

Tail pumping by Eastern Phoebes: an honest, persistent predator-deterrent signal?¹

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ABSTRACT. Eastern Phoebes (*Sayornis phoebe*) persistently pump their tails when perched, and the function of this behavior is unclear. We tested four hypotheses concerning the possible functions of tail pumping, including the (1) balance hypothesis, (2) signal-aggression-to-conspecifics hypothesis, (3) foraging-enhancement hypothesis, and (4) predator-deterrent hypothesis. Eastern Phoebes were monitored from 1 April to 1 August 2006 and 1 June to 1 August 2007 in Madison County, Kentucky. Phoebes were captured in mist nets and marked with unique combinations of colored-leg bands. Each focal phoebe was observed one to two times a week and tail-pumping rates, wind velocity, and perch characteristics were recorded. Our results provided support only for the predator-deterrent hypothesis. Phoebes exhibited a significant increase in tail-pumping rates in the presence of a potential predator (Eastern Screech-Owl, *Megascops asio*), suggesting that tail pumping, along with increased rates of calling, informs potential predators that a phoebe is aware of their presence and, therefore, more difficult to capture. Phoebes, however, tail pump regardless of whether a predator has been sighted and such movement could make phoebes easier to detect. If so, and if a detected phoebe provides no additional cues (calling) to indicate awareness of a predator, an attack might actually be more likely. However, tail pumping may be beneficial, regardless of whether a predator has been detected, if it serves as a continuous, honest predator-deterrent signal. This would be the case if predators learned to associate tail pumping and phoebes, and also learned that phoebes, with their alert posture, small size, and impressive aerial maneuvering abilities, represent low reward, difficult-to-capture prey. If so, then both phoebes and predators would benefit, with phoebes less likely to be attacked and predators not initiating attacks that would waste time and energy and alert other potential prey to their presence.

SINOPSIS. **Movimiento de la cola por *Sayornis phoebe*: una señal honesta y persistente para desalentar a los depredadores**

Sayornis phoebe mueve su cola persistentemente cuando esta perchado, la función de este comportamiento no es clara. Nosotros pusimos a prueba cuatro hipótesis relacionadas con la posible función del movimiento de la cola, las cuales fueron (1) hipótesis del balance, (2) hipótesis de señales de agresión en contra de individuos de la misma especie, (3) hipótesis de la intensificación de búsqueda de alimento y (4) la hipótesis para desalentar a los depredadores. *S. Phoebe* fue monitoreado desde 1 Abril–1 Agosto 2006 y 1 Junio–1 Agosto 2007 en Madison County, Kentucky. *S. Phoebe* fue capturado con redes de niebla y marcado en sus patas con una combinación única de anillos. Cada *S. Phoebe* focal fue observado 1–2 veces a la semana y las tasas de movimiento de la cola, la velocidad del viento y características de las perchas fueron colectadas. Nuestros resultados solo proveyeron soporte para la hipótesis de desalentar a los depredadores. *S. Phoebe* mostraron un notable incremento en la tasa movimiento de su cola ante la presencia de un depredador potencial (*Megascops asio*), lo cual sugiere que el movimiento de la cola, adicional al incremento simultáneo de llamados, informan a depredadores potenciales que *S. Phoebe* esta al tanto de su presencia y consecuentemente será más difícil de capturar. Debido a que *S. Phoebe* mueve su cola sin importar la presencia de un depredador, depredadores potenciales que detecten a un *S. Phoebe* el cual no este proveyendo señales adicionales como llamados o moverse más cerca, puede ser percibido como una indicación que no han sido detectados y probablemente incremente la probabilidad de un ataque. Sin embargo, una posible ventaja del movimiento persistente de la cola, incluso cuando un depredador potencial no ha sido detectado, es que sirve como una señal honesta e igualmente persistente para desalentar a los depredadores. Este sería el caso si potenciales, pero no detectados, depredadores perciben el movimiento de la cola como una señal de que *S. Phoebe*, debido a su postura de alerta, tamaño pequeño (< 20 gms), y habilidades de maniobrabilidad bien desarrolladas, como una dificultad para capturar una presa potencial y como resultado el no atacar resultaría más benéfico (en términos de no perder tiempo y energía) que atacar.

