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ARTICLE

Tail flicking in the black redstart (*Phoenicurus ochruros*) and distance to cover

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Abstract Tail flicking is a common behavior in many bird species, but its function is often unknown. Apart from intraspecific communication, tail flicking could be used during predator–prey communication, e.g., as a signal of prey vigilance or quality. We studied this behavior in the black redstart (*Phoenicurus ochruros*), a species that frequently shows tail flicking and is prone to attacks by ambushing predators that hide in cover. Hence, cover might be perceived as dangerous by this species. We hypothesized that flicking should increase with decreasing distance to cover. We counted the number of tail flicks of individuals and measured their distance to the nearest cover for an ambushing predator. We found that distance to cover had a significant effect on tail flicking behavior, as flicking increased with decreasing distance, but found no difference in flicking frequency between adults and juveniles or between sexes. Consequently, tail flicking is unlikely to signal submission or to be sexually selected in the black redstart. Since tail flicking also occurred in the absence of predators, we consider tail flicking in black redstarts to display vigilance and to be directed towards ambushing predators.

Keywords Vigilance · Ambush predator · Signaling · Predator–prey communication

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Introduction

Many bird species of different taxa are known to pump, flick or wag their tails, which is sometimes observed in, but not restricted to, a sexual context (Fitzpatrick 1998). Other commonly proposed functions of bird tail movements are the communication of social status, vigilance and predator deterrence (Randler 2016). Attacking prey is costly for a predator in terms of time and energy lost for, e.g., mating, and the risk of getting injured irrespective of the success of an attack. Prey, in turn, face the trade-off of minimizing predation risk whilst maximizing the time for foraging, mating and parental care. Hence, both predator and prey could benefit from a signal that discourages predators from attacking in situations where the chance of a successful attack is low (Broom and Ruxton 2012).

If tail movements serve as a pursuit-deterrent signal, movements should be related to the presence of a predator and the distance between predator and prey. Moreover, the signal should affect the behavior of the predator, e.g., cause it to abandon an attack. Indeed, there are various studies showing that tail movement rates increase when a predator is present or is simulated by an experimental stimulus (Griffin et al. 2005; Murphy 2006; Randler 2007; Jones and Whittingham 2008; Carder and Ritchison 2009). Further, Woodland et al. (1980) found a relationship between tail movements and predator distance in eastern swamphen (*Porphyrio porphyrio*) as birds increased flicking with decreasing predator distance. Nevertheless, there is also unsupported evidence for the pursuit-deterrent function as individuals also flick their tails when predators are absent, which favors the hypothesis of tail movements being an individual's quality advertisement. In the latter case, tail movements should not only occur in the absence of predators, but also be related to a bird's body condition and vigilance. Alvarez et al. (2006) found a relationship between physical condition and tail flicking rate in moorhens (*Gallinula chloropus*), as individuals in better condition displayed higher rates than less healthy individuals. Other studies showed that tail movements are related to an individual's vigilance, whereby more vigilant individuals tended to flick faster than others (Ryan et al. 1996; Alvarez et al. 2006; Randler 2006).

For prey, proximity to cover might be protective, as it allows animals to escape quickly from predators; but it might also be obstructive and increase predation risk as it may allow predators to launch an ambush attack undetected by its prey (Lazarus and Symonds 1992). Therefore, distance to cover can create a gradient in predation risk and gives the opportunity to assess adjustments in anti-predator behaviors such as vigilance (Pulliam and Mills 1977).

Hence, we focused in our study on the effect of variation in distance to cover on the frequency of displayed tail movements in the black redstart (*Phoenicurus ochruros*). We conducted field observations to investigate this relationship and, more specifically, we hypothesized that redstarts show an increased number of tail flicks as the distance to cover decreases.

The black redstart frequently shows an up- and downward movement of its tail (henceforth called "tail flicking"). Males have blackish, females and juveniles grey coloration, and all individuals display a bright red tail. Moreover, redstarts forage in semi-open habitats such as meadows and gardens, and are prone to ambushing predators that are concealed in bushes and trees. Domestic cats and sparrow hawks (*Accipiter nisus*) are two of the most common predators of the black redstart. Sparrow hawks successfully prey on 11–575 black redstarts year^{-1}, depending on the area (summarized by Uttendörfer 1952). In addition, adult black redstarts, as well as their eggs and nestlings, are prone to predation by cats (Weggler and Leu 2001). Both domestic cats and sparrow hawks are common in southwest Germany and have been seen in our study area. Hence, we assumed that the black redstart experiences predation risk from these species in our study area.

