Received: 25 October 2018 | Revised: 20 February 2019 | Accepted: 11 March 2019

DOI: 10.1111/eth.12867

RESEARCH PAPER

WILEY ethology

Flight initiation distance and escape behavior in the black redstart (*Phoenicurus ochruros*)

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Funding information
Gips-Schüle Stiftung

Editor: L. Fusani

Abstract

There are many anti-predatory escape strategies in animals. A well-established method to assess escape behavior is the flight initiation distance (FID), which is the distance between prey and predator at which an animal flees. Previous studies in various species throughout the animal kingdom have shown that group size, urbanization, and distance to refuge and body mass affect FID. In most species, FID increases if body mass, group size or distance to refuge decreases. However, how age and sexual dimorphism affect FID is rather unknown. Here, we assess the escape behavior and FID of the black redstart (*Phoenicurus ochruros*), a small turdid passerine. When approached by a human, males initiated flights later, that is allowing a closer approach than females. Males of this species are more conspicuous, and therefore, may exhibit aposematism to deter potential predators or are less fearful than females. Additionally, juveniles fled at shorter distances and fled to lower heights than adults. Lastly, concerning escape strategy, black redstarts, unless other passerine birds, fled less often into cover, but rather onto open or elevated spots. Black redstarts are especially prone to predation by ambushing predators that might hide in cover. Hence, this species most likely has a higher chance of escaping by fleeing to an open spot rather than to a potentially risky cover.

KEYWORDS
age, antipredator behavior, black redstart, dichromatism, escape strategies, flight initiation distance

1 | INTRODUCTION

According to life-history theory, reproductive success is greatly affected by anti-predator behavior (Caro, 2005). Therefore, animals need to adapt and optimize their behavior to current situations to maximize (future) reproductive success. Besides environmental factors, predation is a major cause of animal mortality. Consequently, effective self-defense against predators can greatly affect survival and future reproduction. There are three key elements of self-defense (a) avoiding detection which typically involves hiding and camouflage strategies (b) evading capture by applying an appropriate escape strategy and (c) predator deterrence. While hiding and camouflage rather rely on visual cues such as shape and color, the other two defense mechanisms are based on an animal's immediate behavior. When a predator approaches, prey faces the decision whether to flee or not (Bonnot et al., 2017). Fleeing thereby can hold the cost of interrupting feeding or social interactions as well as the direct energetic costs of fleeing, but a successful escape might increase the future reproductive success. Remaining at a given place to avoid the costs of fleeing on the other hand holds the cost of an increasing predation risk. According to Ydenberg and Dill (1986) prey should flee when the cost of fleeing equals the cost of remaining, whereby the cost and benefits of escaping can vary temporally and spatially (Kotler, Brown, & Bouskila, 2004; Lima & Bednekoff, 1999; Mikula et al., 2018; Winnie & Creel, 2007). In animals, there is a great variety of anti-predatory escape strategies (Lima & Dill, 1990; Stankowich

TABLE 1 Hypotheses tested in the current study and outcome variables

Hypothesis	Reference	Outcome variable
Conspicuousness-hypothesis: Usually males are more colorful and more conspicuous and flee earlier. We expect males to have larger DF and EH	Thiel et al., (2007), Lailvaux et al., (2003)	FID, EH, DF
Experience-hypothesis: We expect differences between juveniles and older individuals due to different experience with predators	Smith et al., (1984), Whiting et al., (2003)	FID, EH, DF
Flock-size hypothesis: We expect birds in flocks to have a higher FID than single birds or birds in smaller flocks	Stankowich & Blumstein, (2005)	FID, DF
Urbanization hypothesis: Differences in FID are expected along an urban gradient, thus the nearer the birds to the city center, the lower the FID	Battle et al., (2016)	FID, DF
Fearfulness hypothesis: Escape height reflects fearfulness and is correlated with FID; Birds higher above the ground flee later	Björvik et al., (2015)	FID with EH FID with SH
Safe place hypothesis: Distance to a refuge (nearest cover): Short distance to a potential refuge should decrease the risk of predation and, therefore, decrease FID	Stankowich & Blumstein, (2005) Tätte et al., (2018)	FID
Escape strategy: Black redstarts may flee onto rooftops or in open areas, rather than within the center of a bush	Kalb & Randler, (2017)	Escape into cover vs. open
Technical aspects		
No relationship between FID and DF in lighter species	Tätte et al., (2018)	FID with DF
Positive correlation between SD and FID	Tätte et al., (2018), Blumstein, (2003)	SD with FID

Note. FID: Flight initiation distance, the distance at which an individual flees; DF: Distance fled from the flushing point to the landing point; EH: escape height, to which height an individual fled. SD: starting distance; the distance from which the approach began. SH: starting height, the height at which the bird initially perched.

