



# Corvids exhibit dynamic risk assessment during escape

Kunter Tätte, Anders Pape Møller, Raivo Mänd

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### Abstract

It is widely accepted that stationary prey are able to carefully assess the risk levels associated with an approaching predator to make informative decisions on when to escape. However, little is known about subsequent decision-making process. We set out to compare whether escape durations of three species of corvids differ depending on how a human observer (in the role of a predator) behaves after the escape has begun. When birds were being followed during escape, escape durations were the longest, escape trajectory was modified the most during escape, and a larger proportion of individuals changed from terrestrial to aerial escape strategy compared to observations where birds were not followed. Mean horizontal escape angle of ca 120° was also a potential indication that monitoring the threat is taken into account when deciding on the escape trajectory. While there were some differences between the behaviour of these three closely related species, the general patterns supported the notion that birds dynamically assess risk during escape to find an optimal balance between getting caught and spending too much time and energy on escaping. Further research using different predator-prey combinations or making comparisons between habitats could help understand the generality of our results.

<b>Keywords</b>	antipredator behaviour; birds; Corvidae; escape behaviour; escape duration; risk assessment
<b>Corresponding Author</b>	Kunter Tätte
<b>Corresponding Author's Institution</b>	University of Tartu
<b>Order of Authors</b>	Kunter Tätte, Anders Moller, Raivo Mänd
<b>Suggested reviewers</b>	Nadine Kalb, Kenta Uchida, Yves Bötsch, Jose Nunes

## Submission Files Included in this PDF

### File Name [File Type]

Cover letter - with title page\_26.11.2019.docx [Cover Letter]

Response to Reviewers 26.11.2019.docx [Response to Reviewers]

HIGHLIGHTS 25.11.2019 -clean.docx [Highlights]

DRA Abstract 15.10.2019.docx [Abstract]

DRA Manuscript 25.11.2019\_CLEAN.docx [Manuscript File]

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Author statement.docx [Author Statement]

## Submission Files Not Included in this PDF

### File Name [File Type]

Electronic Supplementary Table S1.xlsx [Table]

Electronic Supplementary Table S2.xlsx [Table]

Electronic Supplementary Table S3.xlsx [Table]

Electronic Supplementary Table S4.xlsx [Table]

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**Cover letter**

Kunter Tätte  
University of Tartu  
Vanemuise 46, EE-51014 Tartu, Estonia  
Tel: +372 5665 1177  
kunter.tatte@gmail.com

November 26, 2019

Dear Prof. Bolhuis,

We have now addressed all the minor comments by Reviewer 2. In addition, we did some small updates to Fig. A2 and its legend to improve readability.

I have also added the title page of the manuscript to the second page of this cover letter.

Yours sincerely,

Kunter Tätte

## **Corvids exhibit dynamic risk assessment during escape**

Kunter Tätte<sup>1\*</sup>, Anders Pape Møller<sup>2</sup>, Raivo Mänd<sup>1</sup>

<sup>1</sup> University of Tartu, Institute of Ecology and Earth Sciences, Department of Zoology, Estonia

<sup>2</sup> Ecologie Systématique Evolution, Université Paris-Sud, CNRS, AgroParisTech, Université Saclay, France; Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, College of Life Sciences, Beijing Normal University, Beijing 100875, China

**Abbreviated title:** Risk assessment during escape

**Declarations of interest:** none.

### **\*Correspondence:**

Kunter Tätte

e-mail: kunter.tatte@gmail.com

Tel.: +372 5665 1177

Addr.: Vanemuise 46, EE-51014 Tartu, Estonia

## **-Reviewer 2**

-

The authors have done an excellent job addressing the comments on their initial submission. The statistical approach is greatly improved and my other main concerns are satisfied.

**Response:** Thank you!

A few minor comments:

**-Highlights:** Please add a first point with some idea of the hypothesis tested. The conclusion here could also benefit from some mention of why that is relevant.

**Response:** Great suggestion! Added: “This study examined whether birds adjust escape plans while fleeing”.

**L44:** I agree that FID tests are “immensely popular”, but I’m not sure about that particular description here – “commonly used”, perhaps?

