out, and the movement through the arc consisted of several discrete steps rather than a single smooth motion. Because I had not observed this particular display previously and because the novel display was performed in a different context from the typical wag display, I recorded occurrences of the display and behaviors following the display to attempt to elucidate the signal information in the atypical display.

## LITERATURE OVERVIEW

### Taxonomy and General Morphology

Momotidae is a small family of Coraciiform birds currently restricted to the New World tropics. Motmots are small to medium sized birds with large heads and weak feet (Smith 1976). The bill, which is serrated to varying degrees, is 50-60 percent of the length of the entire skull, and the nostrils are situated close to the frontal feathers (Korzun *et al.* 2004, Pascatto and Donatelli 2003, Snow 2001, Wetmore 1968). Motmots have short, round wings with twenty-one remiges (Murie 1872). The wing shape may limit the distance they can fly and disperse (Skutch 1947, Gaumer 1881-1882, Reyes *et al.* 2009), and motmots are not thought to be able to fly as far as five kilometers (Snow 2001). Motmots in the genus *Momotus* have twelve tail feathers, or retrices, whereas the other motmots have ten (Murie 1872, Wetmore 1968). Except for the Tody motmot (*Hylomanes momotula*), the strongly graduated tail of an adult motmot is about 60 percent of the body length (Murphy 2005). The middle two feathers in most species, aside from the Tody motmot, the blue-throated green motmot, and some populations of the *Baryphthengus* motmots, are distinctively racket-tipped. Graduated tails are the most costly to elongate due to the increase in drag produced without changes in the amount of lift generated (Balmford *et al.*

1993), and tails that are heavier further away from the body may be aerodynamically costly as well (Tubaro *et al.* 2005).

There are six genera recognized in the family and around nine to fifteen species, which suggests that Momotidae are a genetically isolated remnant of a once larger group (Lindholm 1991). While motmots moved from North America down into South America (Chapman 1923), fossil evidence from the Oligocene in Switzerland suggests an Old World origin for the family (Olsen 1976). Momotidae was present in the New World by the late-Miocene (8 MYA), based on a fossil humerus from Florida, which was indistinguishable from that of a modern momotid due to features on the proximal head and pectoral muscle attachment (Becker 1986). By the Pleistocene, motmots had reached Brazil (Sick 1993).

Stiles (2009) measured plumage and vocalization characteristics of the blue-crowned motmot *Momotus momota*, a species which, at times, has been separated into upwards of twenty species (Graham 2010). Based on his measurements, Stiles (2009) suggested subdividing *M. momota* into at least five species, a move accepted by the South American Classification Committee. In 1955, two different members of the *M. momota* complex produced a pair of hybrid offspring at a zoo (Hawkins 1955). Captive populations may be useful for studying whether members of the *M. momota* complex have genetic incompatibilities or specific behaviors reinforcing reproductive isolation.

Motmot body plumage consists primarily of blended shades of green, olive, chestnut, buffy, tawny, and rufous shades (Skutch 1945, 1947, 1964, 1971). However, the angle of light can make distinguishing colors more difficult (Chapman 1923), and birds will blend into the foliage under lower light conditions (Skutch 1947). Except for the Tody motmot (*Hylomanes* *momotula*), adult motmots have a patch of black feathers, sometimes bordered with blue, on the chest (Skutch 1945, 1947, 1964, 1971). The chest badge of *M. momota*, consist of one to five feathers (Stiles 2009). Young motmots, however, typically lack the black chest badge (Larcombe 1991, Orejuela 1977, Skutch 1947, 1964, 1971, Stiles 2009).

The brightest coloration on the members of the *M. momota* complex is the iridescent blue crown or diadem (Tristam-Valentine 1895, Graham 2010), which can be seen even under low light conditions (Wetmore 1968). Similarly, the eyebrow feathers of the turquoise-browed motmot are described as “the most arresting color on the birds” (Skutch 1947). When Skutch observed a turquoise-browed motmot under the light of an incandescent flashlight, he described the majority of the plumage as appearing grey, but the crown reflecting to the point that he expected it to glow in the dark (Skutch 1947). The keel-billed motmot is described as having “electric-blue” eyebrows as well (Miller 1994). The greenish-blue patch of brow feathers on the mostly olive Tody motmot is described as the only spot of color on the bird that reflects in dim light (Wetmore 1968). It is interesting to note that Tody motmots are found eating *Morpho* butterflies frequently (Stiles and Skutch 1989), since Wetmore (1968) remarked on mistaking the blue feather patch for a butterfly. The diadem of juvenile blue-crowned motmots tends to be greener than adult birds with an indistinct border (Stiles and Skutch 1989, Graham 2010). Young Tody motmots have a smaller blue eyebrow than adult birds however young broad-billed motmots, which lack blue brow markings as adults, have a short blue eyebrow (Stiles and Sktuch 1989).

Sexual dimorphism, in which males and females of a species can be easily distinguished, is minimal in motmots, as is expected in socially monogamous species. Males of the *M. momota* group are, on average, larger than females, but not significantly (Stiles 2009); however, turquoise-browed motmot males are significantly heavier than females, averaging 1.6 grams heavier than females (Murphy 2005). The wire length on male turquoise-browed motmots is ten percent longer than female wire length (Murphy 2005, Murphy 2007a, Murphy 2010). Stiles (2009) found no evidence for differences between male and females of the *M. momota* complex in plumage color or pattern. Female keel-billed motmots have more mustard colored chest plumage, whereas males are greener (Jones 2003, Miller 1994).

## Habitat

Momotidae occur from Mexico to Argentina, and the genus *Momotus* is found throughout the range of the family (Chapman 1923, Lindholm 1991). The majority of species prefer tropical lowland habitats, but two species, the blue-throated and highland motmots, are found in montane forests of Middle and South America (Greeney *et al.* 2006, Snow 2001, Stiles 2009, Skutch 1945). The keel-billed, broad-billed, and Tody motmots are obligate primary forest dwellers (Miller 1994, Snow 2001), but the blue-crowned motmot can live in secondary growth, gardens, and can be found foraging around buildings and other human disturbances (Skutch 1964) as well as sandy beaches and coffee plantations (Orejuela 1977). Russet-crowned and turquoise-browed motmots prefer semi-arid habitats where they can reach high population densities, these motmots can be found in disturbed areas as well (Amadon and Eckelberry 1955, Chapman 1923, Orejuela 1980, Skutch 1947, Snow 2001).