& Blumstein, 2005). The optimal strategy for a species can be influenced by various factors such as the predator itself (species, sex, size,), the distance between prey and predator, the relative speed of prey and predator, the perceived predation risk by the prey as well as the internal state of the prey (e.g., fuel load, muscle size, condition, etc.; Hedenström & Rosén, 2001).

To assess different escape strategies and fearfulness responses as an individual difference trait within, as well as comparatively between species it is common to measure the flight initiation distance (FID), that is the distance at which an individual flees in case of an approaching predator. FID is known to be affected by numerous factors including flock size, urbanization, distance to refuge and body mass (Stankowich & Blumstein, 2005; Tätte, Møller, & Mänd, 2018).

In this study, we investigated if and how flock size, distance to suburban fringe and distance to cover affect the escape behavior of the black redstart (*Phoenicurus ochruros*). These factors are known to influence the flight initiation distance in other bird species. Further, we tested four hypotheses regarding the experience (predicted by age), sexual dimorphism, fearfulness and the general escape strategy (Table 1) of our study species. In this species, males have a conspicuous blackish body coloration, whereas females and juveniles show a grey coloration. The black redstart usually breeds in urban and rural habitats and forages in semi-open habitats (Bairlein, 1983; Gedge, 2003). In the following paragraphs, we describe each of our tested hypothesis briefly and explain how it could apply to our study species.

Animals in larger groups usually flee at a greater distance (Stankowich & Blumstein, 2005; flock-size hypothesis) because large flocks may be able to detect an approaching predator earlier (Boland, 2003) and hence take flight earlier. Some species on the other hand are more tolerant of approaching threats when in a large group because animals may feel safer in groups ("dilution effect," Cresswell, 1994), which can lead to a decreased FID. As the black redstart does not live in permanent flocks, we expect our findings to be in line with Stankowich and Blumstein (2005); that is, birds in flocks have a higher FID than single birds or birds in smaller flocks.

In general, individuals may feel saver when nearer to a refuge, which results in a lower FID (Stankowich & Blumstein, 2005; safe place hypothesis). Concerning the escape strategy of the black redstart, there might be some differences to other passerines (Kalb & Randler, 2017): Many small passerines flee into cover to hide from predators (Lima, 1993; Pulliam & Mills, 1977). Nonetheless, where birds seek cover seems to depend on their escape tactic. Lima (1990) for example showed that White-crowned sparrows (*Zonotrichia leucophrys*) sought cover in response to a raptor attack whereas lark buntings (*Calamospiza melanocorys*), which usually opt an aerial escape tactic, did not. Black redstarts living close to human settlements are especially prone to ambushing predators such as cats (Hölzinger, 2018; Weggler & Leu, 2001). Therefore, we assume that black redstarts in areas with a high abundance of terrestrial predators flee to elevated spots or into open areas rather than within the center of vegetation (Kalb & Randler, 2017).

Further, urbanization is known to affect the flight behavior of many animals and it is generally hypothesized, that animals in urban habitats have lower flight initiation distances than animals in rural habitats. This may be due to a higher habituation to human presence or ecological trade-offs due to habitat quality, such as food availability or habitat obstruction that might hamper predator detection and hence decrease FID (Battle, Foltz, & Moore, 2016, Bjørvik, Dale, Hermansen, Munishi, & Moe, 2015, Bonnot et al., 2017, Randler, 2008a, Randler 2008b; Tätte et al., 2018, urbanization hypothesis). In our study area, the black redstart often breeds close to human settlements and hence is accustomed to human presence. Therefore, we expect differences in FID along an urban gradient with birds nearer to the city center having the lower flight initiation distances.