**Response:** Changed to “commonly used”.

**L60-61:** Escape duration should be the time elapsed between flight initiation and return to the original position (or, perhaps, resuming pre-stim activities). Flight time would be the variable related to distance fled. This distinction seems to be present in the Methods & Results.

**Response:** We must politely disagree on this suggestion. While “flight time” has indeed been used in Collop et al. (2016) and Holmern et al. (2016, Behav. Ecol.) to describe antipredator escape responses, it is commonly used to describe any aerial movement in birds, bats, and flying insects (as shown by searches on ISI Web of Knowledge). “Escape duration”, however, should clearly indicate that this is the time elapsed during fleeing and that it can include terrestrial escapes as well. For example, a reviewer in another journal once asked us to change the phrase “takes flight” because he/she thought that it was a term related only to aerial escapes. We are not aware of studies that use “escape duration” as a measure of escape that includes the time it takes for the animal to return to the original position, as you suggested. Returning to the original location is usually not considered a part of the predatory sequence (e.g. Endler 1991).

**L61:** Sentence fragment – can delete or incorporate into previous sentence.

**Response:** Deleted

**L85-87:** It would be helpful to include the directions of these FID differences from Cooper (e.g. slow approach-small FID, fast approach-large FID?) to give some context to your question & results.

Response: We have now specified that slow approaches result in short FID and fast approaches in a long FID (line 86).

**L91:** The two commas here are unnecessary.

Response: Removed the commas.

**L91-97:** This is pedantic and I apologize, but “studies” appears 4 times in this section (plus L104). Suggest an initial conditional, and then just discuss the findings.

Response: Now that you have pointed it out, it really does sound bad. We have changed the phrasing, so that “studies” is used only once in the beginning.

**L107-108:** This statement is very strong – such that I think a thorough, systematic review of the literature (including a complete list of databases, search terms, returned items, rejected items, criteria for rejection, etc.) is required to make it. Please tone down the absoluteness.

Response: Indeed, we may have been too hasty in our judgement. There might be studies out there that we have not stumbled upon (due to a different choice of keywords, for example). We have deleted the first two sentences of this paragraph.

**L150:** Escape AT greater distances, or escape TO greater distances?

Response: We have now made it clear by writing out: “larger species tend to have longer distance fled” (line 144).

**L151-152:** This sentence is unwieldy – just to say that “species” was included as a categorical factor in the analysis.

Response: We simplified the sentence a bit. Now it states: “We also examined whether there are any interspecific differences in how risk is assessed”.

**L206:** The two commas in this sentence are unnecessary.

Response: Deleted the commas.

**L355:** Which dependent variable?

Response: Now it says “escape angle” instead of “dependent variable”.

**L518:** “outsmart” is rather subjective.

Response: Ok, removed. “Outmanoeuvre” should be enough to deliver the message.



## HIGHLIGHTS

- This study examined whether birds adjust escape plans while fleeing
- Following corvids during their escape increased escape duration
- Corvids that were followed made larger turns during escape
- Corvids switched from terrestrial escape to aerial escape more often when followed
- Results suggest that prey continue to monitor predators during escape

## **ABSTRACT**

It is widely accepted that stationary prey are able to carefully assess the risk levels associated with an approaching predator to make informative decisions on when to escape. However, little is known about subsequent decision-making process. We set out to compare whether escape durations of three species of corvids differ depending on how a human observer (in the role of a predator) behaves after the escape has begun. When birds were being followed during escape, escape durations were the longest, escape trajectory was modified the most during escape, and a larger proportion of individuals changed from terrestrial to aerial escape strategy compared to observations where birds were not followed. Mean horizontal escape angle of ca 120° was also a potential indication that monitoring the threat is taken into account when deciding on the escape trajectory. While there were some differences between the behaviour of these three closely related species, the general patterns supported the notion that birds dynamically assess risk during escape to find an optimal balance between getting caught and spending too much time and energy on escaping. Further research using different predator-prey combinations or making comparisons between habitats could help understand the generality of our results.

