

January 2016

American Kestrels (*Falco sparverius*) may use tail-pumping to maintain balance

Joshua Suich
Eastern Kentucky University

Follow this and additional works at: <http://encompass.eku.edu/etd>

 Part of the [Behavior and Ethology Commons](#), and the [Ornithology Commons](#)

Recommended Citation

Suich, Joshua, "American Kestrels (*Falco sparverius*) may use tail-pumping to maintain balance" (2016). *Online Theses and Dissertations*. 432.
<http://encompass.eku.edu/etd/432>

This Open Access Thesis is brought to you for free and open access by the Student Scholarship at Encompass. It has been accepted for inclusion in Online Theses and Dissertations by an authorized administrator of Encompass. For more information, please contact Linda.Sizemore@eku.edu.

Possible functions of tail-pumping by American Kestrels (*Falco sparverius*)

By

Joshua Suich

Thesis Approved:



Chair, Advisory Committee



Member, Advisory Committee



Member, Advisory Committee



Dean, Graduate School

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a Master's degree at Eastern Kentucky University, I agree that the Library shall make it available to borrowers under rules of the Library. Brief quotations from this thesis are allowable without special permission, provided that accurate acknowledgment of the source is made. Permission for extensive quotation from or reproduction of this thesis may be granted by my major professor, or in [his/her] absence, by the Head of Interlibrary Services when, in the opinion of either, the proposed use of the material is for scholarly purposes. Any copying or use of the material in this thesis for financial gain shall not be allowed without my written permission.

Signature Joshua Smith

Date 11/29/16

American Kestrels (*Falco sparverius*) may use tail-pumping to maintain balance

By

Joshua Suich

Bachelor of Science
Bryan College
2008

Submitted to the Faculty of the Graduate School of
Eastern Kentucky University in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE
December 2016

Copyright © Joshua Suich 2016
All Rights Reserved

ACKNOWLEDGMENTS

I thank Dr. Gary Ritchison for helping me design this project and giving me the chance to work with cool falcons! I am also thankful for helpful critiques of manuscript drafts. I also thank Dr. David Brown and Dr. Charles Elliott for serving on my committee. Special thanks goes to my undergrad professor, Dr. Laurence Fleming, who encouraged me to pursue graduate school and has been very supportive throughout the process. I also thank all my friends in the bird lab for making me laugh, encouraging me, and being like a family. Finally, I'm very grateful for the support and encouragement of my parents, who have always been there for me.

ABSTRACT

When perched, several species of small falcons, including American Kestrels (*Falco sparverius*), often pump their tails, but the possible function of this behavior is unknown. My objective was to use observations and experiments to examine the possible function(s) of tail-pumping by American Kestrels. Fieldwork was conducted from March 2015 to December 2015 at the Blue Grass Army Depot in Madison County, Kentucky. During observations of focal kestrels, I noted their behavior (e.g., landing on a perch, hunting, or consuming prey), including when and how often they pumped their tails (i.e., rapid movement of the tail down, then back up to its original position). Kestrels typically tail-pumped when landing on a perch (mean = 4.1 ± 0.2 pumps per 10 sec) and consuming prey (mean = 2.4 ± 0.2 pumps per 10 sec). When hunting, kestrels tail-pumped at higher rates during the 30 sec prior to attacking (mean = 1.1 ± 0.3 pumps), then they did in the 30-60 sec interval before an attack (mean = 0.3 ± 0.1 pumps). During experiments where kestrels were presented with models of a conspecific and a predator (Cooper's Hawk, *Accipiter cooperi*), I found no difference in likelihood of tail-pumping prior to and during the presentation. These results suggest that tail-pumping by American Kestrels is not used to communicate with conspecifics or as a predator-deterrent signal. Rather, kestrels appear to tail-pump to help maintain balance on perches when landing and consuming prey. In addition, prior to attacking prey, kestrels typically bob their heads (possible to aid in judging distances), and tail-pumping may help them maintain stability as they head-bob and prepare to attack.

TABLE OF CONTENTS

CHAPTER	PAGE
I. INTRODUCTION	1
II. METHODS	4
III. RESULTS	10
IV. DISCUSSION	13
LIST OF REFERENCES.....	18

LIST OF TABLES

TABLE	PAGE
1. Wind-velocity categories based on the Beaufort scale	5

LIST OF FIGURES

FIGURE	PAGE
1. Mean number (\pm SE) of tail pumps per 10 sec by American Kestrels engaged in different behaviors	10
2. Example of female American Kestrel tail-pumping (moving tail downward from top to bottom) while consuming prey.....	15

CHAPTER I

INTRODUCTION

Many species of birds perform various tail movements, and the functions of these movements are often unclear. Some birds are thought to use tail-fanning movements and the flashing of tail-spots to create changes in light exposure that may startle and expose hidden prey. For example, Painted Redstarts (*Myioborus pictus*) extend their wings and fan their tails to flush insects while foraging (Jabłoński 1999), and Hooded Warblers (*Setophaga citrina*) flick their tails and flash bright tail spots to flush insect prey and increase their foraging success (Mumme 2014).