Key words: aggression, balance, foraging, predator, *Sayornis phoebe*, signal

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Among several species of birds, individuals regularly move their tail and the reason for such movements are not always apparent. In some species, tail movements may aid in foraging

and serve as a predator deterrent. For example, Willie Wagtails (*Rhipidura leucophrys*) rapidly move their tail from side-to-side when foraging for insects on the ground. Such movements may aid in prey capture because the shadows cast by the wagging tail create rapid changes in light intensity that could startle and flush ground-dwelling insects (Jackson and Elgar 1993). Moorhens (*Gallinula chloropus*) flick their tails up and down to reveal a contrasting rump patch (Wood 1974), and the rate of tail-flicking increases when a predator is detected. In addition, Moorhens in a better physical condition flick their tails faster (Alvarez 1993), and Alvarez et al. (2006) suggested that tail-flicking signals a Moorhen's awareness of a potential predator and provides predators with information about the bird's physical condition. Using tail movements to signal awareness of a predator and physical condition requires energy, but higher-quality Moorhens benefit because tail-flicking requires less energy than fleeing from predators (Alvarez et al. 2006). Similarly, Turquoise-browed Motmots (*Eumomota superciliosa*) perform a tail display in the presence of predators that may serve as a pursuit-deterrent signal (Murphy 2006, 2007).

Eastern Phoeebes (*Sayornis phoebe*) pump their tail by quickly lowering the tail and then slowly raising it (Weeks 1994). Eastern Phoeebes persistently tail pump when perched and do so throughout the year during social interactions with conspecifics as well as when alone and foraging, preening, or patrolling (Smith 1969, Weeks 1994, Ritchison, pers. obs.). Smith (1969) hypothesized that tail pumping by phoebes in such diverse contexts not only indicated a possible conflict of tendencies but also suggested the behavior could help them maintain balance. Because the function of tail pumping by Eastern Phoeebes is currently unknown, our objective was to test a series of hypotheses concerning this behavior. Specifically, we monitored phoebes during the breeding season and conducted a series of experiments to determine if tail pumping was used for balancing, signaling aggression to conspecifics, foraging enhancement, or deterring predators.

METHODS

Field work took place from 2 April to 30 July 2006 and 2 May to 22 June 2007 at the

Blue Grass Army Depot (BGAD) in Madison County, Kentucky. Most Eastern Phoebes in Kentucky are migratory, returning to breeding territories in central Kentucky during March and early April. Most phoebes leave the area for wintering sites by mid-October (Weeks 1994).

Mist nets were used to capture Eastern Phoebes, with males lured into nets by broadcasting conspecific songs from a speaker placed below the net and females were captured by placing nets near nest sites. The sex of each captured phoebe was determined (based on the presence of either a brood patch or cloacal protuberance) and standard morphological measurements (wing chord, tarsus length, tail length, and mass) were taken. All captured phoebes were fitted with a U.S. Geological Survey numbered, aluminum leg band and a unique combination of three colored plastic bands to permit identification of individuals.

We observed and conducted experiments with 57 Eastern Phoebes during our study, but not all individuals were used to test each hypothesis (balance hypothesis [$N = 40$, 18 females and 22 males], signaling-aggression-to-conspecific hypothesis [$N = 15$ males], foraging-enhancement hypothesis [$N = 20$, 9 females and 11 males], and deterring-predators hypothesis [$N = 22$, 10 females and 12 males]). Focal individuals were observed between 06:30 and 14:30 and observation periods were 0.5–1 h in duration. During focal bird observations, we observed phoebes with binoculars at distances of 15–50 m. During observations, the number of tail pumps was recorded by speaking into a cassette recorder and, later, using a stopwatch, the tail-pumping rate was calculated as the number of tail pumps/min. A tail pump was defined as one movement of the tail downward followed by an upward return to or near its original position.