## 1. INTRODUCTION

A large variety of antipredator adaptations exist in the animal kingdom, but one of the most common is escape, considering that even morphologically or chemically well protected species still often turn to escape when encountering a predator (Hatte et al. 2001; Polo-Cavia et al. 2008). The safest way to avoid being injured or depredated is to distance oneself from predators. However, escape can be costly if it interrupts a fitness enhancing activity, such as foraging, courting, or defending its territory, and escape itself can be costly in energetic terms (Ydenberg & Dill 1986). Therefore, it is necessary for prey to correctly assess the degree of predation risk posed by a predator or other threatening stimulus to avoid unnecessary costs (Ydenberg & Dill 1986). In other words, while an underestimation of risk could be lethal for prey, an overestimation of risk would be costly as well – especially if the prey reveals itself to a predator that had no prior intent of attack (Broom & Ruxton 2005).

The first and most recognized economic model of escape behaviour was a simple graph by Ydenberg & Dill (1986), illustrating the changes in the costs of fleeing and remaining of a stationary prey when approached by a predator. The model predicted that the optimal distance for escape would be when the cost of fleeing is equal to the cost of remaining. This model has been updated by Blumstein (2003) to distinguish the risk assessment zone (Zone II in Fig. 1) from the zone where risk is not assessed due to overly long distance between prey and predator (Zone III in Fig. 1), and from the zone where escape is immediate due to short distance (Zone I in Fig. 1). These models have been made to predict flight initiation distance (FID) – the remaining distance between prey and

predator at the moment of escape. FID has become a commonly used measure of fearfulness and has been used for various taxa to test hypotheses about decisions made under threat of predation (Cooper & Blumstein 2015). Most studies that make use of FID use a human observer as an approaching predator (Stankowich & Blumstein 2005) because humans and human-caused disturbances can also be considered a form of predation risk (Frid & Dill 2002). FID is a consistently repeatable personality trait (Carter et al. 2010; Holtmann et al. 2017; López & Martín 2015), but it is also affected by extrinsic factors, such as the speed, size, and directness of an approaching predator (Stankowich & Blumstein 2005). Moreover, FID is negatively correlated with the density of pedestrians (Mikula, 2014; Stankowich & Blumstein 2005), which is likely to be a result of both habituation and risk allocation (Rodríguez-Prieto et al. 2008b). Population level differences in FID, such as urban boldness, can also be explained by microevolutionary changes (Møller 2008) or phenotypic sorting (Holtmann et al. 2017).

Another important parameter of escape is distance fled (Tätte et al. 2018), or – when measured in time units – escape duration or flight time (Collop et al. 2006).. Distance fled has received little attention in escape models (Cooper & Blumstein 2015, p. 57) and is often regrettably neglected when the costs of escape are discussed (Tätte et al. 2018). Cooper & Pérez-Mellado (2004) have suggested that distance fled could be similarly modelled as FID, with one slope predicting risk of predation, and the other predicting cost of leaving a resource (as in Fig. 1). However, it is unclear whether distance fled is decided upon the moment of escape, or whether prey continuously, during escape, assess the

risk of predation and other costs of escape to decide on the final destination. In addition, the so-called zigzagging escape during chase (characterized by frequent turns) is typically attributed to increasing unpredictability of escape (Domenici & Ruxton 2015, p. 213), and not seen as a series of informed corrections to escape trajectory. The question of dynamic risk assessment (DRA) has been briefly discussed in relation to FID (Cooper 1998; Cooper 2006a; Bateman & Fleming 2014), time spent in refuge (Martín & López 2005), and distance fled (Bateman & Fleming 2014; Collier & Hogdson 2017), but there seems to be ambiguity about what is dynamic assessment and what is not.

Cooper (1998) was possibly the first to point out that the economic model of escape (Ydenberg & Dill 1986) does not account for rapidly changing risk curves, after studying how lizards react to sudden turns by an approaching human. The first study to have purposefully tried to demonstrate DRA in escape behaviour was by Cooper (2006a), who examined how lizards change their FID in relation to the speed of an approaching predator. More specifically, Cooper (2006a) tested whether switching his walking speed from slow to fast, and from fast to slow during approach have a different effect on FID from not changing speed midway. It was evident that slow and fast-slow speeds resulted in a highly similar short FID, and fast and slow-fast speeds had a similar long FID. Cooper (2006a) concluded that FID depends only on the final approach speed, and that this was strong evidence for his hypothesis that prey continuously assess the predation risk when encountering a predator.