Other birds appear to use tail movements to communicate with conspecifics. For example, rates of tail-flicking by adult Dusky Moorhens (*Gallinula tenebrosa*) are higher than those of juveniles, suggesting that tails are used to indicate social status in a flock (Ryan et al. 1996). Sogge et al. (2007) found that Willow Flycatchers (*Empidonax traillii*) responded to conspecific playback with aggressive visual displays that included tail-pumping, i.e., rapidly raising then slowly lifting their tails. Male Elegant Trogons (*Trogon elegans*) engage in tail-raising displays both during courtship and during aggressive interactions with other males (Bitton and Doucet 2014). These tail displays may simultaneously act as a predator-deterrent by signaling awareness to predators and discouraging pursuit (Bitton and Doucet 2014).

In addition to Elegant Trogons, several other species of birds repeatedly wag or flick their tails as an apparent signal of vigilance to predators. Randler (2006) found that tail-wagging by White Wagtails (*Motacilla alba*) was associated with alert behavior, and Murphy (2006) reported that Turquoise-browed Motmots (*Eumomota superciliosa*) performed tail-wagging displays in the presence of predators, suggesting that tail-

wagging may act as a pursuit-deterrent signal. Similarly, Eastern Phoebes (*Sayornis phoebe*) and Black Phoebes (*Sayornis nigricans*) tail-pump at faster rates when exposed to predators, suggesting that tail-pumping indicates readiness for escape flight (Carder and Ritchison 2009, Avellis 2011). Alertness-signaling has also been reported in several species in the family Rallidae (Woodland et al. 1980, Alvarez 1993, Alvarez et al. 2006, Randler 2007). Alvarez et al. (2006) found a positive correlation between body condition and tail-flicking rates among Eurasian Moorhens (*Gallinula chloropus*). By signaling awareness of a predator's presence, high-quality moorhens may be discouraging pursuits and conserving energy by avoiding escape flights (Alvarez et al. 2006).

Tail-pumping has been observed in several small species of raptors (e.g., Maclean 1970, Tarboton 1978, Kemp and Crowe 1994, Kemp and Van Zyl 1998, Kemp and Vidhidharm 1998). Tail-pumping by Black-thighed Falconets (*Microhierax fringillarius*) may act as an excited post-flight display (Kemp and Crowe 1994). Kemp and Vidhidharm (1998) found that male White-rumped Pygmy Falcons (*Polihierax insignis*) tail-pumped in response to playback of the calls of conspecific males, suggesting that tail-pumping may function as an aggressive territorial warning to potential intruders. Tarboton (1978) reported that Black-shouldered Kites (*Elanus axillaris*) tail-cocked while searching for prey. Mendelsohn and Jaksic (1989) suggested that this behavior may serve to deter rival kites from a hunting area. Tail movements in raptors may also be used during intrasexual interactions. Maclean (1970) observed tail-wagging by female Pygmy Falcons (*Polihierax semitorquatus*) during submissive displays to males, and Spottiswoode et al. (2004) noted that Pygmy Falcons tail-wagged during courtship rituals. Tail movements may also help falcons maintain their balance on a perch, as suggested by Debus (2012), but studies testing possible connections between bird tail movements and balance are rare (Randler 2016).

American Kestrels (*Falco sparverius*; hereafter kestrels) pump their tails when perched in trees or on utility lines. Although often mentioned as a characteristic useful for identifying kestrels in the field (e.g., Tekiela 2001, Stokes and Stokes 2010, Crossley 2011), the function of such tail-pumping is unclear. In the lab, Mueller (1974) found that kestrels tail-pumped more frequently in response to presentation of live mice than model mice, and suggested that tail-pumping may be an instinctive pre-attack behavior. Bird and Palmer (1988) noted that, after fledging, young kestrels sometimes changed perches frequently and, prior to doing so, performed exaggerated head-bobbing and tail-pumping intention movements. Given the proposed functions of tail-pumping in other species of birds and reports of tail-pumping among several species of small falcons and kites, tail-pumping by kestrels may represent more than an instinctive behavior or intention movement. Thus, my objective was to use a combination of observations and experiments to examine the possible function(s) of tail-pumping by male and female American Kestrels. I tested four hypotheses for tail-pumping by kestrels, including balance, pre-attack, conspecific communication, and predator-deterrent hypotheses

CHAPTER II

METHODS

Fieldwork was conducted from March to December 2015 at the Blue Grass Army Depot (BGAD) in Madison County, Kentucky. The BGAD (6070 ha) consists primarily of open fields and scattered woodlots.

Typical kestrel nesting densities in the U.S. range from 0.11 to 1.74 pairs/km² (Bird and Palmer 1988), so I assumed that resident kestrels remain in their territories throughout the year and, in addition, that male and female kestrels observed at least 1.3 km apart were different pairs or different kestrels. Smallwood (1988) found no evidence that kestrels gave up their territories in 1283 sightings of kestrel interactions.