Balance hypothesis. To determine if phoebes use tail pumping to maintain balance on a perch, we monitored the rate of tail pumping by focal birds on perches that differed in degree of stability and at different wind velocities. Focal individuals ($N = 18$ females and 22 males) were monitored during randomly selected 5-min observation periods. At 30-s intervals, wind velocity was measured using a wind meter (Kestrel 2000, Neilsen Kellerman, Chester, Pennsylvania). To minimize the possible effects of vegetation and other barriers on wind velocity, we monitored phoebes and

measured wind velocity at least 5 m from the nearest vegetation.

Because the potential effect of wind is related to both its impact on a focal phoebe (i.e., the wind exerting a force against the bird's body) and the substrate on which a phoebe is perched, we measured the relative stability of the focal phoebe's perch immediately after each observation. Perch stability was measured using a Pesola spring scale (Ben Meadows, Janesville, Wisconsin) and was defined as the force (g) needed to move a perch a distance of 5 cm. At the point where the phoebe was perched, the scale was attached (by a small clamp) and then pulled downward until the perch site was displaced 5 cm. At the end of the 5-min observation period, we immediately measured wind velocity at the point where the focal phoebe was perched. If wind velocity at the phoebe's location differed by more than 2 kph from our last reading, the observation was not used in subsequent analyses of the possible effect of wind velocity on the rate of tail pumping. We examined the possible relationship between tail-pumping rate and both wind velocity and perch stability using correlation analyses.

Signal-aggression-to-conspecifics hypothesis. Male Eastern Phoebes are territorial (Weeks 1994) and changes in tail-wagging rates could play a role in territory defense by serving as an aggressive signal to conspecific males. To test this hypothesis, we conducted a series of playback experiments with 15 territorial males. Male phoebes defend nest sites and nearby areas that serve as foraging sites (Weeks 1994). Although territory boundaries were not delineated, all experiments were conducted within 25 m of active nests (incubation or nestling period) or the known location of recently fledged young (during periods when females were likely not fertile). During playback experiments, a 3-min recording of a phoebe song was played to simulate trespassing on the focal male's territory by another male. Each experiment was 9 min in duration and was divided into 3-min preplayback, playback, and postplayback periods. During the playback period, songs of a conspecific male were broadcast over a speaker at volumes typical of singing males.

To avoid pseudoreplication, we prepared as many playback tapes as there were focal males ($N = 15$). Male Eastern Phoebes were recorded in different locations on the BGAD and these

recordings were used to generate playback tapes. Recordings were made using a cassette recorder (Sony TCM-50DV, Tokyo, Japan) and microphone (Sennheiser, Old Lyme, Connecticut). A different tape with recordings of a different male was used for each playback experiment. To ensure the focal male was not exposed to the recorded male prior to experimentation, we used a recorded male with a territory that was at least 500 m from the focal male's territory for each playback. During each 3-min period of each playback experiment, we monitored the focal male and noted (1) the number of tail pumps, (2) distance from the playback speaker (at 20-s intervals), (3) distance of closest approach to the speaker, (4) number of songs uttered, (5) number of calls uttered, and (6) number of flights of at least 1 m. Kruskal-Wallis tests were used to compare the behavior of phoebes during the preplayback, playback, and postplayback periods.

Foraging-enhancement hypothesis. Tail pumping could potentially enhance foraging success by causing insects on or near a phoebe's perch to take flight, thereby becoming accessible to a foraging phoebe. If tail pumping flushes insects, we predicted that, for approximately 1 min after landing on a new perch, phoebes would be especially aware of insects that might flush from or near their perch in response to the newly arrived wagging tail. Thus, if the foraging-enhancement hypothesis is correct, we predicted that initial forays (short flights from a perch to capture an insect in midair) by phoebes would be shorter than later forays when phoebes would be searching for insects at greater distances from the perch. During 30-min observation periods, we noted the length of time a phoebe was on a perch and then estimated the distance of the subsequent foray to the nearest meter.