Other studies that have attempted to demonstrate DRA in escape have been done by making successive approaches towards prey after its escape. Bateman

& Fleming (2014) and Collier & Hogdson (2017) found that grasshoppers change their escape strategies over successive approaches depending on the perceived risk of predation. While it was shown that risk of predation is quickly recalculated, it was unclear whether risk was assessed in real time during escape or just before each escape. If even a momentary delay can be enough to make new accurate risk assessments, as shown in Lind et al. (2002), then a methodology using repeat approaches cannot be regarded as a continuous pursuit. That is, new escape decisions could still have been made before each escape. The cost of remaining could have increased each time because of the heightened perception of predation risk from previous escape attempts. Behaviour in these experiments on grasshoppers changed dynamically, but possibly not in the way originally hypothesized by Cooper (1998, 2006a).

While there is plenty of evidence to suggest that prey do indeed monitor approaching predators before initiating flight (Stankowich & Blumstein 2005; Cooper & Blumstein 2015), the extent to which they monitor while fleeing is less clear. For example, some lizards stop shortly after escape, and subsequently turn their heads to the side to monitor and assess risk (Cooper 2008). While some species, e.g. the Eurasian woodcock (*Scolopax rusticola*), do have a 360° view of their surroundings (Martin 1994), most birds tend to have a blind area at the back of their head (Martin 2007), including corvids (Fernández-Juricic et al. 2010). Furthermore, visual acuity varies in different parts of the visual field, forcing birds to move their heads or eyes when monitoring their surroundings (Fernández-Juricic 2012). Thus, DRA during escape would put requirements on the movement of the head, or on the escape trajectory. Indeed, escape angles

that allow continuous tracking of predator during escape are common in several taxa (Domenici & Ruxton 2015). However, birds, though poorly studied regarding horizontal escape trajectories, have been characterized by having two peaks: 180° to maximize distance from the predator (sometimes followed by a turn towards the predator to fly over it), and 90° for rapid evasion from predator's line of attack (Domenici et al. 2011).

The goal of the current study was to test whether escape by birds change in a way consistent with DRA when escaping from predators – that is, to study the ability to adjust escape plans in real time according to the actions of predators. For that, we made three different types of approaches: "halt" – the potential predator (human) comes to a halt when the bird initiates escape; "forward" – approach is continued in a straight line after escape begins; "chase" – the bird is chased during escape (Fig. 2, see Materials and methods for details). Perceived risk of predation was assessed by measuring escape duration. We predicted that the time spent on escape will be the shortest in the case of approach type "halt", intermediate with type "forward", and the longest with type "chase". If prey would not continue risk assessment during escape, then there would be no significant variation among different approach types as the destination would be pre-fixed. In addition, we set out to further examine the patterns of escape durations by including potential covariates and factors – such as FID, escape angles, species identity, and escape strategy (see Materials and methods) – in a linear mixed-effects analysis. Furthermore, we took interest in finding potential predictors of initial escape angle and angular change during escape as these variables could provide additional explanations for the variation in escape

routes. Three relatively similar species of corvids were used in the study: the hooded crow (*Corvus cornix*), the rook (*Corvus frugilegus*), and the Eurasian jackdaw (*Coloeus monedula*). We selected corvids because their high cognitive abilities (Cramp et al. 2004; Emery & Clayton 2004) should favour DRA, and larger species tend to have longer distance fled (Tätte et al. 2018), which gives them more time to assess risk. We also examined whether there are any interspecific differences in how risk is assessed. Studying how animals react to different stimuli under threat of predation helps to understand how human-caused disturbances could affect the well-being of wild animals (Frid & Dill 2002).

## **2. MATERIAL AND METHODS**

### **2.1 Study system**

The study was conducted in two major Estonian cities, Tartu (58°23'N 26°43'E) and Tallinn (59°26'N 24°44'E) from May to July, 2018. We set out to collect data until we had at least 90 behavioural observations of each corvid species. The final data set consisted of 90 hooded crows, 108 rooks, and 126 Eurasian jackdaws. Potential resampling of individuals was minimized by not visiting the same locations (e.g. parks, streets) more than once. Observations were conducted between 8 AM and 5 PM under similar weather conditions (no precipitation, wind speed less than 6 m/s, temperature 11–22 °C).