Where the ranges of the blue-crowned motmot and the rufous-capped motmot, *Baryphthengus ruficapillus*, overlap, *B. ruficapillus* is found in tall forest while *M. momota* is found in denser vegetation and secondary growth (Willis 1981). The rufous motmot and the broad-billed motmot, though similar in coloration, have been found nesting close to one another and are apparently not disturbed by each other (Skutch 1971, Snow 2001). On the Yucatan peninsula, *M. momota* is more common than *E. superciliosa* in taller, moist forests, while *E. superciliosa* is more prevalent in scrubby woodlands (Orejuela 1977).

## Status and Conservation

While the majority of motmots are considered common and listed as "least concern", one species of motmot is listed as vulnerable. The keel-billed motmot, *Electron carnatium*, is the rarest of the motmots and, as an obligate forest-dwelling bird, *E. carnatium* faces problems of habitat loss (Miller and Miller 1996), and there appear to be fewer females than males (Miller 1994). Hybridization with broad-billed motmots, *E. platyrhynchum*, may occur when mates are scarce (Miller and Miller 1996). The high site fidelity exhibited by *E. carnatium* and other motmots may reduce the likelihood of locating a mate.

High site fidelity and limited dispersal abilities decrease gene flow between populations. The russet-crowned motmots, *Momotus mexicanus*, that depend on a good breeding site for reproductive success showed a high level of genetic variation between populations 25 km apart (Reyes *et al.* 2009). With less than a single migrant per generation, *M. mexicanus* and other motmots may face problems associated with inbreeding or hybridization with related species (Miller 1994, Miller and Miller 1996), when population density becomes too low or mates become too rare.

Habitat destruction or modification may not affect all motmots equally. While *M. momota* is considered a highly adaptable species (Orejuela 1977, Skutch 1964, Wetmore 1968, Graham 2010), the keel-billed motmot, rufous motmot, and blue-throated green motmot are considered to be vulnerable to deforestation (Miller 1994, Miller and Miller 1996, Renner 2005, Skutch 1945, Wetmore 1968). Both the turquoise-browed motmots and blue-crowned motmots have made use of land modified for human use (Skutch 1947, Skutch 1964), but when they occur together, the more colonial turquoise-browed motmots may be able to exclude blue-crowned motmots from secondary growth (Orejuela 1977).

Skutch (1983) suggested that the destruction of the highland forest habitat of the blue-throated green motmot, *Aspatha gularis*, could drive the species to extinction. However, Renner (2005) found that *A. gularis* was more commonly observed in secondary growth and edges than mature forests and suggested that *A. gularis* was a poor indicator of primary forest. Despite their ability to survive in secondary growth, the population density of *A. gularis* may be rather low (Renner, 2005).

It may be possible to establish captive breeding programs for the more vulnerable motmots in the future, although only the blue-crowned motmots are known to have reproduced in captivity. Bates and Busenmark (1977) stated that motmots are hardy and do well in captivity once habituated to a domestic diet. In the United States, blue-crowned motmots have been kept in captivity since 1903 (Lindholm 1991). *M. momota* has been kept in London zoos since at least 1877 (Snow 2000, Tristam-Valentine 1895) and in private collections since at least 1860 (Salvin 1873). *M. momota* have reproduced in zoos in the United States since 1951 (Graham

2010, Griswold 1956, Lindholm 1991), and in 1970 captive *M. momota* reproduced in the United Kingdom (Roots 1970).

## Food and Feeding

Members of Momotidae tend to be sit-and-wait predators; birds will perch in the shade until sallying to capture prey (Snow 2001). Aerial sallies are more successful for turquoise-browed motmots (*Eumomota superciliosa*) than blue-crowned motmots (*Momotus momota*) (Orejuela 1980, Thurbur and Komar 2002, Solano-Ugalde and Arcos-Torres 2008) that will instead chase prey to the ground. Blue-crowned motmots engage in more widely foraging techniques than turquoise-browed motmots (Orejuela 1977). Rufous motmots, rufous-capped motmots, Tody motmots, broad-billed motmots, highland motmots, and blue-crowned motmots have all been observed following army ant raids (Greeney *et al.* 2006, personal communication with Anjali Kumar and Richard LaVal 2010, O'donnell *et al.* 2010, Skutch 1964, Skutch 1971, Wetmore 1968, Willis 1981); normally only single birds or pairs are seen at a raid. Smaller motmots are more insectivorous than larger birds (Remsen *et al.* 1993). Both *E. superciliosa* and *M. momota* have been observed foraging on moths attracted to artificial lights at night (Thurbur and Komar 2002, Solano-Ugalde and Arcos-Torres 2008) and at moth traps. Kleptoparasitism, in which one individual steals the prey captured by another, has not been found in motmots (Brockman and Barnard 1979), and motmots are not known to take prey they have not captured (Mauricio Garcia-C. and Zahawi 2006).

Motmots will typically beat food held in the beak against either a perch or the ground prior to swallowing the item whole. Stiles (2009) suggested that the beating behavior is an innate behavior in motmots; he observed motmots beating bread as well as live prey. Unlike raptors, motmots do not tear prey apart (Chacoń-Madrigal and Barrantes 2004), and feet are not used for prey handling (Mauricio Garcia-C. and Zahawi 2006). Predatory attacks by motmots on vertebrate prey and prey models are directed towards the neck region (Brodie III 1993, Delgado-V and Brooks 2003, Smith 1976).

While motmots take a large number of insects as well as some fruit (Remsen *et al.* 1993, Snow 2000, Skutch 1964), the large bill and relatively small legs may be more adapted for handling vertebrate prey (Smith 1976). Lizards, snakes, frogs, scorpions, and snails are captured and eaten by motmots fairly often. A wide variety of fruits and arils are consumed by motmots, including *Ficus*, *Ehretia*, and *Bursera* (Scott and Martin 1984), Lauraceae (Greeney *et al.* 2006), Arecaceae (Skutch 1964), and nutmeg arils (Howe 1981, Skutch 1964). Additionally, reports of more unusual dietary items are not uncommon in the literature.

Master (1999) observed a pair of rufous motmots (*Baryphthengus martii*) capture and consume a poison dart frog in the wild. *B. martii* stomachs have also been found containing a fish and a crab (Remsen *et al.* 1993). *Momotus momota* have been reported eating a hummingbird (Mauricio Garcia-C. and Zahawi 2006), a nestling variable seedeater (Reid and Sánchez-Gutiérrez 2010), a bat (Chacoń-Madrigal and Barrantes 2004), a shrew (Sandoval *et al.* 2008), and mice in the wild and in captivity (Delgado-V and Brooks 2003, Larcombe 1991, Hawkins 1955, Roots 1970). Cheese (Delacour 1926, Skutch 1983) and bread (Murie 1872, Stiles 2010) have been taken by tamer blue-crowned motmots; captive motmots have eaten minnows and crayfish (Hawkins 1955) as well as poison dart frogs (Master 1999). Reid and Sánchez-Gutiérrez (2010) reported observing the predation event of an *M. momota* on a rice rat, although the rat was roughly a third the size of the motmot.  Orejuela (1980) found that *M. momota* ate a higher proportion of ground arthropods than *Eumomota superciliosa*, while actively flying insects in Hymenoptera and Lepidoptera were preferred by *E. superciliosa*. Skutch (1947) remarked on how *E. superciliosa* ate colorful butterflies that other birds avoided even as nestlings.  Masters (1992), however, found that, while not initially averse to eating moths injected with high quantities of a chemical found in adult butterflies from the tribe ithomiinae, *M. momota* would learn to reject unpalatable moths on taste.  The colorful butterflies avoided by other birds may be members of the *Morpho* genus, a group on which the motmots are likely predators (Stiles and Skutch 1989, Young 1971).