Materials and methods

Behavioral observations were conducted by N. K. in the non-breeding season of redstarts (August and September 2016) in the vicinity of Böblingen, Pforzheim and Tübingen, Baden-Württemberg in southwest Germany. The observation sites were widely distributed so that every bird was observed only once (black redstarts are quite common in this part of southwest Germany). During observations, the minimum distance from the observer to an observed redstart was 10 m. Focal individuals showed no obvious signs of disturbance. To avoid the effects of group size on predator-related behavior, single individuals only were observed. Upon detection, the number of tail flicks was counted until the bird changed its spatial position or flew out of sight. Hence, observation times varied between individuals [mean observation time (s), 89.4 ± 14.7]. A tail flick was defined as an upward and downward movement of the bird's tail, and the number of tail flicks was counted by clicking with a counter each time a bird flicked its tail upwards. We also recorded the clicks with a continuously running digital voice recorder.

After each observation, the distance from the bird to the closest cover for a potential ambushing predator (i.e., the nearest tree or bush) was measured by counting steps (average length 63 cm). In the few cases where an area was not accessible, we estimated the distance in meters. Lastly, the geographic location of the study sites, time, weather, and sex and age of each individual were dictated into the voice recorder at the end of each observation. The individuals were identified as: adult male, adult female or juvenile. Because we observed focal animals in the field it was not possible to record data blind. In total, we observed 38 black redstarts: ten juveniles, 16 males and 12 females.

Analysis

First, voice recordings were used to determine the number of tail flicks, and observation time per individual bird recorded until the bird was out of sight. Second, we calculated the flicking ratio per 60 s for each bird to correct for different observation times. Finally, we performed a generalized linear model (GLM) in SAS JMP 16 using a normal distribution and an identity link to determine the relationship between flicking ratio and distance to cover. Hence, we used flicking ratio as the response variable and included distance to cover and sex and age (male, female, juvenile) as fixed factors. Further, we added weather (sunny vs. cloudy), date, time (morning = 7 a.m.–12 a.m.; afternoon = 12 a.m.–4 p.m.; evening = 4 p.m.–8 p.m.) and location as random effects in the model. All graphs were created with R (R Core Team 2016).

Results

On average, black redstarts flicked 16.3 (SD 7.72) times within 60 s and had a mean distance of 8.1 m (SD 7.38) to cover. The number of tail flicks per 60 s was significantly related to the distance to cover (GLM, $F = 5.72$, $df = 1$, $p = 0.0168$, estimate −0.423, SE 0.172) but not to sex or age (GLM, $F = 2.547$, $df = 2$, $p = 0.2799$, estimate 3.067, SE 1.905). Black redstarts showed an inverse relationship between distance to cover and tail flicking (Fig. 1)

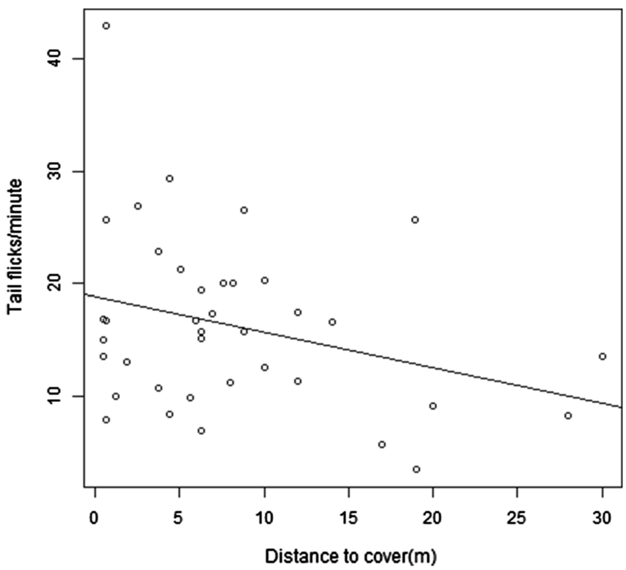

Fig. 1 Number of tail flicks per minute depending on the distance to cover. Birds showed a higher rate of tail flicks the closer they were to cover

with a higher flicking rate when nearer to obstructive cover.

Discussion

A number of studies have investigated the function and context of tail flicking in different species to test the most frequent hypothesized functions of flicking [e.g., feeding, mate choice, predator context; reviewed in Randler (2016)].