The hooded crow, the rook, and the Eurasian jackdaw are common species in Estonian cultural landscapes, but have often been persecuted by humans (Elts et al. 2018). The hooded crow and the rook are similar in size (44–47 cm in length), while the Eurasian jackdaw is 75% smaller than the two (33–34 cm)



(Cramp et al. 2004). Smaller birds usually have a shorter FID (Blumstein 2006) and distance fled (Tätte et al. 2018), and that is the case for the Eurasian jackdaw as well, compared with the other two species (Livezey et al. 2016; Tätte et al. 2018). The Eurasian jackdaw and the rook are typically colonial, while the hooded crow is territorial (Cramp et al. 2004). All three species almost wholly forage on the ground and can be seen flocked together when foraging or roosting (Cramp et al. 2004). Picking food from the surface is the most frequent foraging behaviour for the Eurasian jackdaw and the hooded crow, while deep probing the soil is the most frequent for the rook (Waite 1984).

## **2.2 Starting distance**

Upon finding a corvid on the ground, we measured the starting distance (i.e. the distance between the observer and the bird) with Laser Rangefinder PROSTAFF 3i (Nikon Vision Co., Ltd., Tokyo, Japan; measurement range 7.3–590 m, accuracy 0.1 m). We avoided starting distances that were considerably shorter than 30 m because with short starting distances, there is a risk that the bird is already in the zone of maximum risk where prey immediately escape when spotting a predator (Fig. 1; Blumstein 2003). Furthermore, unpublished data from our previous studies indicates that the three selected species of corvids very rarely have FIDs longer than 24 m in Estonian urban areas (6 observations out of 486). In the present study, starting distances ranged from 28.0 m to 59.4 m and the median was 33.7 m (1<sup>st</sup> quartile 31.3, 3<sup>rd</sup> quartile 37.4). We also recorded the activity of the focal bird. Out of the total 323 observations in this study, 278 (86.1%) focal birds were foraging, 27 (8.4%)

were resting, 16 (5%) were eating, 1 (0.3%) was grooming itself, and 1 (0.3%) was vocalizing.

### **2.3 Approach type**

Next, we approached the focal bird at a normal walking speed (about 1.3 m/s), but the termination of approach depended on the approach type. We approached birds in three ways: (I) approach until the bird initiated escape (defined as “halt”); (II) approach was continued in a straight line after escape begins (regardless of the escape direction of the bird) until the bird stops or the observer reaches the initial location of the bird (defined as “forward”); and (III) the bird was followed during escape until it stopped (defined as “chase”) (Fig. 2). For approach type “forward”, the initial location of the bird was selected as the termination point because often it is not possible to continue walking indefinitely beyond the initial spot due to obstacles such as trees, fences or buildings. The order in which approach types were executed followed a continuous loop, i.e. “halt”-“forward”-“chase”-“halt”-“forward”-“chase” etc. Eliciting an escape response causes only a brief disturbance for urban birds that should not significantly differ from the daily disturbance involuntarily caused by pedestrians.

### **2.4 Flock size**

Flock size was estimated as the number of individual corvids in a 15 m radius of the focal bird (chosen as the one closest to the observer), similarly to e.g. Guay et al. (2013), Samia et al. (2017) and Tätte et al. (2018). Other individuals from that flock were not experimentally approached. However, on some occasions, when flocks were few and large (extending over the 15 m radius), multiple

individuals from these extended flocks were approached. The latter was done only when it was clear that the second individual showed no visible alert behaviour (i.e. head-up posture) after the first one had escaped, and when there was at least 30 m of starting distance to the second individual. In addition, the observer waited at least two minutes before initiating the new approach to further minimize potential carryover effects.