## Predators

Natural predation events are uncommon to observe; however, birds of prey, snakes, cats, and bats have been recorded consuming momotids.  A roost of false vampire bats, *Vampyrum spectrum,* consumed several turquoise-browed motmots during a four-month study (Vehrencamp *et al.* 1977).  Felines, including feral cats, will hunt motmots (Leck 1979, Murphy 2006), to the point of causing the local extinction of *M. momota* (Leck 1979).  While snakes may compose part of the diet of several motmots (Smith 1976, Skutch 1964), other snakes, usually as nest predators, will consume motmots (Murphy *et al.* 2010, Orejuela 1977, Scott and Martin 1986). Additionally, boas will capture adult birds.  Owls have been recorded as hunting *E. superciliosa* near Mayan ruins (Scott and Martin 1986), and Greeney *et al.* (2006) observed a collared forest-falcon, *Micrastur semitorquatus*, attack and consume a highland motmot.  Other likely predators include grey foxes, ctenosaurs, coatis, weasels, and humans (Murphy 2006, Murphy *et al.* 2010, Orejuela 1977, Willis 1981).

## Breeding

The courtship behavior of the blue-crowned motmot occurs in the fall when burrow excavation begins (Skutch 1964). The turquoise-browed motmot, *Eumomota superciliosa*, however, courts and makes socially monogamous pairs during the early spring a few months before laying begins (Murphy 2007b, Skutch 1947), and pairs are regularly maintained across several years (Murphy 2007b, Martin *et al.* 1989). Courting motmots will duet together (Skutch 1947, Skutch 1971, Snow 2001, Hawkins 1955) and wag their tails more rapidly than usual (Wagner 1950, Hawkins 1955, Lindholm 1991). Inanimate objects such as twigs or pieces of green leaf may be displayed (Skutch 1964, Graham 2010, Wetmore 1968), which may be a symbolic version of mate feeding behaviors seen in other courting motmots (Skutch 1947, Masters 1999, Orejuela 1977).

Motmots nest in curved, unlined, and uncleaned burrows that can be located in earthen banks, natural recesses in caves, burrows of other animals, and wells; nesting pairs can be found either singly or, in some species, in dense colonies (Alves *et al.* 1998, Greeney *et al.* 2006, Gaumer 1881-1882, Martin and Martin 1980, Scott and Martin 1986, Miller 1994, Skutch 1947, 1964, 1945, 1971, Murphy 2007a, 2007b, 2008a, 2008b, Murphy *et al.* 2010, Orejuela 1977). Both *Eumomota superciliosa* and *Electron carnatium* have utilized archaeological ruins as nesting sites (Miller and Miller 1996, Miller 1994, Martin and Martin 1980, Scott and Martin 1986, Scott and Martin 1983, Martin and Martin 1985). Excavation begins during the fall prior to nesting for the blue-crowned motmot (Skutch 1964), but not until March in the turquoise-browed motmot (Orejuela 1977, Skutch 1947, Murphy 2007b). The blue-throated green motmot, the only species to use the nest burrows outside of the breeding season, begins excavation a few months after the young leave (Skutch 1945, Snow 2001). Motmots show high site fidelity; birds will frequently return to previously used holes or banks several years in a row (Skutch 1945, Martin and Scott 1989, Reyes *et al.* 2009).

The selection of a suitable location to nest, where the burrow will not collapse or flood, is an important factor in determining reproductive success (Skutch 1971, Reyes *et al.* 2009, Roots 1970). Motmots will nest until they successfully raise a single brood per year in the wild; however multiple broods can be raised in captive populations (Martin and Martin 1980, Roots 1970, Hawkins 1955). Only biparental care is observed in motmots, although females may invest more in excavation, brooding, and feeding (Skutch 1947, Alves *et al.* 1998, Martin and Martin 1985, Orejuela 1977); older siblings or non-parent birds helping at the nest have not been recorded (Murphy *et al.* 2010).

Eggs are laid in the nest chamber at the end of the tunnel every other day (Scott and Martin 1983). The blue-crowned motmot lays between one and four eggs in captivity, and can successfully raise all young when there is enough food available (Lindholm 1991). The highland motmot lays two eggs at the entrance before the nest chamber (Greeney *et al.* 2006), while three to five eggs appears to be common in the other species. Skutch (1945) found that the blue-throated green motmot usually laid three eggs, and the keel-billed motmot nest examined by Miller (1994) had three eggs as well. *E. superciliosa* females lay between three and five eggs, with four being the most common clutch size with a usual loss of a single offspring (Scott and Martin 1986, Skutch 1947).

Motmots hatch naked and with eyes closed (Wetmore 1968, Graham 2010, Scott and Martin 1986, Skutch 1947, 1964, 1945, 1971). Only the blue-throated green motmot, *Aspatha gularis*, grows down (Skutch 1945, Snow 2001), which may be an advantageous adaptation for these birds which live in colder climates than the other members of the family.

Adults are usually cautious when approaching the nest to feed young (Larcombe 1991, Skutch 1945, 1947, 1964, 1971, Amadon and Eckelberry 1955, Roots 1970). One parent will feed the nestlings more than the other (Alves *et al.* 1998, Martin and Martin 1985, Orejuela 1977, Skutch 1947). Nestlings are initially fed with insects; fruit and vertebrate prey are introduced as the nestlings become older (Alves *et al.* 1998, Scott and Martin 1986, Graham 2010, Wetmore 1968, Snow 2001, Skutch).

While mortality is highest during incubation (Murphy *et al.* 2010), causes of nestling mortality include predation by snakes, falling from the nest, parasitic maggots, starvation, and nest invasion by fire ants (Miller 1994, Murphy *et al.* 2010, Scott and Martin 1986). Ctenosaurs and tarantulas are also suspected causes of nestling mortality (Murphy *et al.* 2010, Orejuela 1977, Skutch 1964). Though the nest is not cleaned otherwise, dead nestlings are removed from the nest by the parents (Larcombe 1991, Miller 1994, Scott and Martin 1986, Skutch 1945).