If insects are more likely to be flushed shortly after the arrival of a phoebe on a perch, then we predicted that phoebes should tail pump at higher rates immediately after landing on a perch. To test this prediction, during a subset of observation periods, we determined the tail-pumping rates of focal phoebes at 30-s intervals and recorded total perch time to determine if there was any change in rates with increasing time on a perch. Possible differences between initial and later foray distances and in tail-pumping rates relative to time on perches

were examined using repeated measures analysis of variance.

Predator-deterrent hypothesis. Tail pumping by Eastern Phoebes may serve as a signal to predators. To test this hypothesis, we performed predator trials using a nonreleasable (alive, but blind in one eye) Eastern Screech-Owl (*Megascops asio*). For each trial, a platform mounted about 1.5 m above ground on a metal rod was placed in a phoebe territory within 25 m of either an active nest or fledglings when no adult phoebes were in view. Each predator trial consisted of two 4-min periods (prepresentation and presentation). The prepresentation period began when it appeared that a phoebe was in position to see the platform. The presentation period began when, after the 4-min prepresentation period, the owl was placed on the platform. During each 4-min period, we monitored the focal phoebe and noted (1) the number of tail pumps, (2) distance from the owl platform (at 20-s intervals), (3) distance of closest approach to the platform, (4) number of songs uttered, (5) number of calls uttered, and (6) number of flights of at least 1 m. The behavior of phoebes during the predator prepresentation and presentation periods was compared using Wilcoxon tests.

All statistical analyses were conducted using the Statistical Analysis System (SAS Institute 1999) and results were considered significant when $P < 0.05$. Values are reported as means \pm SE.

RESULTS

Balance hypothesis. We found no relationship between the rate of tail pumping and either wind velocity ($r = -0.11$, $P = 0.48$; $N = 40$) or perch stability ($r = -0.21$, $P = 0.37$; $N = 20$). In addition, overall, we found no difference in the mean tail-pumping rates of males and females ($z = 0.44$, $P = 0.66$).

Signaling-aggression-to-conspecifics hypothesis. We found no differences among periods (preplayback, playback, and postplayback) in tail-wagging rates ($H_2 = 0.1$, $P = 0.97$), distance from the playback speaker ($H_2 = 0.7$, $P = 0.71$), distance of the closest approach to the speaker ($H_2 = 1.4$, $P = 0.49$), number of songs uttered ($H_2 = 0.7$, $P = 0.71$), or number of flights of at least 1 m ($H_2 = 1.1$, $P = 0.58$).

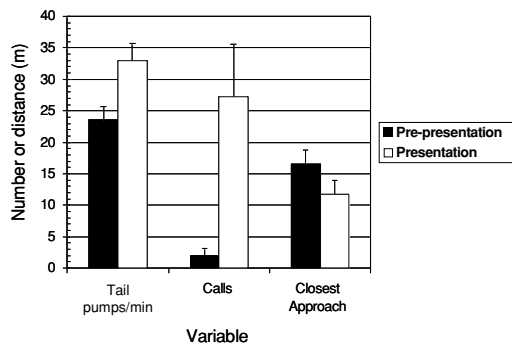


Fig. 1. Mean tail-pumping rate, number of calls, and closest approach (m) to platform for Eastern Phoebes during the prepresentation (no owl present) and predator-presentation (Eastern Screech-Owl present) periods.

Foraging-enhancement hypothesis. To test this hypothesis data, perch times of actively foraging focal phoebes were divided into three categories: ≤ 15 s, 16–30 s, and ≥ 30 s. Among these categories, we found no difference in the mean foray distance ($F_{2,12} = 2.1$, $P = 0.16$). Tail-pumping rates of phoebes with perch times up to 30 s in duration versus birds with perch times greater than 30 s in duration did not differ ($F_{1,11} = 2.2$, $P = 0.06$).