I attempted to observe each focal kestrel at least twice a week at varying times during the day. Because kestrels have large territories, observation periods lasted as long as I could maintain visual contact with a kestrel. I attempted to maintain a sufficient distance from kestrels (about 35 - 40 m) so my presence would not influence their behavior. Binoculars (8X42) were used to aid in observing kestrels. In addition, I used a video camera and tripod during observations and, when a focal kestrel was perched, I began video-recording the kestrel and continued observing with binoculars.

While video-taping observations, I noted the time and verbally described the behavior of the kestrel (hunting, resting, preening, or consuming prey). I also noted each time a focal kestrel tail-pumped, with tail-pumping defined as a rapid downward motion of the tail followed by an upward thrust to its initial position. The presence of potential predators and conspecifics was also noted and their distance (m) from the focal kestrel was estimated using known reference points (e.g., distance between utility poles). I also

noted the sex of conspecifics and any known relationship (mate, fledgling, or intruder) to the focal kestrel.

Balancing hypothesis – To determine if kestrels tail-pump to help maintain their balance on perches (i.e., use their tails to generate a moment to counterbalance the torque generated around their rotational axis; Romero-Pujante et al. 2005), I monitored tail-pumping rates of focal birds on different types of perches (tree branches, utility wires, and utility poles) and at different wind velocities. Following the methods of Carder and Ritchison (2009), focal kestrels were monitored during randomly selected 5-min observation periods. At 1-min intervals during observation periods, wind velocity was measured using a wind meter (Kestrel 2000, Neilsen Kellerman, Chester, PA). For analysis, wind velocities were categorized based on the Beaufort scale (Table 1).

Table 1. Wind-velocity categories based on the Beaufort scale.

Category	Wind speed (km/hr)
1	< 1
2	1.1 – 3
3	3.1 – 6
4	6.1 – 10
5	10.1 - 16

Source: <http://www.spc.noaa.gov/faq/tornado/beaufort.html>.

I also examined the possible effect of different behaviors on tail-pumping rates, including pre-attack (30-60 sec period before an attack) and attack (0-30 sec period before an attack) behavior, consuming prey, and landing on a perch. As a control, I determined tail-pumping rates when kestrels were not engaged in any of these behaviors. Tail-pumping rates were determined per 10 sec intervals for these behaviors.

Because individual kestrels were observed on multiple occasions, I used repeated-measures analysis of variance to examine the possible effect of sex, perch type, wind velocity, and behavior on tail-pumping rates.

Pre-flight or pre-attack hypothesis – Smallwood and Bird (2002) noted that, after locating prey, kestrels frequently bob their heads (possibly using parallax to aid in judging distances), then tail-pumped as “. . . a ritualized flight-intention behavior.” However, tail-pumping prior to initiating attacks might also help kestrels maintain stability as they head-bob and prepare to initiate an attack. If so, tail-pumping rates would be expected to be higher for kestrels head-bobbing and initiating attacks from less stable perches or during periods with greater wind velocity. To test this hypothesis, I examined the possible effect of perch type and wind velocity on tail-pumping rates of kestrels prior to initiating attacks. Perch types included trees, poles, and powerlines, and wind velocity was determined within 2 min of when a kestrel initiated an attack. Tail-pumping rates were determined during the period beginning when a kestrel initiated head-bobbing and ended when an attack was initiated (i.e., the kestrel left its perch). I used repeated measures ANOVA to examine the possible effects of perch-stability category and wind-velocity on tail-pumping rates of kestrels initiating attacks.

Conspecific-communication hypothesis – To determine if tail-pumping might signal aggression or submission to conspecifics, a speaker (placed within 30-40 m of focal kestrels) was used to play back conspecific calls to focal kestrels. The vocal repertoire of kestrels consists of three calls: chitter, klee, and whine (Johnsgard 1990). Whine and chitter calls are generally limited to the breeding season and given during interactions between pairs of kestrels. Klee calls are given throughout the year and appear to signal aggression (Smallwood and Bird 2002). Therefore, to examine the possible use of tail-pumping to as a conspecific signal, I used playback of klee calls. Recordings of these calls were obtained from the Macaulay Library of wildlife sounds

(Cornell Lab of Ornithology; <http://macaulaylibrary.org/>) and subsequently used for playback experiments. I used calls of four different individuals during experiments to avoid pseudoreplication. Winland (2016) found no difference in the characteristics of the klee calls of male and female American Kestrels so calls of male, female, or kestrels of unknown sex were obtained from the Macaulay Library and used in experiments.

Following the procedure described by Carder and Ritchison (2009), each conspecific call experiment consisted of two 3-min periods: pre-playback and playback. Prior to some experiments, a study skin of a male American Kestrel was placed on a 1.5-m-high pole next to the playback speaker and about 30 – 40 m from the focal kestrel (to minimize the likelihood of the kestrel leaving its perch due to my presence). During other experiments, a study skin of a female kestrel was used to test for possible differences in behavioral responses between the sexes, including signs of submission, as suggested for female Pygmy Falcons (Maclean 1970).

During each experiment interval, I determined tail-pumping rates of focal kestrels. In addition, I noted other behaviors that might indicate aggression or submission, including the (1) mean distance from speaker or model (20-s intervals), (2) distance of closest approach to the study skin, and (3) number of each type of call.