Young will leave the nest between twenty-four and thirty-eight days after hatching (Alves *et al.* 1998, Scott and Martin 1986, Skutch 1971, Snow 2001). Though similar in size to adults when they leave the nest, fledgling motmots have shorter tails and bills, and, in several species, lack the black breast markings (Hawkins 1955, Larcombe 1991, Orejuela 1977, Roots 1970, Skutch 1947, 1964, 1971, Stiles 2009). Captive fledglings begin to feed themselves after about a week (Graham 2010, Roots 1970) and were independent and able to hunt live prey a little under a month after leaving the nest (Root 1970, Hawkins 1955, Graham 2010) and Orejuela (1977) also found that wild motmots remained dependent on food brought by parents for four to six weeks after fledging. Skutch (1945) observed a captive blue-throated green motmot, the only species of motmot that uses tunnels as a roosting site outside of the breeding season, making motions similar to those used by adults digging tunnels when the bird was between two to three months old, implying that young blue-throated green motmots are independent by that time.

## Behavior

Tail wagging is a behavior common to all motmots, Skutch (1971) referred to the pendulum-like, stereotypic motion as the “typical motmot gesture”. When a motmot gives a wag-display, the tail is moved smoothly in an arc of about 100 degrees (Murphy 2006). Explanations for the display, which draws attention to the motmot (Beebe 1910, Skutch 1947, 1964), consist of the bird being “stimulated but not frightened” (Wetmore 1968), “strongly excited” (Skutch 1964), when the bird’s attention is attracted (Wagner 1950), and “when aware of danger or the presence of man” (Gaumer 1881-1882), or as a predator-directed pursuit-deterrent signal (Murphy 2005, 2006, 2007a.). Wagging is more intense during the breeding season (Lindholm 1991, Wagner 1950). It may also be used as a dishonest signal of awareness of potential predators prior to feeding nestlings (Murphy 2007a).

Motmots do not bathe in water puddles on the ground, but the sound of rain will stimulate bathing actions in perched birds (Smith 1977). In captivity, motmots will bathe in running water from a hosepipe (Lindholm 1991). However, dust bathing appears to be common in the family, even outside of arid regions (Sick 1993, Skutch 1964, Skutch 1971, Smith 1977), and may serve to reduce endoparasites such as feather lice.

Motmots demonstrate high site and mate fidelity, nesting in or by the same location several years in a row, often with the same mate (Chapman 1923, Miller 1994, Reyes 2009, Murphy *et al.* 2010, Scott and Martin 1989, Martin *et al.* 1989). Turquoise-browed motmots exhibit low levels of territorial behavior (Martin and Martin 1980), only defending the nest entrance from conspecifics (Orejuela 1977).

Vocalizations maintain territory boundaries (Orejuela 1977, Miller 1994) and displays of aggression are more common than fighting, which rarely occurs (Skutch 1964). Aggressive displays observed in the turquoise-browed motmot include: displaying a yellow leaf and piston-like scooting at the nest entrance (Murphy 2008a), as well as spreading the turquoise brow feathers while flattening the crown, this is either accompanied with a “snore call” or a partially opened beak (Smith 1977, Orejuela 1977). Murphy (2008a) observed that more chases took place between members of the same sex in *Eumomota superciliosa*, however both in Orejuela’s (1977) conspecific playback trials and in captive situations (Larcombe 1991, Lindholm 1991, Hawkins 1955), paired blue-crowned motmots approach conspecific invaders together.

## MATERIALS AND METHODS

### Study organism

Blue-crowned motmots are medium-sized (39 cm), omnivorous, neotropical birds that occur from northeastern Mexico to Peru and northern Argentina (Skutch 1964, Stiles and Skutch 1989). While the *Momotus momota* species complex has recently been subdivided into several species due to differences in physical and vocal characters (Proposal 412 to South American Classification Committee), most literature does not yet distinguish between these species and they likely have similar behaviors. The blue-crowned motmots are highly adaptable birds that can be found not only in primary forests, but also in secondary growth forests, gardens, and foraging around buildings and other human disturbances (Skutch 1964). The plumage appears monomorphic between the sexes. On motmots in Monteverde, the crown is black bordered by a wide band or diadem of iridescent blue, the mask is black with a blue margin, the chest is tawny, and the back is a green that blends into a dark blue along the tail feathers, the racket tips are dark blue (Skutch 1964).

Despite the ability of blue-crowned motmots to persist around human disturbances, predation by domestic cats, an ambush predator, induced the local extinction of blue-crowned motmots in a small preserve in Ecuador (Leck, 1979). Several characteristics make the blue-crowned motmot vulnerable to ambush predators. The shape of the tail may impair flight performance for motmots; elongated and graduated tails such as the tail of the blue-crowned motmot are aerodynamically inefficient (Balmford *et al.* 1993) and the heavier distal end of the racket-tipped feathers imposes more detrimental effects on flight performance (Tubaro *et al.* 2005). Additionally, the short, rounded wing shape seen in motmots may limit the distance they can fly (Skutch 1947, Snow 2001). Larger birds, such as motmots with impaired flight or escape ability may be more vulnerable to ambush predators (Jones *et al.* 2009). Like all other motmots, the blue-crowned motmot nests in tunnels in banks or roadside cuts and will often forage on the ground (Skutch 1964, Snow 2001). Blue-crowned motmots are more territorial than turquoise-browed motmots (Orejuela 1977). Territoriality is a predictable behavior that may make individuals easier for predators to locate (Young 1971).

Blue-crowned motmots lay their eggs in March or April, and because the eggs hatch about three weeks later and the young do not leave until roughly a month after hatching (Skutch 1964), all of the birds I observed for my stimulus presentation trials were either adults or yearlings. The population of birds that I observed in Monteverde were often heard calling to one another between dawn and dusk, even during the middle of the day. Additionally, the birds I observed were frequently in close proximity to buildings or roads, and were likely habituated to human presence.

Like other motmots, the blue-crowned motmot will give a wag-display in which the bird moves its tail smoothly in an exaggerated side-to-side motion (Figure 1) covering an arc of about 100 degrees (Murphy 2006). At times, the blue-crowned motmot will hold the tail far to one side outside of the normal arc area (Figure 2) (Skutch 1964).