Predator-deterrent hypothesis. Because we found no differences between responses of males and females for any variable during either the prepresentation ($P \geq 0.47$) or presentation ($P \geq 0.08$) periods, we analyzed responses for both sexes combined. We found a significant difference between prepresentation and presentation predator trial periods in tail-pumping rate ($z = 2.5$, $P = 0.012$), number of calls uttered ($z = 3.1$, $P = 0.002$), and distance of closest approach ($z = 2.4$, $P = 0.018$; Fig. 1). However, neither the number of songs uttered ($z = 0.1$, $P = 0.94$) nor the number of flights of at least 1 m ($z = 0.6$, $P = 0.54$) differed between periods.

DISCUSSION

Balance hypothesis. Our results indicate that Eastern Phoebes did not tail pump to help maintain balance. Similarly, Romero-Pujante et al. (2005) found that tail length did not influence the ability of Bearded Tits (*Panurus biarmicus*) to balance on a perch. Male

Bearded Tits with experimentally shortened tails (by 2 cm), experimentally lengthened tails (by 2.5 cm), and unaltered (control) tails did not differ in their ability to balance while moving through reeds, suggesting that tail length did not influence balance abilities (Romero-Pujante et al. 2005). In addition, if tail pumping were important for birds attempting to maintain balance on a perch, then many other species of birds would also exhibit tail-pumping behavior.

Signal-aggression-to-conspecifics hypothesis. Male Eastern Phoebes in our study did not increase tail-pumping rates in response to the playback of conspecific songs, suggesting that tail pumping does not signal aggression. In addition, Smith (1969) noted that phoebes did not always tail pump during aggressive encounters. Weeks (1994) further noted that territorial disputes between male phoebes involved vocalizing and chasing, and that threat displays consisted of “song and various 2-note calls.” Investigators have similarly reported that tail movements by Turquoise-browed Motmots (Murphy 2006), Moorhens (Alvarez 1993), and Purple Gallinules (*Porphyryula martinica*; Alvarez 1993) did not vary during interactions with conspecifics and, in addition, Randler (2007) found that the rate of tail-flicking by Moorhens decreased after being exposed to the call of a conspecific. Such results suggest that tail movements in these species, as in Eastern Phoebes, do not signal aggression to conspecifics.

Foraging-enhancement hypothesis. Tail pumping by Eastern Phoebes in our study did not appear to aid in foraging. Similarly, Randler (2006) studied the tail-wagging behavior of White Wagtails (*Motacilla alba*) and concluded that prey flushing was an unlikely function of such behavior. Because White Wagtails tail-wagged regularly when preening and clearly not searching for prey, and there was a negative correlation between tail wagging and pecking rates, Randler (2006) concluded that tail wagging by wagtails did not cause potential prey to flush.

Predator-deterrent hypothesis. Eastern Phoebes in our study tail pumped at higher rates when a potential predator was nearby, suggesting that such behavior may serve as a pursuit-deterrent signal. Smith (1969: 316) observed similar behavior by Eastern Phoebes, noting that “a potential predator near the nest evokes tail-wags.” Several species of birds appear to use

tail movements as pursuit-deterrent signals. For example, the tail-flicking behavior of Moorhens appears to function as a pursuit-deterrent signal (Alvarez 1993, Alvarez et al. 2006, Randler 2007). Male and female Moorhens tail flick at faster rates not only after detecting an approaching predator (Alvarez 1993, Alvarez et al. 2006) but also when the call of a predator was broadcast over a speaker (Randler 2007). In addition, Moorhens in a better overall physical condition tail flicked at faster rates, suggesting tail-flicking rate is an honest signal of individual quality as well as an honest signal of vigilance (Alvarez et al. 2006).