In our study, there was no significant difference between the sexes, rendering the sexual selection hypothesis unlikely. Nonetheless, the non-significant effect in our study could have been caused by the small sample sizes for each sex. Differences between the sexes may occur because males are more conspicuous than females, and thus should be more prone to predation. However, males may also show aposematism (Götmark and Unger 1994).

We found higher tail flicking in the black redstart when nearer to cover where an ambushing predator may have hidden, i.e., birds seem to be more vigilant when close to cover. If tail flicking is a display of vigilance, it should also occur if no predator is visible and be related to body condition as well as vigilance (Randler 2016). Various studies found supportive evidence for this hypothesis, as flicking is shown year-round (Randler 2006, 2007) and is related to body condition (Alvarez et al. 2006). Given the fact that we did not spot any predator during our observations, but flicking still occurred, we favor tail flicking in black redstarts as a display of vigilance and directed towards ambushing predators.

Our results add knowledge to various previous studies which investigated the relationship between vigilance and distance to cover in the context of foraging (Lima 1987; Díaz and Asensio 1991; Pöysä 1994). Beauchamp (2010) found that sandpipers (*Calidris pusilla*) were less vigilant as the distance to obstructive cover increased, and foraged farther away from cover (Beauchamp 2015). These results suggest that bird species foraging in open habitats perceive a decrease in predation risk as the distance to cover increases. Moorhens (*Gallinula chloropus*) increase tail flicking when farther away from cover (Alvarez 1993). However, the perception of cover is different in moorhens and passerines. Moorhens flee to reedbeds near the water (Lima 1993), where their predators do not usually hide, thus they may perceive cover as shelter (especially because they have the possibility to flee into water), while passerines may perceive cover as more dangerous.

Many passerine birds are known to stay close to and rush to vegetative cover when attacked (Pulliam and Mills 1977; Lima 1993), and often depend on vegetative cover to hide from predators. Sparrows, for example, are reluctant to venture from or feed away from cover (Schneider 1984; Lima 1987). However, a study by Lima (1987) showed that in three species of finches the distance to cover while feeding was strongly affected by the type of cover. Birds fed farther away from cover when it was hard to see into compared to open cover, i.e., easy to see into. These results suggest that birds adapt their behavior according to aspects of cover that might influence the risk of predation. Cover might simply hinder a bird's vision so that it has to move away from it to increase the chance of predator detection. Alternatively, cover could conceal an actual predator, thus being close to cover may increase the risk of predation. The fact that birds that passed through cover had the tendency to feed closer to it than birds that did not pass through it suggests that the avoidance of/distance to cover is a reflection of the perceived risk of predation (Lima et al. 1987).

White-crowned sparrows (*Zonotrichia leucophrys*) fed only close to, or in, cover, whereas lark buntings (*Calamospiza melanocorys*) avoided feeding in cover and even fed in its complete absence (Lima 1990). Moreover, these two species differed in their reaction to attacks by raptors: sparrows sought cover when attacked by raptors, whereas buntings, which usually use an aerial escape tactic, never did.

Black redstarts tend to flee onto rooftops or fences rather than into bushes or trees when attacked, e.g., by cats (personal observation). Consequently, redstarts seem not to rely as strongly on cover as a safe hiding place as other small bird species. Proximity to cover might instead be perceived by redstarts as a potential predation risk, as a predator could launch an attack from within the cover itself. Black redstarts often forage in semi-open areas, such as meadows, where tail flicking is most likely visible to predators even at long distances. Therefore, tail flicking has the potential to (1) signal to a predator that a bird is vigilant and/or in good condition, and consequently that an attack is likely to be unsuccessful; or (2) in a worst-case scenario, attract additional predators. If flicking increases the likelihood of being detected by a predator, birds should minimize tail flicking, especially when in open habitat. This could also explain our results, where birds flicked their tails less the farther they were from cover. In this way, birds could minimize the risk of attracting predators. In addition, if flicking is directed towards ambushing predators, as hypothesized by us, a redstart should rather flick its tail when close to cover than when in the open.

Another proposed function of tail flicking is the display of submission, thus less dominant or subordinate individuals should display a higher flicking rate than dominant individuals (Craig 1982). In our study, as we focused only on individual black redstarts, flicking as a signal of submission also seems unlikely in this species. As we focused on single individuals, we did not assess the function of group size, which is known to affect vigilance (Barnard 1980; Elgar et al. 1984). Hence, further studies are needed to test if tail flicking in black redstarts changes in the presence of conspecifics.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical note This study complies with all the relevant laws of Germany.

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