## Study area

I conducted trials in human altered edge habitats (gardens, lawns, parking lots, regenerating pasture, and roadsides) in the premontane and lower montane wet forest life zones between 1100 m and 1550 m on the Pacific slope in Monteverde, Puntarenas, Costa Rica (Haber 2000). Trials occurred when motmots were encountered in areas between the Estacion Biologia, the butterfly garden, and the cheese factory. However, most trials were concentrated in the Bajo del Tigre neighborhood, the Bajo del Tigre visitor center area, the Estacion Biologia, and around the Monteverde Conservation League main office, locations where I estimated there to be between five to ten birds within calling distance.

### Stimulus presentation trials

Upon locating a blue-crowned motmot, I stopped and waited for twenty seconds to allow the bird to become accustomed to my presence. During encounters with motmots in Monteverde prior to the start of my trials, I noticed that the birds usually resumed normal behavior after about twenty seconds. If wagging occurred prior to the trial starting, I moved back one meter from the bird and waited another twenty seconds, repeating this as necessary until wagging due to human presence stopped. If the bird moved farther away but remained where I could see it, I stayed in place and began the acclimatization period again. Following the acclimatization period, I ran a trial with the individual.

Trials lasted for three minutes or until the subject left the area. Trials occurred between 0530 and 1700 hours during fifteen days at the end of the dry season between the eighth of April and the first of May 2010. All trials occurred with a distance of 2 to 12 m between myself and the subject. Stimuli were presented between 1.5 to 2 m above ground level in most trials; visual stimuli were presented lower if it would place the stimulus closer to the bird's eye level and auditory stimuli were usually presented from about 1.5 m above ground level. Because I was unable to distinguish individual birds except in the presence of plumage aberrations, I ran as many trials on an individual bird as possible at one time and avoided replication with individuals distinguished by obvious plumage characteristics. I ran 100 trials, 25 of each treatment.

I presented the subject with one of four treatments: 1) a model of a predatory bird; 2) a model of a non-predator; 3) the call of a predatory bird; and 4) the call of a non-predatory, non-threatening bird. In every trial, I recorded the following behaviors over the course of the three minute interval: 1) presence or absence of the tail-wag display behavior in response to stimulus; 2) whether the bird fled or remained following the stimulus; 3) whether a bird approached me during the trial; and 4) foraging events. Wag-displays were counted if the tail was moved dramatically to at least one side. Events in which the tail stayed at one side were recorded as half-beats and part of the wag-display. I defined "departure from the trial" as a bird leaving my field of vision, either by flying away or moving into a more concealed location. Foraging was defined as flight from the perch either to the ground or to a vertical object and then to the ground, regardless of whether or not the bird obtained food.

As the non-predator model, I used a study skin of the Ruddy Pigeon, *Patagioenas subvinacea,* a non-threatening species, attached to a small branch to simulate a perched bird. My predator model was originally a cardboard cutout of a Roadside hawk*, Buteo magnirostris*, also attached to a stick. The original predator model proved to be less durable than necessary and, for the remaining visual predator model trials, I used a plush owl as a model.

For my playback trials, I downloaded the calls of *B. magnirostris* and *P. subvinacea* from Xeno-canto.org onto an iPod. Portable speakers were used to broadcast the calls from the iPod and the calls were looped to play repeatedly through the trial.

### Statistical analysis

Chi-squared tests were used to test for significant differences between the number of birds in Monteverde that (i) performed a wag display, (ii) stayed or left, (iii) participated in a foraging event, or (iv) approached me during the trial for each treatment. To control for variation between sites, I ran a model in JMP with treatment and location as fixed effects to see if there was a significant difference between treatments in a response variable.

### Zoo observations

Between October and November of 2010, I conducted a series of observations on a group of captive blue crowned motmots at the Denver zoo. A few of the captive birds demonstrated a different tail display that I had not observed in the wild motmots in Monteverde. I watched the birds at the Denver Zoo with remote-controlled security cameras that had been placed within their enclosure prior to the start of my study. The atypical display was characterized by a fanned tail moving in discrete intervals in an arc (Figure 6), and this display was frequently followed by an attack on the camera. Two individuals, one male and one female, in a group of three off-display juvenile motmots demonstrated the fanned tail display. I recorded the number of times that I observed the display, the amount of time the displaying bird spent displaying, and the percentage of displays that were followed by the bird flying into or attacking the camera.

## RESULTS

I found a significant difference in the number of wag-displays among treatments, with more wag displays in response to a visual predator than any other treatment ($\chi^2 = 16.531$, p=0.0009, df = 3; Figure 3). While only 44% of the predator visual trials elicited wagging, predator visual and playback trials accounted for 80% of tail wagging. One wag display observed was not included in the analysis because the trial was interrupted by the arrival of several motmots and the identity of the bird displaying was uncertain. Two half wags that were immediately followed by the bird leaving the perch to forage were not included as wag displays due to the low probability of the wag being connected to the presented stimulus. Thus the total number of trials in which wagging was related to the stimulus was 18. When I ran a model in JMP with location and treatment as fixed effects, I found that location was very insignificant (p= 0.94) whereas the treatment was significant (p= 0.0009). Thus site had no effect on whether an individual wagged from my presented stimulus.

I observed 36 trials in which the motmot remained in sight of the models throughout the trial (Figure 4). The treatment did not influence whether individuals stayed or left the trial area ($\chi^2 = 1.042$, df = 3, p = 0.791). *M. momota* left the trial before three minutes about twice as often as they stayed through the three minutes (36 motmots remained while 64 left).

Twenty-two foraging events were observed while a trial was running, and the number of foraging events observed during trials was significantly different among stimulus categories ($\chi^2 = 9.557$, p = 0.0227, df = 3). Specifically, foraging events were observed during *P. subvinacea* call trials significantly more often than during other treatments (Figure 5). I ran a model in JMP with treatment and location as fixed effects to determine if location had an effect on foraging behavior. I found that location was not significant (p= 0.1677) whereas the treatment was significant (p= 0.0196), thus site did not have an effect on whether a motmot engaged in foraging during a trial whereas treatment type did help to explain if a motmot would engage in foraging during the trial.

I was approached during a trial by the observed motmot on seven occasions, but never observed a motmot approach during either a display of a predator visual or a playback trial of the *B. magnirostris* call. *M. momota* was significantly more likely to approach the stimulus during a *P. subvinacea* call ($\chi^2$ =10.292, p=0.0162, df = 3) than in any other trial type.

In the captive motmots, I observed the fanned and elevated tail, discrete-step tail display (Figure 6) a total of 44 times. The display lasted an average of 9.27 seconds (±9.47 s). Of the displays, 68.2% were followed with the displaying bird flying at the camera. The camera was the apparent receiver of the display based on the orientation of the displaying motmot's gaze.