I used repeated-measures ANOVA to examine the possible effect of playback period (pre-playback and playback) and sex (i.e., of the study skin and focal kestrels) on tail-pumping rates and distances of kestrels from study skins. Kestrels using tail-pumping as an aggressive posture were predicted to utter more klee calls (calls typically given in aggressive contexts; Smallwood and Bird 2002) and move closer to the study skin, particularly those of the same sex as focal kestrels, during playback. Submissive kestrels were not expected to utter klee calls or approach study skins.

Predator-deterrent hypothesis – American Kestrels may tail-pump to signal vigilance and deter pursuit from predators such as larger owls or hawks. Because

kestrels are quick, highly maneuverable birds with sharp talons, predators may find kestrels difficult to capture and may risk injury even if a hunt is successful. If so, then the characteristic tail-pumping of kestrels may represent a means by which potential predators 'recognize' American Kestrels, i.e., other potential prey of similar size do not tail-pump and, as a result, even from a considerable distance, a possible predator may be able to differentiate kestrels (difficult prey) from similar-sized birds (less difficult prey).

To test the predator-deterrent hypothesis, I conducted experiments using study skins of a raptor that could potentially prey on kestrels, i.e., a female Cooper's Hawk (*Accipiter cooperii*; females are larger than males and thus may be more likely to attack a kestrel) and study skins of a raptor that likely presents little or no threat to kestrels, i.e., a male Sharp-shinned Hawk (*Accipiter striatus*; males are smaller than females and thus less likely to attack a kestrel). Two study skins of each of these hawks were used during experiments. I used study skins of Common Grackles (*Quiscalus quiscula*), a large songbird that represents no threat to kestrels and is likely too large to be considered as possible prey, as a control.

Each predator-deterrent experiment consisted of two 3-min periods: pre-presentation and presentation. During the pre-presentation period, I observed focal kestrels and determined tail-pumping rates. After the pre-presentation period, I placed a study skin of one of the test raptors or control (mounted on a 1.5-m-high pole) within visual range (~25 – 40 m) of the focal kestrel, but far enough away to minimize the likelihood of the kestrel flying away. Once it appeared that the focal kestrel would likely have noticed the study skin (by looking in that general direction), I again determined tail-pumping rates for the next 3 min (or until the focal kestrel left its perch to approach the study skin or left the area). Repeated-measures ANOVA was used to examine the possible effects of experimental period (pre-presentation and presentation) and exposure to the different study skins (two hawks plus the control) on tail-pumping rates.

If tail-pumping serves as a predator-deterrent signal, rates were expected to be higher during the presentation of study skins of female Cooper's Hawks.

Statistical analysis – All analyses were conducted using the Statistical Analysis System (SAS Institute 2014). Significance was accepted at $P < 0.05$. All values are reported as means \pm SE.

CHAPTER III

RESULTS

I monitored a total of 43 kestrels (N = 21 males and 22 females) during my study.

A subset of this total number was used to test each hypothesis.

Balance hypothesis

Tail-pumping rate of kestrels (per 10 sec) varied significantly among different behaviors ($F_{4,70} = 30.2$, $P < 0.0001$), with rates highest after kestrels landed on perches (Figure 1).

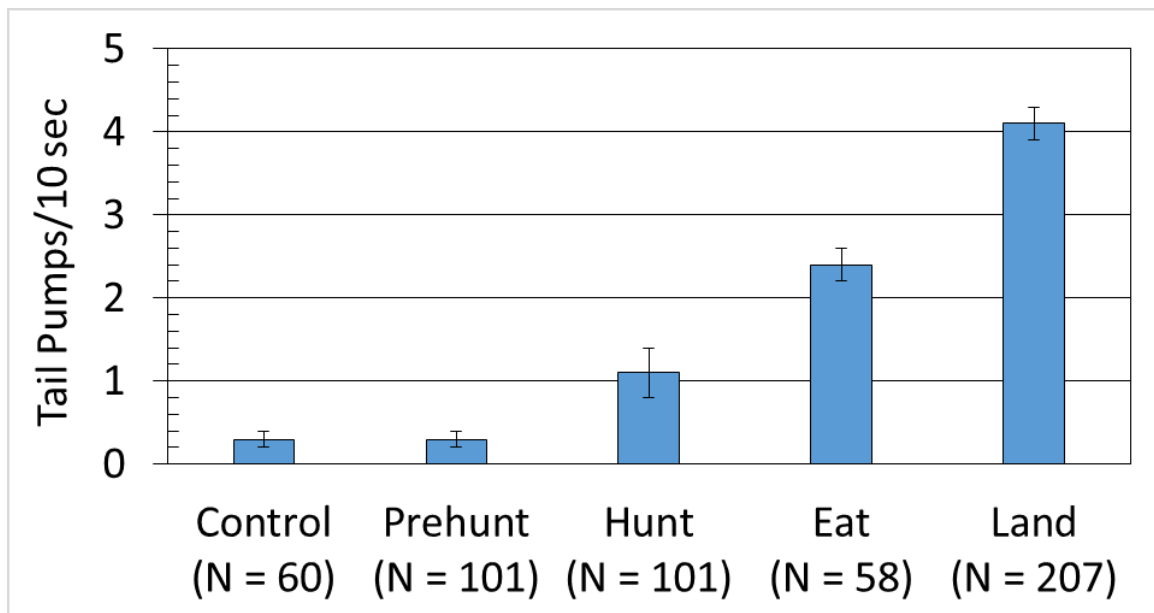


Figure 1. Mean number (\pm SE) of tail pumps per 10 sec by American Kestrels engaged in different behaviors.