Due to sexual dimorphism or plumage dichromatism, there are two contradictory hypotheses with respect to conspicuousness and flight behaviour (conspicuousness-hypothesis) (Møller, Samia, Weston, Guay, & Blumstein, 2016). First, one would assume that more conspicuous individuals within a species are more prone to predation because they can be earlier detected by predators (Slagsvold, Dale, & Kruszewicz, 1995). Second, conspicuous prey may also be considered as aposematic and this would mean that conspicuous individuals are attacked less frequently (Götmark, 1992). In line with the first prediction, more cryptic species have been found to flush at shorter FIDs, for example, in frogs (Blanchette, Becza, & Saporito, 2017; Ozel & Stynoski, 2011). In common flat lizards (*Platysaurus intermedius wilhelmi*), a sexual dichromatic species, more conspicuous males take refuge earlier and have higher FID than females (Lailvaux, Alexander, & Whiting, 2003). In birds plumage vividness was no predictor of FID after controlling for body size (Hensley, Drury, Garland, & Blumstein, 2015). Hensley et al., (2015), however, did not account for differences between sexes, as in species with sexual dimorphism only males were included in the analysis. In capercailles (*Tetrao urogallus*) males are ornamented and larger than females and show higher FIDs (Thiel, Ménoni, Brenot, & Jenni, 2007). In the black redstart males are more conspicuous than females and juveniles. Hence, we expect a difference in flight behavior between the sexes.

Experience with predators changes with age (Smith, Arcese, & McLean, 1984; experience-hypothesis). Hence, one would expect that younger, more unexperienced, individuals flee later than experienced adult individuals. Common flat lizard juveniles have a shorter FID and flee further than adults, which might be related to juveniles having more predators than adults (Whiting, Lailvaux, Reaney, & Wymann, 2003). In birds, it is known that juveniles are often more confined than older ones and younger individuals differ from adults in their anti-predator behavior (Smith et al., 1984). Nonetheless, Stankowich and Blumstein (2005) found no consistent age effects in FID, indicating that this relationship might be species-specific. In the black redstart it is known that more juveniles than adults are victims to cat predation in rural habitats (Hölzinger, 2018). Hence, we expect a difference in flight behavior between adults and juveniles. More specifically, we expected that juvenile black redstarts have a lower FID and shorter maximum distance fled than adult individuals.

Flight initiation distance may also reflect some kind of fearfulness or perceived danger (fearfulness-hypothesis). Consequently, being in an already safe place should reduce FID. Birds perching higher above the ground may perceive an approaching terrestrial predator as less dangerous, and therefore, may flee at lower distances. However, this behavior might also be a species-specific factor as Bjørvik et al., (2015) found perch height to be unrelated to FID. This could be related to the predator species or, more specifically, the hunting strategy of a given predator. For species that are prone to ambushing (terrestrial) predators, such as the black redstart, sitting on higher perches might hold the benefit of an earlier detection of predators that hide in bushes, and therefore, lower the predation risk leading to a decreased flight initiation distance. Species, however, that are more prone to aerial predators might prefer and benefit from starting points closer to the ground. When fearfulness is some kind of an individual difference trait, one could also assume that FID should be correlated with escape height, namely that birds that are more fearful should flee earlier and flee to a higher escape height, as well as to a farther distance. The starting distance at which the approach of predator begins is also known to affect flight behavior as it affects the perceived predation risk (Blumstein, 2003).

Tätte et al., (2018) found distance fled; that is, the actual distance fled from the starting point to the next resting point, to be an important factor that needs to be considered when studying escape behavior of animals. They reported a positive relationship between FID and distance fled for heavier birds but not for lighter species, indicating that the cost of escaping might differ according to body mass due to different energetic costs during fleeing. Because these authors worked on different species with different size/body mass and our study was related to only one species, we considered the hypothesis which Tätte et al., (2018) explicated for a lighter species as the black redstart can be grouped to the lighter species in the framework of Tätte's study.