## DISCUSSION

### The wag-display

Because wagging occurred significantly more often in response to the predator-visual trials than in the other trial categories, tail-wagging in *Momotus momota* appears to be elicited by the presence of a predator that was sighted by the motmot. I observed tail wagging in 44% of the trials in which a potential predator was presented. This was less frequent than the 71% of trials in which Murphy (2006) observed wagging in *Eumomota superciliosa*. This difference may be due to my shorter trial length and models that did not approach the motmot. Some birds are able to moderate their anti-predator response based not only on predator type (Curio *et al.* 1983), but also on apparent predator distance (Curio and Klump 1983). It is possible that wagging occurred less often due to the models appearing as low-risk threats and it is also possible that the distance between the subjects and the stimuli was too small for a signal to have sufficient time to alter a predator's behavior (Hasson 1991, Carder and Ritchison 2009). Despite the lower percentage of wagging observed in the present study, my results still support the conclusion that tail-wagging is directed towards predators and likely functions as a signal to deter attacks from ambush predators.

Predation-deterrent signals are given by potential prey to a potential predator to advertise either awareness of the predator or physical quality of the individual as related to escape ability (Caro 1995). Because predation-deterrent signals draw attention to the location of the signaler, such signals should not be given when the prey has not located the predator (Hasson 1991, Caro 2005, Murphy 2006). Such signals should be conspicuous from a distance great enough to allow the predator to assess the probability of a profitable pursuit and choose to abort attacks on the alerted or high quality and therefore unprofitable prey (Hasson 1991, Carder and Ritchison 2009, Leal 1999).

The wag-display of a motmot draws attention to the bird (Beebe 1910, Skutch 1947, Skutch 1964), and the motion is common to all motmots (Skutch 1971, Stiles and Skutch 1989) throughout the year (Murphy 2006) and different age groups (Skutch 1947). Like other predation-deterrent signals, the wag-display is clear, stereotypic, visible from a distance, and given with or without conspecifics in the area. Most importantly, the wag display occurs significantly more often in the presence of predators or potential predators. Because tail wagging was significantly more likely to occur when the subjects were presented with a visual model of a predator rather than a predator call playback, the predator-elicited wag-display of the motmot likely advertises the motmot's awareness of the predator's location.

Murphy (2007b) suggested that the longer wire length between the feathered portion of the tail on male turquoise-browed motmots is a sexually selected trait and that this wire length may also affect the effectiveness of the wag-display, i.e. a more isolated racket-tip may be more obvious (Hasson 1991). In the blue-crowned motmot, wagging is seen more often during the breeding season (Wagner 1950, Hawkins 1955, Lindholm 1991), which suggests that tail displays or tail condition may serve a role in mate selection in the blue-crowned motmot as well. Additionally, the length of the wire is not a cosmetic decision based on how well a motmot chooses to trim its tail as had previously been speculated (Salvin 1873, Gaumer 1881-1882), but a predetermined trait of an individual (Murphy 2007c). Murphy (2010) found that after removal of the racket-tips from male *E. superciliosa* tails hematocrit (the proportion of blood volume occupied by red blood cells) increased, suggesting that the racket tips on the aerodynamically inefficient (Balmford *et al.* 1993) tail of a motmot carries a cost to individual fitness. Because sexually selected traits that incur a cost are usually honest indicators of individual condition, in that individuals in poor condition are either unable to produce the traits or are unable escape predation and therefore do not survive, future studies may find that those motmots that can 'afford' to wag their tails at predators are in superior physical condition. Thus, predation-deterrent signaling in motmots might not only advertise awareness of the predator, but also information about prey fitness as well; this, however, remains to be tested.

Some predator-directed signals may serve to deflect predator attention more than advertising awareness. Cuban curly-tailed lizards, which, like some other lizards, salamanders, and rodents, can lose their tails, will give a predator-directed signal that may deter pursuit or deflect attack from the body onto the tail (Cooper 2007). It is unknown if tail wagging in motmots also serves a dual purpose of either deterring or misdirecting attack from predators, but it seems unlikely. While Murphy (2010) found that hematocrit levels increased for males of *E. superciliosa* when their racket-tips were removed –unlike in lizards that can drop and re-grow their tails (Batemen and Fleming 2009)– motmots will not re-grow their central tail feathers unless they are fully removed (Murphy 2010). Additionally, Tubaro *et al.* (2005) found that the bare and distal rachis of the central tail feathers on *E. superciliosa*, while not aerodynamically favorable, is reinforced and very strong, making it unlikely to break off during an attack. Furthermore, while conspicuously colored markings may confuse predators and deflect attacks to non-essential body areas (Powell 1982), the most visible color on *M. momota* is not on the racket-tips as might be expected if the tail was used to deflect attack, but on the iridescent crown (Tristam-Valentine 1895, Wetmore 1968, Graham 2010). Greeney *et al.* (2006) observed an attack on a highland motmot (*Momotus aequatorialis*, formerly grouped with *M. momota*) and noted that the predatory falcon directed its initial attack to the motmot's head. Due to the lack of racket regeneration, the reinforced rachis around the rackets, and the more conspicuous coloring on the crown rather than the tail, it seems doubtful that motmots give a wag-display to predators to deflect attacks onto the tail.

Stiles (2009) suggested that the motmots could be divided into two clades, one with *Eumomota*, *Electron*, and *Hylomanes* and one with *Momotus*, *Baryphthengus*, and *Aspatha*. Since the turquoise-browed motmot and the blue-crowned motmot belong to different lineages but use the tail-wag in a similar manner, predator directed tail-wagging may be an ancestral behavior in motmots. Motmots are vulnerable to ambush predators because they are large, slow flying, territorial, and fairly sedentary; the wag-display appears to be a predator-elicited signal used to deter attack by advertising awareness of a predator's location and may also communicate information about individual fitness.

## Fleeing behavior

The observation that birds did not flee at different rates in response to the four different treatments suggests that the potential of being discovered by a predator during the trial periods was less than the cost of flight, which could trigger an attack by either the present predator or an additional unseen predator (Martìn *et al.* 2009, Young 1971). Coloration and sedentary behavior may assist motmots to avoid being detected by predators (Beebe 1910, Skutch 1947, Caro 2005), and the length of a trial may have been insufficient time for a potential predator to discover the bird (Martìn *et al.* 2009). Fleeing is energetically costly, whereas predator-directed signals, such as tail movements in birds, are less energetically costly (Carder and Ritchison 2009). If the predator-directed signal is used to advertise the probability of escape, fleeing may not occur if the predator gives up. Thus, an animal that demonstrates predation-deterrent behavior may be less likely to expend the energy to flee immediately because there may be a reduced probability of an attack (Caro 2005).