Notes: Control consisted of kestrels resting on a perch. Prehunt and Hunt are described in the pre-attack indicator/stability hypothesis. Eat refers to kestrels eating prey on a perch. The Land category was the period right after kestrels landed on a new perch.

A Tukey's post-hoc test indicated that the differences in tail-pumping rates between the pre-hunt and control periods and between hunt and control were not significant; all other two-way comparisons were significant ($P < 0.05$). The interaction between sex and behavior was not significant ($F_{4,16} = 0.2$, $P = 0.96$).

During control periods (i.e., not during the pre-hunting period or when kestrels were landing on a perch, eating, or hunting), wind velocity (with categories 4 and 5 combined because only two kestrels were observed with category 5 wind velocity) had no effect on tail-pumping rates ($F_{3,35} = 0.3$, $P = 0.80$). The interaction between perch type and wind velocity was not significant ($F_{3,9} = 0.1$, $P = 0.97$).

Pre-attack indicator/stability hypothesis

To determine if tail-pumping serves either as a pre-attack indicator or helps stabilize a kestrel before taking flight, I compared tail-pumping rates of kestrels during the period from 30 to 60 sec before an attack (pre-attack period) to rates during the 30-sec interval before an attack ($N = 104$). Mean tail-pumping rates were significantly higher ($F_{1,20} = 8.6$, $P = 0.008$) during the 30 sec before an attack (3.5 ± 0.8) than during the pre-attack period (0.9 ± 0.3). During the 30 sec prior to an attack, I found no effect of sex ($F_{1,11} = 0.3$, $P = 0.59$), wind velocity ($F_{3,26} = 0.6$, $P = 0.63$), or perch type ($F_{2,11} = 1.3$, $P = 0.32$) on tail-pumping rates.

Conspecific communication hypothesis

Overall, I found no difference in the mean number of tail pumps by kestrels during trials ($N = 60$) between the pre-presentation (5.3 ± 2.0) and presentation (2.6 ± 0.6) periods ($F_{1,31} = 1.4$, $P = 0.25$). In addition, the interaction between the period (pre-presentation and presentation) and the type of experiment (female presented with male, female presented with female, male presented with male, male presented female) was not significant ($F_{3,3} = 1.5$, $P = 0.23$). In experiments with female kestrels, mean tail-pumping rates during the pre-presentation and presentation periods were 11.2 ± 6.2 and

2.2 ± 0.4 when presented with a conspecific female, and 1.2 ± 0.8 and 2.1 ± 1.0 when presented with a conspecific male. In experiments with male kestrels, mean tail-pumping rates during the pre-presentation and presentation periods were 3.8 ± 1.0 and 3.6 ± 1.6 when presented with a conspecific female, and 1.6 ± 0.7 and 2.0 ± 0.8 when presented with a conspecific male.

Predator-deterrent hypothesis

Overall, the mean number of tail pumps by kestrels (N = 118) did not differ between the conspecific pre-presentation (5.0 ± 1.2) and presentation (4.7 ± 1.1) periods ($F_{1,23} = 0.03$, $P = 0.87$). In addition, the interaction between period and treatment was not significant ($F_{2,2} = 0.03$, $P = 0.97$). Mean tail-pumping rates during pre-presentation and presentation periods were 4.2 ± 1.9 and 3.4 ± 1.1 for the Cooper's Hawk, 6.4 ± 2.4 and 5.2 ± 1.5 for the Sharp-shinned Hawk, and 4.4 ± 1.8 and 5.6 ± 2.8 for the control (Common Grackle). In addition, during encounters with live potential predators (Cooper's Hawks and Red-tailed Hawks (*Buteo jamaicensis*); N = 37), kestrels averaged only 0.57 ± 0.35 pumps before responding aggressively with attacks and/or klee calls.

CHAPTER IV

DISCUSSION

My results suggest that tail-pumping by American Kestrels does not act as a pursuit-deterrent signal and plays no role in communication with conspecifics. Rather, my results suggest that kestrels pump their tails to maintain balance on perches, primarily when landing, eating, and preparing to attack prey. Although I found no effect of either wind velocity or perch stability of rates of tail-pumping, kestrels in my study did tail-pump at higher rates immediately after landing on perches and when consuming large prey. Similarly, Debus (2012) observed that when a Brown Falcon (*Falco berigora*) perched on a wire it balances ‘. . . precariously while fanning its tail.’ Other species of birds reported to use their tails to maintain balance on perches include American Goldfinches (*Spinus tristis*; Coutlee 1963), Smooth-billed Ani (*Crotophaga ani*; Quinn and Startek-Foote 2000), Red-faced Cormorants (*Phalacrocorax urile*; Causey 2002) and Pelagic Cormorants (*P. pelagicus*; van Tets 1965). Gatesy and Dial (1996) examined tail function in Domestic Turkeys (*Meleagris gallopava*) and noted that they ‘. . . often elevate and abduct the rectrices upon landing to help balance on the perch.’