Lastly, escape behavior may differ between species and/or situations. For example, many bird species flee into cover, despite the fact that cover can be perceived as dangerous or as safe (see Lazarus & Symonds, 1992). In previous work, however, we found that black redstarts may perceive cover as dangerous because their tail flick rate increased with decreasing distance to cover. Other personal observations suggest that black redstarts flee from approaching predators (namely cats) by fleeing to a higher safe place. Also, black redstarts increase their tail flicking in the presence of terrestrial predators. Interestingly, there is no study about the behavior, for example, in fledglings, when predators approach, where freezing might be an adequate behavior (as in other small turdids dwelling in open habitat; Randler, 2013).

2 | METHODS

2.1 | Study area

The study was carried out within the vicinity of Freudenstadt, Baden-Württemberg, SW Germany (Coordinates: 48°28′N, 8°25′O). This is a rural area in the northern Black Forest with many orchard meadows and allotment gardens. The data were collected in different villages in an altitude of 550–800 m. Experiments were carried out during the post-fledging season of the black redstart from 23.6.2017 until 23.8.2017 (on a total of 11 days). Sampling took place from 7:05 until 18:03, but most data were collected throughout the mornings until noon (82%). Every location within the study area was visited only once to avoid pseudo-replication (mean distance (m) between locations ±*SD*: 307 ± 184 m).

2.2 | Sex and age determination

All observations were conducted by a single observer (FA) wearing similar clothing throughout the study period to reduce any effects caused by the observer's appearance.

After detection of a black redstart, the age and sex of each bird was determined using binoculars (Zeiss Conquest 10x42; Carl Zeiss, Wetzlar & Jena, Germany), using the classification given by Nicolai, Schmidt, and Schmidt (1996). For age, we classified the birds in two categories: adult and juveniles, that is, birds in their adult or juvenile plumage. In terms of sex, we classified males (blackish coloration) and females and female-colored (greyish coloration). In our study species young males often have the same greyish plumage coloration as females (cairei plumage). Hence in young individuals it is often not possible to determine the sex of an individual. We also noted the biologically relevant group size (according to Blumstein, Samia, Stankowich, & Cooper, 2015) within the birds that were in visual contact.

2.3 | Human approach

Human approach is a common procedure when studying the escape response of animals as it is comparable to predation risk (Frid & Dill, 2002) and, therefore, offers an easy and reliable method to investigate an individual's reaction to perceived predation risk (Tarlow & Blumstein, 2007; Tätte et al., 2018). The general approach procedure in our study followed the guidelines of Blumstein et al., (2015). Birds were always approached directly by foot and at the same speed, given the well-known influence of predator speed and approach (Stankowich & Blumstein, 2005). The approach was terminated after a birds started to show a flight response.

2.4 | Behavioral parameters

We measured the flight initiation distance, that is, the distance between the observer and the bird when it started to flee. All distances and heights from 10 m onwards have been measured with a Leica Rangemaster 1000-R (Leica, Wetzlar, Germany). Shorter distances were measured by triangulation between two Rangemaster measures or by pace length (five measures of 10 pace lengths measured and averaged: 0.836 m/ pace). Further, we collected data on starting distance for all approaches, that is the distance from which the approach began (Blumstein et al., 2015), and the starting height of the bird above the ground. In cases where birds started from the ground the value zero was assigned. Additionally, we classified the escape strategy as (a) redstarts fled into bushes/trees (to hide in cover) or (b) fled to the outer parts of cover or higher areas, such as rooftops or fences. Distance to a safe place was measured similarly as noted above. We considered bush cover as well as a rooftop as a safe place, because our procedure mimics a terrestrial predator.

2.5 | Urbanization

We measured the distance to suburban fringe as a proxy of urbanization. As we worked in more or less rural habitats (locations in and close to villages with 150–14,900 inhabitants mean ±*SD*, 3,915 ± 5,789), we did not dichotomize into urban and rural but used this continuous measure. This measure is a more reliable assessment of the position of the redstart (outside or inside the villages) and the distance to the closest settlement. Positive values indicate an area outside the settlements, and negative values indicate within settlements.

3 | STATISTICAL ANALYSES

We used SPSS 24.0 (IBM Corp. Released 2016. IBM SPSS Statistics for Windows, Version 24.0. Armonk, NY: IBM Corp) for all analyses. All parametric variables were $\log_{10}$ transformed after the addition of one to achieve a normal distribution.