## **2.5 Escape duration and its predictors**

We noted whether escape was terrestrial, aerial, or both (i.e. the bird switched from terrestrial to aerial escape strategy while fleeing). However, in the statistical models we used a binary escape strategy where terrestrial strategy also includes the strategy “both”, because there were too few observations from the category “both” to make more precise models. Escape duration was measured with a stopwatch from the moment escape was initiated until the bird stopped (even if temporarily) with centisecond (cs) precision. If a bird escaped out of sight (13.3% of cases:  $N = 15$  for approach type “halt”,  $N = 14$  for type “forward”, and  $N = 14$  for type “chase”), counting immediately stopped. Each escape trajectory was drawn onto a circle by visual estimation to measure initial and final escape angle in relation to the observer. Later, the difference between initial and final escape angles was defined as change in escape angle. Whenever possible (93.2% of cases), distance fled was linearly measured in addition to escape duration, as in Tatte et al. (2018), but we preferred to use escape duration as the dependent variable because it is a more precise characteristic when dealing with non-linear escape paths (e.g. zigzag movement). Furthermore, height and type of the chosen refuge (tree, ground,

other, NA) were recorded. We also measured distance to the closest potential refuge (tree, bush, post, or fence), that is at least two meters high, from the initial location of the bird. Lastly, density of trees was calculated as the number of trees (defined as upright single-stemmed plants that are at least two meters high) in a 15 m radius to account for possible habitat effects.

## **2.6 FID-phi**

Instead of ordinary flight initiation distance (FID), we used FID-phi *[note to the Editor: we would like “phi” to be replaced with the corresponding Greek letter in the final version. PDF conversion at the submission site was unable to display the proper symbol.]* that was calculated as the distance approached by the observer in relation to starting distance at the moment the focal bird began escaping. The exact equation of FID-phi was:  $1 - (\text{distance approached} / \text{starting distance})$ . The use of phi index was inspired by Samia & Blumstein (2014), who used it to study the relationship between alert distance and FID, but we modified the equation so that the values can be interpreted similarly to ordinary FID, with larger values indicating an earlier escape. The use of a relative measure was necessary because approach type “chase” did not allow us to directly measure the remaining distance to the bird (and we could not simply subtract the walked distance from starting distance because the birds often moved while foraging). However, due to the almost universal positive correlation between starting distance and FID (Blumstein 2003), that may partly be due to mathematical reasons (Dumont et al. 2012), relative measurement of escape components may provide more informative results (e.g. Samia et al.

2017) that are not biased by mathematical constraints (Samia & Blumstein, 2014).

## **2.7 Statistical methods**

The main hypotheses were tested with general linear mixed models using the library lme4 (Bates et al. 2015) in R version 3.5.2 (R Core Team 2018).

Continuous variables (escape duration, distance to refuge, density of trees, change in escape angle) were  $\log_{10}$ -transformed to make the data conform more closely to the normal distribution. The sample means from the values of starting distance, FID-phi, and escape angle were subtracted to reduce multicollinearity from the included interaction terms. Escape angle was scaled by dividing by two times its standard deviation to put it on a similar scale of units with other predictors (Gelman, 2008). The relationship between escape angle and other variables could be non-linear, because angles below 90° indicate an escape towards the predator and over 90° indicates escape away from the predator, but we have too few observations below 90° to convincingly model such non-linearity. City district was used as a random factor in all models to account for potential site and population specific variation. Function dredge from the library MuMIn (Bartoň 2017) was used to generate all combinations of predictors from the global model. Using the same library, these combinations were then ranked by Akaike information criterion (AIC) values and then model averaging was done on a set of models where  $\Delta AIC < 4$ . Uninformative parameters were removed from the top model set according to the criteria suggested by Leroux (2019). The natural average method was used for model averaging. Estimates of predictors were considered to have support for an

effect on the dependent variable whenever their 95% confidence intervals did not overlap zero. Library emmeans (Lenth 2017) was used for pairwise comparisons with Tukey's method, and for creating corresponding plots of estimated marginal means. Partial residual plots were created with the library visreg (Breheny & Burchett 2017).

Circular statistics and figures were carried out with Oriana 4 software (Kovach 2011). Escape angle data were divided into twenty 18° bins centered at 0°. Escapes to the left and right side were pooled after finding no statistically significant differences between the distributions of the left and right side for any of the three species using Watson's  $U^2$  tests (see Fig. A1 for initial escape directions before pooling). Escape angle of 180° indicates an escape straight away from the human observer, while an angle of 0° indicates escape towards the observer.