In a recent review of tail movements in birds, Randler (2016) noted that studies of the possible role of avian tail movements in maintaining balance were ‘scarce’, but also suggested that if tail movements are important in maintaining balance, birds should move their tails more frequently when on ‘more flexible perches’ and ‘during windy conditions.’ In support of the ‘flexible perch’ hypothesis, Romero-Pujante et al. (2005) found that the tails of Bearded Tits (*Panurus biarmicus*) appeared to be particularly important for balancing when tits were perching on small twigs or branches. Observers have noted that other raptors may also use their tails for balance on ‘flexible perches’

(i.e., small-diameter branches or utility wires), including Merlins (*Falco columbarius*; T. Barksdale, pers. observ., <https://macaulaylibrary.org>, video ML 448705), Aplomado Falcons (*Falco femoralis*; T. Barksdale, pers. observ., <https://macaulaylibrary.org>, video ML 402555), Black-winged Kites (*Elanus caeruleus*; S. Patil, pers. observ., <https://www.youtube.com/watch?v=YHXJuV3wDgg>), and Rough-legged Hawks (*Buteo lagopus*; C. Barrentine, pers. observ., <https://www.youtube.com/watch?v=L62tZAlp6NQ>).

American Kestrels are typically found in open habitats and frequently use utility wires and small branches of trees and shrubs as hunting perches (Smallwood and Bird 2002, Worm et al. 2013). Cruz (1976) noted that kestrels often perched on the exposed upper branches of large trees and Tyler (1938) reported that kestrels tended to use high, exposed perches. The ‘flexibility’ of utility wires and the exposed upper branches of trees and shrubs used as perches by birds would vary with the size and mass of birds. For example, Bobowski et al. (2014) noted that Red-tailed Hawks, with average masses of about 1200 g for females and 1030 g for males, struggled to maintain their balance when perched on utility wires. American Kestrels are much smaller than Red-tailed Hawks, with average masses of about 111 g for males and 120 g for females (Dunning 1993). However, small-diameter branches on the outer portions of trees and shrubs and utility wires, which may be favored by kestrels trying to most effectively scan the ground for prey, might still be ‘flexible’, so that tail-pumping is needed to maintain balance.

Randler (2016) noted that if tail movements are important in maintaining balance, birds should move their tails more frequently ‘during windy conditions’. I found no effect of wind velocity on tail-pumping rates of American Kestrels. However, most observations were made when wind velocities were 4 or less on the Beaufort scale. A 4 on the Beaufort scale is equivalent to a wind velocity of 20 – 28 km/hour, which may not have been sufficient to make balancing on perches difficult for kestrels. In addition, Balgooyen (1976) noted that American Kestrels respond to wind speeds of 32 to 40 km/hour by

leaning into the wind and assuming a more horizontal position to enhance wind flow past the body (Figure 2). Thus, kestrels may not need to increase rates of tail-pumping to maintain balance. In addition, American Kestrels tend to perch significantly lower, where wind velocities may be lower, during periods of high wind (Balgooyen 1976, Mills 1979).



Figure 2. Example of female American Kestrel tail-pumping (moving tail downward from top to bottom) while consuming prey.

Note: The kestrel assumes a horizontal posture because of windy conditions (as indicated by the movement of leaves and branch in the background).

Source: images from a video by Timothy Barksdale on the website of the Macaulay Library, Cornell Lab of Ornithology, Ithaca, NY; <http://macaulaylibrary.org/video/407348>.

In further support of the balance hypothesis, I found that American Kestrels tail-pumped at relatively high rates when consuming prey on perches. The additional mass of a prey item on a perch, using at least one foot to hold the prey item, plus movements made by kestrels as they consume prey may make balancing on perches, particularly small-diameter perches, more difficult and cause an increase in tail-pumping rates. Other raptors that have been observed using their tails for balance when consuming prey on perches include Bat Falcons (*Falco ruficularis*; L. Seitz, pers. observ., <https://macaulaylibrary.org>, video ML 477769) and Cooper's Hawks (*Accipiter cooperii*; M. Cherry, pers. observ., <https://www.youtube.com/watch?v=KpJXFkQoVy4>).

Tail-pumping rates of kestrels in my study were also higher just prior to initiating attacks than during pre-hunting or control periods. Similarly, Mueller (1974) observed kestrels tail-pumping before attacking live mice, and Smallwood and Bird (2002) mentioned tail-pumping by kestrels as a pre-attack ritual, possibly indicating indecision before attacking prey. Tail-pumping while scanning for prey has also been reported in Northern Hawk-Owls (*Surnia ulula*; Duncan and Duncan 2014). Tarboton (1978) reported that Black-shouldered Kites tail-cock prior to attacking prey and suggested that kites were aroused by the prospect of a hunt. Among some species of birds, tail-pumping may also signal an intention to take flight (Andrew 1956). For example, American Goldfinches (*Spinus tristis*) flick their tails prior to taking off from perches (Coutlee 1963).