First, Pearson's correlations were used to test for significant relationships between the (dependent) outcome variables FID, distance fled and escape height. Since these three variables where not correlated with each other (see results) they can be classified as independent which justifies the use of different models to test relationships between the independent and the outcome variables. Second, we used three linear regression models to assess the influence of the independent variables distance to suburban fringe, distance to safe place, flock size, starting height and starting distance simultaneously. As data were incomplete for sex and age, age and sex differences were compared by *t* tests. In this case, means and standard deviations are given. We performed two linear regressions to assess the effect of sex and age on FID while controlling for starting distance as a covariate of FID. For the escape strategy, we conducted a two-way ANOVAs to test for an interaction between age and flock size. We further used an ANOVA for the conspicuousness hypothesis to analyze a possible interaction between sex and flock size. Lastly, the results concerning the escape strategy (open vs. cover) were analyzed with a chi-squared test.

4 | ETHICAL NOTE

This study included no animal keeping, we observed birds in their natural habitat. All observations were in accordance to relevant laws in Germany and guidelines and regulations for nature conservancy.

5 | RESULTS

5.1 | Descriptive statistics

In total, we observed 125 black redstarts (25 adult males, 23 adult females, 2 immature males, 27 female-colored individuals and 48 juveniles). The age and sex of the 27 female-colored individuals could

TABLE 2 Overview of the subsamples used during statistical analysis

Hypothesis	*n*	Description
Flock size	125	All individuals, irrespective of sex or age
Safe place	125	All individuals, irrespective of sex or age
Urbanization	125	All individuals, irrespective of sex or age
Conspicuous	77	Males (n = 27), Females (n = 23) and female-colored (n = 27)
Experience	98	Adults (n = 48), immature (n = 2), juveniles (n = 48)
Fearfulness	125	All individuals, irrespective of sex or age
Escape strategy	125	All individuals, irrespective of sex or age

not be classified. To test some hypotheses, we created subsamples (see Table 2 for an overview). For example, female and female-colored birds were grouped together to test the conspicuousness-hypothesis (N = 50). However, the age and sex of the 27 female-colored individuals could not be classified, hence those individuals had to be excluded from the analysis of the experience hypothesis. Here, adults and immature birds were combined because they both were at least 1 year old and therefore, more experienced birds.

Table 3 shows the mean and the *SD* of the variables used in this study. Detailed results of all conducted regression models (to assess variables simultaneously) are depicted in Table 4.

5.1.1 | Flock-size hypothesis

We found no significant relationship between flight initiation distance and flock size (p = 0.773). However, distance fled was significantly related to flock size (p = 0.011), with individuals in larger flocks fleeing shorter distances.

5.1.2 | Safe place hypothesis

Distance to safe place was not related to the flight initiation distance of birds (p = 0.239). Distance fled was related to distance to safe place (p = 0.008). When a safe place was closer, the distance fled was also smaller.

5.1.3 | Urbanization hypothesis

We found no significant relationship between flight initiation distance and distance to suburban fringe (p = 0.486). Further, distance to suburban fringe was not related to distance fled (p = 0.957) or escape height (p = 0.827).

5.1.4 | Conspicuousness hypothesis

We found sex differences in starting distance and FID. Males were approached at shorter starting distances (22.26 ± 6.60) than females (29.02 ± 14.34; T = −2.127, df = 75, p = 0.037; calculations are based on transformed data). There was a significant effect of sex on the flight initiation distance (F = 9.091, df = 1, p = 0.0035). Thereby, FID was lower in males (11.09 ± 5.03) compared to females (17.27 ± 10.89). FID was unaffected by flock size (F = 0.384, df = 1, p = 0.537). We also did not find a significant interaction between sex and flock size (F = 2.241, df = 1, p = 0.139). For escape height, we found no significant difference between males (2.77 ± 2.38) and females (1.99 ± 1.72, T = 1.769, df = 75, p = 0.081, based on transformed data).