Turquoise-browed Motmots (*Eumomota superciliosa*) are also thought to use a wag display as a pursuit-deterrent signal (Murphy 2006). When encountering a predator, motmots perform a predictable and stereotypical wag-display whereby the tail is rocked side-to-side in a pendulum motion. Murphy (2006) suggested the wag-display functions as a perception advertisement that communicates a motmot’s awareness of a predator, and that motmots may direct the display at ambush predators such as bird hawks, foxes, and cats. Randler (2006) reported that tail wagging by White Wagtails (*Motacilla alba*) also appeared to serve as a pursuit-deterrent signal directed toward ambush predators. Tail wagging and scanning for predators were positively correlated when wagtails were feeding and preening, suggesting that tail wagging serves as an honest signal of vigilance (Randler 2006).

During our study, Eastern Phoebes tail pumped almost continuously while preening and foraging, and Smith (1969) reported similar observations. Young phoebes were even observed tail pumping immediately after landing on a perch after their first flight from nests (Ritchison, pers. obs.). Similarly, tail wagging by White Wagtails is not restricted to situations where a predator has been detected (Randler 2006), and Turquoise-browed Motmots tail wag in the absence of predators (Murphy 2007). Tail wagging or pumping when predators are not present (or at least when a bird is apparently not aware that a potential predator is nearby) would appear to represent a dishonest pursuit-deterrent signal. However, as suggested by Murphy (2007), such dishonest signaling could be maintained by selection if the display is also given in an honest context (i.e., when a predator has been detected), and predators

would generally benefit by abandoning pursuit or ambush when they detect the display.

In the presence of a potential predator, Eastern Phoebes in our study not only tail pumped at significantly higher rates but also uttered more calls and flew closer to the predator. Similar responses, with potential prey providing multiple cues to inform predators that they are aware of their presence, have been reported in many other species (Alvarez 1993, Alvarez et al. 2006, Murphy 2006, Randler 2007). In addition, among species of birds reported to use tail wagging or pumping as a pursuit-deterrent signal, rates of tail movement typically increase after a predator has been detected (Alvarez 1993, Alvarez et al. 2006, Murphy 2006, Randler 2007). Thus, predators detecting potential prey that are tail pumping at relatively slow rates and not providing any additional cues (e.g., calling or moving closer) might actually interpret such behavior as a sign that they have not been detected. If true, tail pumping at variable rates (like Eastern Phoebes) may, in terms of predation risk, be costly. Additional potential costs of tail pumping include the energy required for such behavior and the increased likelihood (due to the tail movements) of being detected by a predator.

However, the persistent tail pumping by Eastern Phoebes (and other tail-pumping species) suggests that the benefits of such behavior outweigh the costs. One possible benefit is that persistent tail pumping serves as an equally persistent signal to aerial predators that phoebes represent a difficult-to-capture prey item. If so, then phoebes benefit because tail pumping deters attacks, some small percentage of which would be successful at, of course, great cost to the phoebe. Flycatchers in general can be recognized by their typical, alert feeding posture (Lima 1993), and phoebes (Eastern, Black [*S. nigricans*], and Say's [*S. saya*] phoebes) in particular can be recognized by their posture and persistent tail pumping. Not all flycatchers, however, tail pump. One possible explanation for that is that larger flycatchers are likely not as maneuverable as smaller flycatchers like phoebes and, therefore, can be more easily captured by avian predators. If so, tail pumping by larger flycatchers would not be favored by natural selection because such behavior would simply increase the likelihood of being detected and captured by an avian predator.

A predator-deterrent signal must be clear, straightforward, and conspicuous to an alert predator (Hasson 1991). A predator must be able to detect the signal from a distance far enough away so that there is enough time to alter their behavior (i.e., decide not to pursue or give up their pursuit). Eastern Phoebes typically forage in open woodlands and woodland edges (Weeks 1994) where tail pumping would be visible even at long distances, thus fulfilling the requirements of signaling theory. Of course, the decision by a predator to not pursue or to give up pursuit of a potential prey item must also provide benefits. For a difficult-to-capture potential prey item, like an Eastern Phoebe, not attacking may be beneficial for a predator because the time and energy invested in an attack is unlikely to result in a successful kill. For ambush predators, like Sharp-shinned (*Accipiter striatus*) and Cooper's (*A. cooperii*) hawks, another possible benefit is that, by not launching an attack (likely unsuccessful) on a phoebe, other, possibly more easily captured, prey in the vicinity are not alerted to the hawk's presence.