Rather than simply serving as a pre-attack ritual or indicating arousal or excitement at the prospect of an attack, tail-pumping by American Kestrels might also help them maintain balance. In addition to tail-pumping, kestrels also tend to 'head-bob' prior to initiating attacks (Balgooyen 1976, Smallwood and Bird 2002). Head-bobbing is thought to play an important role in improving depth perception via motion parallax (Nawrot 2003, O'Rourke et al. 2010b), and may be particularly important for kestrels because they have limited eye movement (1° , O'Rourke et al. 2010a). Head-bobbing

may alter their center of gravity and also cause movement of small diameter, unstable perches. As such, tail-pumping by kestrels may accompany head-bobbing as a way of maintaining their balance prior to initiating an attack.

In summary, my results suggest that American Kestrels tail-pump to maintain balance on perches during active movements such as eating and landing. Kestrels also may use tail-pumping to signal excitement and assist in balance before leaving a perch to launch an attack. As Randler (2016) noted, few investigators have examined the possible use of tail movements by birds as a means of maintaining balance on perches and, as such, additional studies are clearly needed, particularly studies of larger birds that sometimes use 'flexible perches.'

LIST OF REFERENCES

- Alvarez, F. 1993. Alertness signalling in two rail species. *Animal Behaviour* 46: 1229-1231.
- Alvarez, F., C. Sánchez, and S. Angulo. 2006. Relationships between tail-flicking, morphology, and body condition in Moorhens. *Journal of Field Ornithology* 77: 1–6.
- Andrew, R. J. 1956. Intention movements of flight in certain passerines, and their uses in systematics. *Behaviour* 10: 179-204.
- Avellis, G. F. 2011. Tail pumping by the Black Phoebe. *Wilson Journal of Ornithology* 123: 766–771.
- Balgooyen, T. G. 1976. Behavior and ecology of the American Kestrel (*Falco sparverius* L.). *University of California Publications in Zoology* 103: 1-83.
- Bird, D. M., and R. S. Palmer. 1988. American Kestrel. In: *Handbook of North American birds*. Vol. 5: diurnal raptors. Pt. 2. (R. S. Palmer, ed.), pp. 253-290. Yale University Press, New Haven, CT.
- Bitton, P.-P., and S. M. Doucet. 2014. A multifunctional visual display in Elegant Trogons targets conspecifics and heterospecifics. *Behavioral Ecology* 25: 27–34.
- Bobowski, M. M., V. Rolland, and T. S. Risch. 2014. Abundance and distribution of overwintering Red-tailed Hawks and American Kestrels in an agricultural landscape in northeastern Arkansas. *Journal of Raptor Research* 48: 273-279.
- Carder, M. L., and G. Ritchison. 2009. Tail pumping by Eastern Phoebes: an honest, persistent predator-deterrent signal? *Journal of Field Ornithology* 80: 163–170.
- Causey, D. 2002. Red-faced Cormorant (*Phalacrocorax urile*). In: *The Birds of North America Online* (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY.

- Coutlee, E. L. 1963. Maintenance behavior of the American Goldfinch. *Wilson Bulletin* 75: 342-357.
- Crossley, R. 2011. *The Crossley ID guide: eastern birds*. Princeton University Press, Princeton, NJ.
- Cruz, A. 1976. Food and foraging ecology of the American Kestrel in Jamaica. *Condor* 78: 409-412.
- Debus, S. J. S. 2012. *Birds of prey of Australia: a field guide, second ed.* CSIRO Publishing, Collingwood, Australia.
- Duncan, J. R., and P. A. Duncan. 2014. Northern Hawk Owl (*Surnia ulula*). In: *The Birds of North America Online* (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY.
- Dunning, J. B., Jr. 1993. *CRC handbook of avian body masses*. CRC Press, Boca Raton, FL.
- Gatesy, S. M., and K. P. Dial. 1996. From frond to fan: *Archaeopteryx* and the evolution of short-tailed birds. *Evolution* 50: 2037-2048.
- Jabłoński, P. G. 1999. A rare predator exploits prey escape behavior: the role of tail-fanning and plumage contrast in foraging of the Painted Redstart. *Behavioral Ecology* 10: 7-14.
- Johnsgard, P. A. 1990. *Hawks, eagles, and falcons of North America*. Smithsonian Institution Press, Washington, D.C.
- Kemp, A. C., and T. Crowe. 1994. Morphometrics of falconets and hunting behavior of the Black-thighed Falconet *Microhierax fringillarius*. *Ibis* 136: 44-49.
- Kemp, A. C., and A. Van Zyl. 1998. Co-operative breeding by Collared Falconets *Microhierax caerulescens*. *Forktail* 13: 131-32.
- Kemp, A. C., and A. Vidhidharm. 1998. Breeding of the White-rumped Pygmy Falcon. *Wilson Bulletin* 110:71-76.
- Maclean, G. L. 1970. The Pygmy Falcon *Polihierax semitorquatus*. *Koedoe* 13: 1-21.