## Foraging behavior

Foraging behavior occurred significantly more often during trials with control calls than in any other trials. This observation indicates that normal behavior was not interrupted after hearing a calling pigeon, while hearing a predator and seeing either a predator or the control visual bird did interrupt normal behavior. Not only are some predators more likely to attack foraging individuals, but animals occupied with foraging reduce vigilance and are also less likely to react to approaching predators (Krause and Godin 1996). Because *M. momota* are large and sedentary birds, presumably requiring less relative energy intakes compared with smaller birds, the risk of predation by an ambush predator may be greater than the risk of starvation (Jones *et al.* 2009). Therefore, it would be more beneficial to pause foraging in response to unusual events than to risk reduced vigilance. Presumably, foraging occurred during control call trials because pigeons calling are not an unusual occurrence for *M. momota* individuals in Monteverde.

### Approach behavior

The absence of an approach by birds during the course of either a predator visual trial or a predator call trial is consistent with prior observations that motmots did not move towards a predator (Murphy 2006). Some species or younger individuals will inspect predators, a strategy that apparently works to deter predation, yet is energetically expensive and carries an increased risk of mortality (Caro 1995, Caro 2005). Because motmots are large, slow-flying birds and thus likely to have impaired escape behavior (Jones *et al.* 2009), it may be fatal to approach a potential predator.

Blue-crowned motmots have been recorded consuming other birds (Skutch 1964, Mauricio Garcia-C. and Zahawi 2006, Reid and Sánchez-Gutiérrez 2010). Although it is possible for motmots to consume vertebrate prey up to one-third their mass (Reid and Sánchez-Gutiérrez 2010), it seems improbable that the more massive (Dunning 2008) *Patagioenas* *subvinacea* would be potential prey for *M. momota* because motmots consume prey whole rather than ripping and tearing (Chacoń-Madrigal and Barrantes 2004). Motmots likely did not approach the predator trials due to the potentially fatal consequences of predator inspection and foraging is an improbable explanation for the approaches during control trials.

## Possible sources of error

The visual acuity of *M. momota* may be more powerful than assumed; it is possible that the predator models used in this experiment were too crude to elicit anti-predation signals as frequently as expected. While Murphy (2006) used an approaching human as a predator, my models remained in place throughout the trial. Additionally, it has been noted that the iridescent blue crown of *M. momota* shows up even in dim lighting (Wetmore 1968). This may be more visible to the avian species I used as models that are sensitive to the violet and blue end of the spectrum (Mullen and Pohland 2008). Thus, while it may appear as though the tail wagging of *M. momota* draws attention to the fairly cryptic bird, *M. momota* may not be as cryptic to an avian predator and head motions alone may be sufficient to advertise awareness to such predators.

While Murphy (2006) was able to use humans to solicit predator-directed signals from *E. superciliosa*, it is unlikely that the motmots in Monteverde would respond the same way. Unlike Murphy's study site in an abandoned limestone quarry in a reserve, my study took place in human-modified areas, usually near buildings or roadsides. Because *M. momota* can become tame and habituated to people (Delacour 1926, Hawkins 1955, Hundley and Mason 1965, Larcombe 1991), I assumed that the birds in Monteverde were likely habituated to people and would not view people as predators as consistently as they did for Murphy (2006). However, it is possible that my presence could have altered their predator response behaviors and in future studies it may be better to use a longer acclimatization period, even up to an hour. To attempt to avoid repeating only one stimulus on individual birds over the course of several days, I tried to run as many treatments consecutively on a single bird during an encounter. Running multiple different stimuli could have affected the responses of the motmots. Future studies should use color-banded birds to distinguish individuals and treatments should be spaced out over several days to avoid having treatments affect one another.

## The fanned tail display

Because the fanned tail display was frequently followed by an attack on the camera, it appears as though this atypical display signals aggressive intent. This is interesting because not only was this display not been mentioned in the literature I reviewed, but also because motmots rarely fight in the wild (Skutch 1964). Usually motmots use vocalizations and aggressive displays to maintain territories (Orejuela 1977, Miller 1994). Aggressive signals that have been described in motmots include chasing (Murphy 2008a, Orejuela 1980), displaying a dead leaf in the bill (Murphy 2008a), and spreading the brow feathers while giving either a “snore call” or a partially opened beak (Smith 1977, Orejuela 1977). I suggest that the fanned tail display is another, maybe overlooked or rarely occurring, aggressive signal used by some, perhaps more territorial, motmots.

Because territorial disputes in which fighting occurs can result in injury to both parties, behaviors that establish dominance without combat are advantageous (Smith 1973). Threat displays are stereotyped actions and, should the receiver fail to respond appropriately, may result in attack (Moynihan 1955). The displays I observed were directed towards the camera, the eventual recipient of attack, which was unable to properly respond to displays. Juvenile birds of territorial species can demonstrate ritualized aggressive displays at an early stage to establish dominance in captivity (Smith 1973), and since dispersal distances may be short for motmots (Reyes *et al.* 2009), aggressive juveniles may be more successful at establishing a territory in the wild (Raihani *et al.* 2008) without traveling too far.

### Future directions

While I found support for the hypothesis that the typical wag display of motmots is used to deter predation by stalking or ambush predators, tail wagging may also serve a courtship purpose (Wagner 1950, Lindholm 1991), and the honesty (i.e. whether it is given to predators that have been sighted) of the signal (Murphy 2007a) should require more study. Future research into the motmot's wag display as a pursuit-deterrent signal should use live predators, perhaps naive predators that learn how to respond to a connection between signaling behavior and unprofitability of pursuit (Young 1971). Using live predators as a stimulus will be realistic enough to elicit a response from the motmot, and it may be possible to study the strength of the signal in deterring predation (Caro 1995) and to assess whether predators can learn to avoid an unprofitable chase to determine if the predator directed signal serves to actually deter predation. It may be interesting to use multiple potential predators to examine if motmots can adjust their tail display based on differences between predators. The use of banded birds in future studies would reduce the chance of replicating trials with the same individual over several days.

Unusual tail displays may be an artifact of captivity or they may be used in a brief time of life or under rare circumstances. Ideally, the display behaviors of motmots should be studied, both in the wild and in captivity, between fledging and successfully raising a brood multiple times and between different species of motmots.

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FIGURES

FIGURE 1. The tail-wag display of the motmot. In a display, the tail moves in approximately a 100-degree arc from side one side to the other.

FIGURE 2. During a half-wag display, a motmot may move the tail to one side and hold it there for an extended period of time.