5.1.5 | Experience hypothesis

Age differences were significant in both, starting distance and FID. We started approaching juveniles at shorter distances (21.68 ± 9.02) compared to older individuals (26.42 ± 12.27; T = 2.271, df = 96, p = 0.025, based on transformed data). Also, FID was lower in juveniles (9.94 ± 5.078) compared to older individuals (14.38 ± 8.91, T = 2.962, df = 96, p = 0.004; based on transformed data). Lastly, juveniles tended to have a lower escape height (1.78 ± 1.52) than adults (2.34 ± 2.07, T = 1.85, df = 96, p = 0.067, based on transformed data). When controlling for starting distance as covariate of FID, the results remained marginally significant (Table 5), thus confirming the previous analyses.

5.1.6 | Fearfulness hypothesis

FID showed no significant relationship with starting height (p = 0.46), but escape height was related to starting height (p = 0.016).

TABLE 3 Descriptive statistics of the sampled variables

	N	Minimum	Maximum	Mean	*SD*
Flock size	125	1	5	1.99	1.07
Start height above ground (m)	125	0.00	3.00	0.67	0.77
Distance to a safe place (m)	125	0.84	44.00	9.23	9.05
Starting distance (m)	125	9.20	70.00	24.74	11.56
Flight initiation distance (m)	125	1.67	55.00	13.12	8.59
Escape height (m)	125	0.00	10.00	2.07	1.84
Distance fled (m)	125	0.50	50.00	10.56	8.17
Distance suburban fringe (m)	125	−225.00	750.00	59.58	178.89

Note:. suburban fringe was coded 0, negative values indicate nearer to the city center, positive values refer to outside the city.

TABLE 4 Regression models for flight initiation distance (FID), distance fled and escape height as dependent variables

Model Statistics	Flight initiation distance R^2corrected = 0.407, F = 18.037, df = 5,119, p = 0.001		Distance fled R^2corrected = 0.101, F = 3.772, df = 5,119, p = 0.002		Escape height R^2corrected = 0.022, F = 1.564, df = 5,119, p = 0.176	
	β	p	β	p	β	p
Constant	–	0.336	–	0.001	–	0.028
Distance to suburban fringe (m)	−0.054	0.486	−0.005	0.957	−0.022	0.827
Distance to a safe place (m)	0.084	0.239	0.235	**0.008**	−0.12	0.189
Flock size	−0.022	0.773	−0.24	**0.011**	−0.001	0.989
Starting height	0.054	0.46	0.046	0.609	0.23	**0.016**
Starting distance	0.658	**<0.001**	−0.067	0.47	0	0.997

Note. Significant independent variables are depicted in bold.

TABLE 5 Regression models for sex and age effects, controlling for starting distance

Model Statistic	FID (model with sex) R^2corrected=0.615, F = 61.739, df = 2,74, p = 0.001		FID (model with age) R^2corrected=0.362, F = 28.572, df = 2,95, p = 0.001	
	β	p	β	p
Constant	–	0.007	–	0.272
Starting distance (lg)	0.745	0.001	0.555	0.001
Sex/Age	0.141	0.058	−0.164	0.051

5.1.7 | Technical aspects

There was a significant relationship between FID and starting distance (p = 0.001). Also we found no relationship between the dependent outcome variables; FID and escape height: r = −0.064; FID and distance fled: r = 0.068, escape height and distance fled: r = 0.076.

5.1.8 | Escape strategy

Most redstarts fled to a safe place, but they did not hide in it but rather sat outside, on top of a bush, tree or anthropogenic structures, such as buildings or fences (109 open, 19 hidden; p < 0.001 binomial test). There were no sex differences (χ^2 = 1.460, df = 1, p = 0.411). The results of the one way-ANOVA revealed a significant effect of age on the escape strategy (F = 4.305, df = 1, p = 0.041). Juveniles were hiding more often in deep cover compared to adults who preferred visible flight posts (χ^2 = 5.181, df = 1, p = 0.029). We found no significant effect of flock size on escape strategy (F = 2.85, df = 1, p = 0.095) nor a significant interaction between age and flock size (F = 0.02, df = 1, p = 0.888).

6 | DISCUSSION

In this study, we investigated the relationship between flock size, distance to suburban fringe and distance to safe place and the flight initiation distance of the black redstart. Further, we tested if and how experience (predicted by age), sexual dimorphism and fearfulness influence the escape behavior of our study species. Lastly, we collected data on the general escape strategy of the black redstart.