- Mendelsohn, J., and F. Jaksic. 1989. Hunting behaviour of Black-shouldered Kites in the Americas, Europe, Africa and Australia. *Ostrich* 60: 1-12.
- Mills, G. S. 1979. Foraging patterns of kestrels and shrikes and their relation to an optimal foraging model. Ph.D. dissertation, University of Arizona, Tucson, AZ.
- Mueller, H. C. 1974. The development of prey recognition and predatory behaviour in the American Kestrel *Falco sparverius*. *Behaviour* 49: 313–24.
- Mumme, R. L. 2014. White tail spots and tail-flicking behavior enhance foraging performance in the Hooded Warbler. *Auk* 131: 141–149.
- Murphy, T. G. 2006. Predator-elicited visual signal: why the Turquoise-browed Motmot wag-displays its raked tail. *Behavioral Ecology* 17: 547–53.
- Nawrot, M. 2003. Depth from motion parallax scales with eye movement gain. *Journal of Vision* 3: 841-851.
- O'Rourke, C. T., M. I. Hall, T. Pitlik, and E. Fernández-Juricic. 2010a. Hawk eyes I: diurnal raptors differ in visual fields and degree of eye movements. *PLoS ONE* 5: e12802.
- O'Rourke, C. T., T. Pitlik, M. Hoover, and E. Fernández-Juricic. 2010b. Hawk eyes II: diurnal raptors differ in head movement strategies when scanning from perches. *PLoS ONE* 5: e12169.
- Quinn, J. S., and J. M. Startek-Foote. 2000. Smooth-billed Ani (*Crotophaga ani*). In: *The Birds of North America Online* (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY.
- Randler, C. 2006. Is tail wagging in White Wagtails, *Motacilla alba*, an honest signal of vigilance? *Animal Behaviour* 71: 1089–1093
- Randler, C. 2007. Observational and experimental evidence for the function of tail flicking in Eurasian Moorhen *Gallinula chloropus*. *Ethology* 113: 629–639.

- Randler, C. 2016. Tail movements in birds—current evidence and new concepts. *Ornithological Science* 15: 1–14.
- Romero-Pujante, M., H. Hoi, and D. Blomqvist. 2005. The importance of tail length for habitat use in the Bearded Tit *Panurus biarmicus*: an experimental study. *Ibis* 147: 464-470.
- Ryan, D. A., K. M. Bawden, K. T. Bermingham, and M. A. Elga. 1996. Scanning and tail-flicking in the Australian Dusky Moorhen (*Gallinula tenebrosa*). *Auk* 113: 499–501.
- SAS Institute. 2014. SAS university edition: installation guide for Windows. SAS Institute Inc., Cary, NC.
- Smallwood, J. A. 1988. A mechanism of sexual segregation by habitat in American Kestrels (*Falco sparverius*) wintering in south-central Florida. *Auk* 105: 36–46.
- Smallwood, J. A., and D. M. Bird. 2002. American Kestrel (*Falco sparverius*). In: *The Birds of North America Online* (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca, NY.
- Sogge, M. K., T. J. Koronkiewicz, C. van Riper, and S. L. Durst. 2007. Willow Flycatcher nonbreeding territory defense behavior in Costa Rica. *Condor* 109: 475-480.
- Spottiswoode, C., E. Herrmann, O. A. E. Rasa, and C. W. Sapsford. 2004. Co-operative breeding in the Pygmy Falcon *Polihierax semitorquatus*. *Ostrich* 75: 322-324.
- Stokes, D. W., and L. Q. Stokes. 2010. *The Stokes field guide to the birds of North America*. Little, Brown and Co., New York, NY.
- Tarboton, W. R. 1978. Hunting and the energy budget of the Black-shouldered Kite. *Condor* 80: 88-91.
- Tekiela, S. 2001. *Birds of Kentucky: field guide*. Adventure Publications, Cambridge, MN.
- Thomas, A. L. R. 1995. *On the tails of birds*. Ph.D. dissertation, University of Lund, Lund, Sweden.

- Tyler, W. M. 1938. Eastern Sparrow Hawk. In: Life histories of North American birds of prey, part 2 (A. C. Bent, ed.), pp. 106-121. U. S. National Museum Bulletin 170, Smithsonian Institution, Washington, D.C.
- Van Tets, G. F. 1965. A comparative study of some social communication patterns in the Pelecaniformes. Ornithological Monographs No. 2.
- Winland, M. 2016. Vocalizations of adult American Kestrels: effect of breeding stage, sex, and context on call use and call characteristics. M.S. thesis, Eastern Kentucky University, Richmond, KY.
- Woodland, D. J., Z. Jaafar, and M.-L. Knight. 1980. The 'pursuit deterrent' function of alarm signals. *American Naturalist* 115: 748-753.
- Worm, A. J., M. M. Bobowski, and T. S. Risch. 2013. Perch-type characteristics of overwintering Red-tailed Hawks (*Buteo jamaicensis*) and American Kestrels (*Falco sparverius*). *Journal of the Arkansas Academy of Science* 67: 159-162.