### 3. RESULTS

#### 3.1 *Escape strategy and refuge type*

During escape, more individuals changed their escape strategy from terrestrial to aerial for approach type "chase" (34/43) compared with approach type "halt" (5/39) as indicated by the Chi-square test of independence,  $\chi^2$  (1,  $N = 82$ ) = 33.38,  $p < 0.001$ , and also compared with approach type "forward" (7/46),  $\chi^2$  (1,  $N = 89$ ) = 33.95,  $p < 0.001$ . There was no significant difference in escape strategies between approach type "halt" and "forward",  $\chi^2$  (1,  $N = 85$ ) = 0.1,  $p = 1.00$ . Previously listed  $p$ -values were adjusted with the Bonferroni correction. Preference for refuge types was equally distributed among approach types "halt", "forward", and "chase",  $\chi^2$  (6,  $N = 323$ ) = 3.58,  $p = 0.734$ , with ground

being the most frequently used choice (56.5%, 64.2%, and 56.6%, respectively), followed by trees (17.6%, 16.5%, and 21.7%, respectively).

### **3.2 Escape duration**

Escape duration was strongly positively correlated with distance fled,  $r = 0.79$ ,  $N = 301$ ,  $p < 0.001$  (Fig. A2). The global model for escape duration contained the following predictors and their interactions (indicated by an asterisk): *Approach type \* Species + Approach type \* Escape strategy + Approach type \* FID-phi + Escape angle \* Species + Distance to refuge + Starting distance \* Species + Density of trees + Flock size*. Density of trees and flock size were removed from the top model set (i.e. models with  $\Delta AIC < 4$ ) as these variables had little statistical impact, were not directly related to main hypotheses, and could be classified as uninformative parameters (model selection tables can be found in the Electronic Supplementary Tables S1-S4) (Leroux, 2019).

Pairwise comparisons (using estimated marginal means from the model), showed that, for all three species, escape duration for approach type “halt” was significantly shorter than for approach type “chase”, while there was a significant difference between approach types “halt” and “forward” only for the hooded crow (Fig. 3; Table 1 & A1). Escape duration for approach type “forward” was significantly shorter than for approach type “chase” for the Eurasian jackdaw and the rook but not for the hooded crow (Fig. 3, Table 1). Compared among all species, escape duration for approach type “chase” was significantly different from approach types “halt” and “forward” for both terrestrial and aerial escape strategies (Fig. 4; Table 2). Approach types “halt” and “forward” did not differ significantly from each other for either escape strategy

when analysed among all species (Fig. 4; Table 2). While aerial escape strategy, compared to terrestrial escape strategy, increased escape duration for approach types “halt” ( $\beta = -0.174$ ,  $SE = 0.051$ ,  $p < 0.001$ ) and “forward” ( $\beta = -0.125$ ,  $SE = 0.044$ ,  $p = 0.005$ ), it showed an opposite trend for approach type “chase” ( $\beta = 0.100$ ,  $SE = 0.047$ ,  $p = 0.035$ ).

The interaction between escape angle and species showed that the relationship between escape angle and escape duration was positive only for the rook (Fig. A3; Table A1). Similarly, the relationship between starting distance and escape duration was positive only for the rook (Fig. A4; Table A1). There was also a significant interaction between approach type and FID-phi as the relationship between FID-phi and escape duration was positive only for approach type “halt” (Fig. A5; Table A1). Distance to the closest refuge was positively correlated with escape duration (Table A1). The density of nearby trees and flock size did not affect escape duration (Electronic Supplementary Table S1).

### **3.3 Escape angle**

The global model for escape angle contained the following predictors and their interactions (indicated by an asterisk): *FID-phi \* Species + Escape strategy \* Species + Distance to refuge + Starting distance \* Species*. Multi-model inference found no reliable relationships between the chosen predictors and escape angle (Table A2).

The mean escape angles (after pooling escapes to the left and right side; see Material and methods) were as follows: 123.4, 95% CI [118.0, 128.8] for the Eurasian jackdaw (Fig. 5a), 118.1°, 95% CI [111.4, 124.8] for the hooded crow



(Fig. 5b), and 117.9°, 95% CI [111.3, 124.5] for the rook (Fig. 5c). The distributions of the escape angles for the three species did not differ statistically from each other ( $p$ -values > 0.05 for all Watson's  $U^2$  tests).