Flock size was not related to flight initiation distance. However, we found distance fled to be related to flock size as birds in larger flocks fled shorter distances than single individuals or individuals in small flocks. This is in contrast to our expectations but in line with findings by Cresswell (1994). Birds in larger flocks might feel safer, as the individual predation risk decreases with increasing flock size.

The flight initiation distance was not related to distance to safe place (i.e., rooftops, fences, etc.). This is in contrast to our expectations as we expected a decreasing FID when individuals are closer to a safe place. Nonetheless, distance fled was related to distance to safe place as birds fled shorter distances when closer to a safe place.

We also found no relationship between distance to suburban fringe as a measure of urbanization and FID (urbanization hypothesis). This is in contrast to findings by Battle et al., (2016) where birds in urban habitats had shorter FID. However, this may be owed to the fact that we worked in a generally rural habitat, so that the differences within and outside of a settlement may not be as striking as in a comparison of a large city with rural habitats (Randler, 2008a; Randler 2008b).

Concerning the conspicuousness hypothesis, we found differences between males and females, with males initiating flights later, that is, allowing a closer approach. Further, we found no difference in escape height, but a trend (p = 0.081), whereby males tended to have higher escape heights than females. Our results are in contradiction to a study on capercailles (*Tetrao urogallus*), where males are ornamented and substantially larger than females. Here, males showed higher FIDs (Thiel et al., 2007). However, this is not counterintuitive, because the sexual dimorphism in capercaillies is both, in weight/size and plumage, whereas there is only a substantial difference in plumage in the black redstart. Also, female capercaillies are among the most cryptic species, and cryptic species take flight at the latest moment (Gabrielsen, Blix, & Ursin, 1985). Lastly, our contradicting results could be explained by the fact that capercailles are terrestrial whereas redstarts are not.

Studies on mobbing behavior, a behavior, where prey species, especially passerines, approach a predator, showed that males approached the predator closer than females, especially in the presence of a female (Curio, Klump, & Regelmann, 1983). Hence, in our study, males might flee later from a low-risk predator (i.e., approaching human) to signal male quality to conspecifics. However, we did not find a significant interaction between flock size and sex, indicating that this was not the case in our study. Nonetheless, we cannot exclude that the advertisement of phenotypic quality might play a role concerning FID, as flock size does not account for how many females or males where present in the flock. Future studies are therefore necessary to investigate if the presence of females in a flock might affect the FID of males.

With respect to the experience hypothesis, our study showed that juveniles fled at shorter distances and had lower escape heights. Assuming that adult birds had survived predation at least for 1 year, and that mortality during the first year is relatively high in songbirds, we propose that the shorter FID and lower escape heights in juveniles is maladaptive and that birds with such lower flight distances may be more prone to predation. Indeed, a study by Kullberg and Lind (2002) showed that great tit (*Parus major*) fledglings do not differentiate in their behavior between a model of a perched predator and a model of a non-predator. Therefore, we assume that the human approach in our study indeed elicits a similar response in young black redstarts as the approach of a terrestrial predator would.

We hypothesized that escape height reflects fearfulness and therefore is correlated with FID. We found starting height and escape height to be unrelated with FID. This is in line with findings by Bjørvik et al., (2015) who found perch height to be unrelated to FID. Therefore, in our study species escape height does not seem to be a measure of fearfulness as suggested by Uchida, Suzuki, Shimamoto, Yanagawa, and Koizumi (2017). This might be the case because we studied a bird, while Uchida et al., (2017) focused on squirrels. Furthermore, FID showed no significant relationship with starting height. Therefore, starting perch height might not be related to fearfulness but rather to predator detection and vigilance. Krams (2001) showed that chaffinches (*Fringilla coelebs*) usually sit and sing in more open habitats where they are prone to predators but also can improve anti-predatory vigilance as predator detection is not obstructed by vegetation. This might be also the case in the black redstart. Lastly, there is the possibility that reaction to a human approach like in our study might rather reflect boldness than fear, especially in rural habitats, where birds are accustomed to human activity.