In a survey of tactics used by birds to escape from predators, Lima (1993) noted that little information was available concerning tactics used by flycatchers and suggested, as one possible explanation, that flycatchers may rarely be preyed upon because their alert postures deter attacks by predators. In support of this, Lima (1993) cited observations of attacks by falcons on an Eastern Phoebe (Bent 1942) and an Eastern Kingbird (*Tyrannus tyrannus*; de Kiriline Laurence 1949) that were unsuccessful because the flycatchers employed "their well-developed aerial maneuvering abilities to avoid capture." In a review of the food habits of North American raptors, Sherrod (1978) noted only four reports of phoebes as prey items, i.e., two Say's Phoebes taken by Swainson's Hawks (*Buteo swainsoni*), one Say's Phoebe taken by a Peregrine Falcon (*Falco peregrinus*), and one *Sayornis* sp. plus a report of "phoebes" in the diet of Broad-winged Hawks (*Bufo platypterus*). In addition, Weeks (1994) reported an unsuccessful attack on a phoebe by a Sharp-shinned Hawk and also noted that, for Eastern Phoebes during the breeding season, mortality due to avian predators appeared to be "insignificant." Although clearly not conclusive, such observations suggest that phoebes may be difficult for avian predators to capture and, if so,

tail-pumping phoebes, and perhaps other species that tail wag or pump persistently, for example, Torrent Tyrannulets (*Serpophaga cinerea*), Sooty Tyrannulets (*S. nigricans*), Greater Wagtail-tyrants (*Stigmatura budytoides*), Many-colored Rush-tyrants (*Tachuris rubrigastra*; Smith 1971), may be supplementing their typically alert posture with an even more visible signal to predators that they will be difficult to capture. If correct, then tail pumping may represent a persistent and honest predator-deterrent signal.

Avian prey species should be adapted to maximize their chances of escaping from an attacking predator and, for adult birds, aerial predators typically represent the greatest threat. One important strategy for minimizing predation risk is to maximize vigilance; nonvigilant animals react more slowly to attacks by a predator (Krause and Godin 1996, Hilton et al. 1999) and slower reacting individuals are more likely to be killed when attacked (Krause and Godin 1996). Although not quantified, birds, such as phoebes, that hawk insects must spend considerable time on elevated perches scanning for insect prey and, in so doing, may also be able to spend time scanning for predators. As suggested by Lima (1993), the "alert feeding posture" of flycatchers, including phoebes, may deter attacks because predators consider the alert posture and associated scanning behavior as indicators of vigilance. Perhaps making them even less attractive as potential prey, Eastern Phoebes are rarely on the ground and are relatively small (mean mass = 16.9 g for females and 19.7 g for males; Weeks 1994). An examination of the hunting behavior of Sharp-shinned Hawks revealed that attack success rates were significantly lower for potential prey that were perched or in flight (compared to prey on the ground) and that small birds under about 20 g were largely absent from their diet (Roth et al. 2006).

A vigilant bird may be attacked by an aerial predator and, depending on their position relative to the predator, will attempt to escape. Two possible, and common, avian escape tactics are to either out-manuever the predator using rapid turns (Howland 1974) or dive away from the predator (Hedenström and Rosén 2001). Such tactics require rapid acceleration and maneuverability, characteristics favored by natural selection to enhance the foraging efficiency of aerial insectivores like phoebes (Warrick 1998, Hedenström and Rosén 2001). This combi-

nation of vigilance plus flying abilities comparable to or exceeding those of many aerial predators, along with their small size, may help explain why phoebes are attacked by predators infrequently (and, apparently, captured even less frequently) and also explain the evolution of the persistent and honest predator-deterrent signal (i.e., tail pumping) apparently employed by phoebes.

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