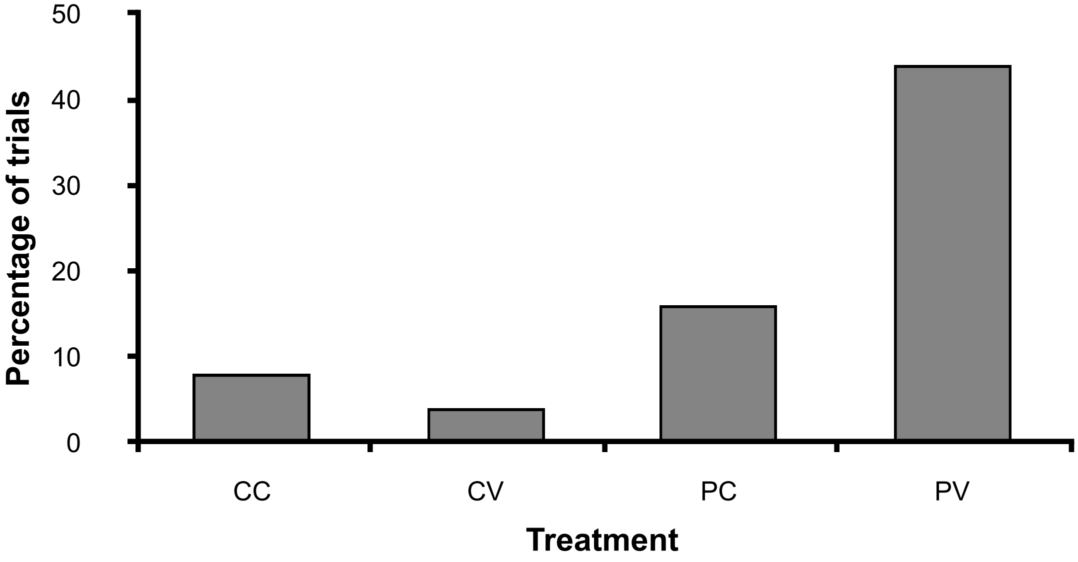

FIGURE 3. Tail wagging by *M. momota* in response to four different stimuli. The percentage of trials (n=25 for each trial) during which wagging occurred compared across the treatment categories. Abbreviations are as follows: Non-predator control call (CC), Non-predator control visual (CV), predator call (PC), and predator visual (PV).

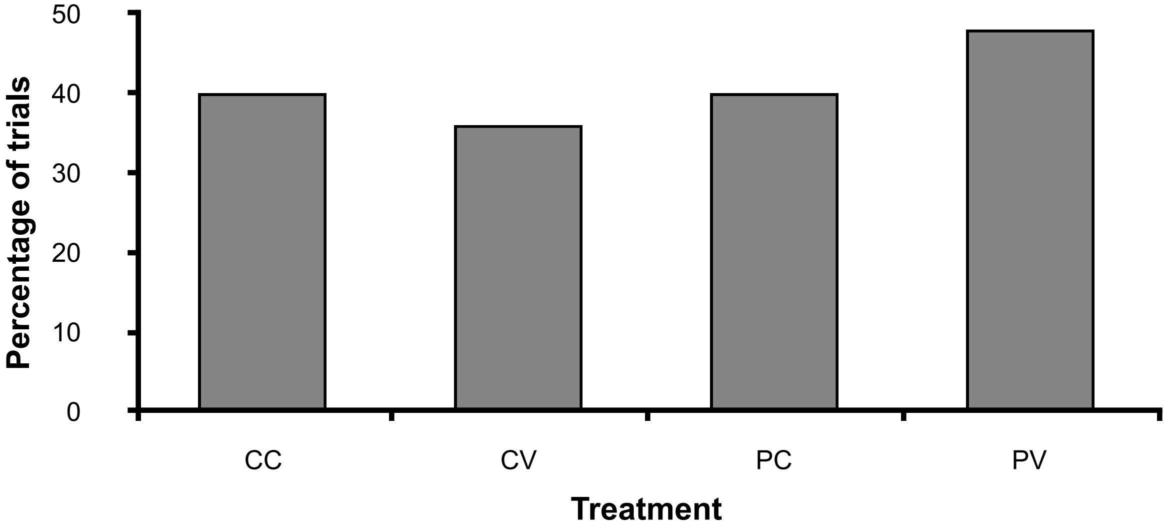

FIGURE 4. Percentage of trials (out of n=25) in which the subject *M. momota* remained in the area compared across the treatment categories. Abbreviations are as follows: Non-predator control call (CC), Non-predator control visual (CV), predator call (PC), and predator visual (PV).

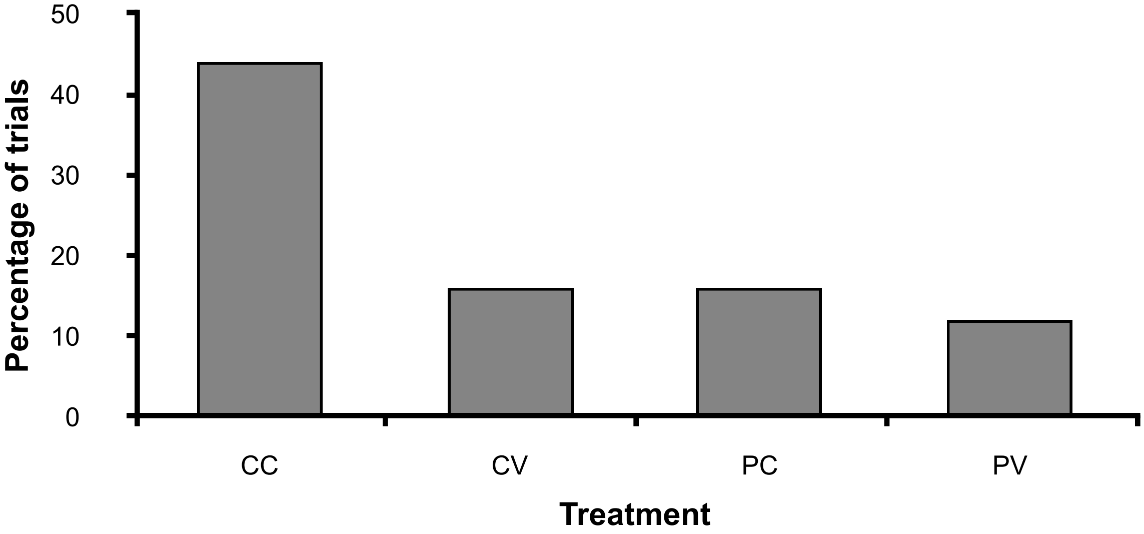

FIGURE 5. Percentage of trials (out of n=25) in which the subject *M. momota* was observed foraging during the trial. Abbreviations are as follows: Non-predator control call (CC), Non-predator control visual (CV), predator call (PC), and predator visual (PV).

FIGURE 6. The fanned tail display. An unusual tail display that I observed associated with aggressive action. The tail is held up and fanned out while it jerks along through discrete steps along an arc rather like a sprinkler head.

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