The escape strategy of black redstarts in our study met our assumptions as birds escaped more frequently to open structures such as rooftops or fences rather than into cover. In addition, starting height and escape height were significantly positively related, suggesting that disturbed birds or birds under the risk of predation flee to a higher place, rather than remaining on the same height level or flee to a lower one. This is in line with previous work on black redstarts, suggesting that cover may be perceived as dangerous because an ambushing predator may hide in it (Kalb & Randler, 2017). However, juveniles fled more often into cover (bushes, trees) than adults, which might be related to juveniles being generally more unexperienced in a predation context. We further found no significant interaction between age and flock size, that is, the escape strategy of juveniles was most likely unaffected of whether it was accompanied by older, more experienced birds or not. In general, the escape strategy of black redstart in our study area is contradictory to the escape behavior of most other small passerines that usually flee into cover (Lazarus & Symonds, 1992). This might be explained by a difference in predation pressure, that is, in rural habitats small passerines, such as great tits and blue tits, are more prone to predation by avian predators (Galeotti, Morimando, & Violani, 1991; Zawadzka & Zawadzki, 2001), whereas black redstarts are more prone to terrestrial predators including cats (Hölzinger, 2018). Therefore, an interesting aspect would be to study how redstarts react in response to a flying avian predator, such as sparrowhawks (*Accipiter nisus*). In this case, it should be better to flee into vegetation (bush), but this has yet to be tested. Moreover, one might compare the escape strategy of black redstarts of areas with changing abundance of aerial and terrestrial predators. Here, one might observe that redstarts adapt their escape strategy to the most abundant predator type (i.e., terrestrial or aerial).

Starting distance had a significant and large effect on FID, which is known from many studies (Blumstein, 2003; Stankowich & Blumstein, 2005). The relationship was strong, which may be owed to the fact that we did the study in more rural habitats. Starting height and FID seem weakly related or even unrelated in urban habitats because birds have to adjust their behavior (e.g., vigilance and feeding time) to the “noisy” urban habitat (Tätte et al., 2018). In addition, starting distance was unrelated to distance fled. Our study species is small and light (with an average weight of about roughly 20 g; Bezzel, 1993), thus, we expected the results similarly to Tätte et al., (2018) study, who reported that lighter and smaller species show no correlation in this respect.

Concerning the measured outcome variables, starting distance, distance fled and escape height, we found a high explained variance in the FID statistics (40%), rendering this variable a more important one compared to both others. Least explained variance was achieved with escape height (2%), suggesting that when time is constraint, FID is the most important variable to measure, followed by distance fled (10%).

In our study, we chose the black redstart because usually, one can separate adult plumage into the two sexes, and, most juveniles are identifiable as juveniles. Thus, this species is good to test our predictions. However, some individuals could not be reliably identified and had to be omitted from the specific analyses. In the best case, future work should focus on sexually dichromatic species where juveniles are also easily distinguished from females. At best, sexual dichromatism should also be visible already in the juvenile phase to apply a 2 × 2 analysis. Alert distances could not be measured because the black redstart is a continuous visual forager, that is, the bird does only shortly lower its head when picking at prey (invertebrates) and then takes up an upright position where it is continuously vigilant (see Barbosa, 1995 for a discussion about head-up positions, vigilance and foraging strategies).

As we found males to flee later than females, we propose future studies to focus more on possible sex differences in flight behavior. Especially in species with sexual dimorphism, researches should focus also on the possibility that sex differences might not only be explained by a difference in conspicuousness, but also by sexual selection, for example, bolder males, which is an important personality aspect. This could be, for example, investigated by comparing the FID of males with the number of matings and/or breeding success. If males flee later in risky situations to advertise male quality, males with lower FID should have a higher reproductive success.

ACKNOWLEDGEMENTS

This study was supported by the Gips-Schüle Stiftung. The funder had no influence on the study and on the results. We further thank two anonymous reviewers for their helpful suggestions regarding this manuscript.

CONFLICT OF INTEREST

All authors report no conflict of interest.

AUTHOR CONTRIBUTIONS

CR, NK & FA designed the study, FA collected the data, CR made the statistical analyses, CR, NK and FA discussed the results, and all authors contributed to the writing of this paper.

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How to cite this article: Kalb N, Anger F, Randler C. Flight initiation distance and escape behavior in the black redstart (*Phoenicurus ochruros*). *Ethology*. 2019;00:1–9. https://doi.org/10.1111/eth.12867