### **3.4 Change in escape angle**

The global model for change in escape angle during escape contained the following predictors and their interactions (indicated by an asterisk): *Approach type \* Species + Approach type \* Escape strategy + FID-phi + Escape duration + Starting distance \* Species*. Multi-model inference, coupled with pairwise comparisons of estimated marginal means, showed that the change in escape angle depended on approach type, with the change in escape angle being larger for approach type III than for approach type "halt", but a significant difference was found only for terrestrial escape strategy (Fig. 6; Table A3 & A4). Change in escape angle was positively related to escape duration (Table A3). FID-phi, starting distance, and the interaction between approach type and species did not have support for a relationship with change in escape angle.

## **4. DISCUSSION**

### **4.1 Overview**

The main goal of the current study was to examine whether birds dynamically adjust escape behaviour during escape according to the perceived risk of predation. The most apparent finding to emerge from this study was that corvids can easily differentiate between a predator (in this case, a human observer) that pursues (approach type "chase") and one that immediately stops approaching when the bird initiates escape (approach type "halt"), by increasing time spent escaping (Fig. 3), by making larger adjustments in escape trajectory (Fig. 6),

and by more frequently changing from terrestrial to aerial escape strategy. Surprisingly, the Eurasian jackdaw and the rook did not show clear differences in escape duration between approach type “halt” and approach type “forward” (where the predator continues moving to the initial location of the bird but does not chase it), while the hooded crow did (Fig. 3; Table 1). Another interspecific difference was that the relationship between escape angle and escape duration was positive only for the rook, while no clear relationship was found for the other two species (Fig. A3). The relevance of DRA during escape is clearly supported by the current findings, but the results also suggest that even closely related species have different escape strategies or use different cues for evaluating risk.

#### **4.2 Indicators of dynamic risk assessment**

Studies have shown that, when a stationary prey is being approached by a predator, the prey will assess the costs related to fleeing and not fleeing to decide on the optimal distance at which to escape (Stankowich & Blumstein 2005; Cooper 2006a). However, very little is known about cost assessment during escape. Before the present study, research on birds suggested that birds either maximize distance from the predator by escaping at 180°, or escape at 90° for rapid evasion (Domenici et al. 2011). These peaks do not give an impression that monitoring predators is important to birds during escape. In our study, all three species had an average initial escape angle close to 120° with no distinctive peaks (Fig. 5), which most likely represents a middle ground between maximizing distance, being unpredictable, and monitoring the predator (Hall et al. 1986; Domenici & Blake 1993).

Several other results also suggest that corvids keep an eye on the actions of the predator even after initiating escape. Most importantly, escape duration increased when the intentions of the predator became more threatening (Fig. 3). These results reflected those of Cooper (2006b) and Collier & Hogdson (2017), who found that distance fled increases in grasshoppers when the approaching human is more persistent. While the choice to use terrestrial escape strategy usually indicates a two to five times shorter distance fled in birds (Rodriguez-Prieto et al. 2008a; Tatte et al. 2018), our study shows that this is not always the case: escape duration was the longest for birds that used terrestrial escape when being followed (Fig. 4a). Yet, escape duration differed between approach types independently of escape strategy (Table 2), meaning that even flying individuals are likely to monitor predators to make necessary changes to escape duration. However, only birds using terrestrial escape showed a significant increase in the angular change when being chased, after controlling for escape duration that was a significant predictor of angular change (Fig. 6a; Table A3). A similar, albeit not significant trend was visible for aerial escape as well (Fig. 6b), although it seems that manipulating escape trajectory is more important during terrestrial escape. The latter is expected, considering that terrestrial escape was slower (Fig. A2). In general, prey are usually slower than predators because of their smaller size, but make up for it by having smaller turning radii and higher turning rates (Domenici & Ruxton 2015).

#### ***4.3 Escape duration in relation to escape angle***

Escape duration was also related to initial escape angle but only for the rook. Contrary to our expectations, the rook showed an increase in escape duration

when escaping at more obtuse angles (Fig. A3). We initially expected that escape angles away from the predator would decrease the time needed to reach a safe distance. However, a possible explanation is that the rook, when sensing low risk of predation, makes a short evasive manoeuvre to the side with the option to continue monitoring the predator, but, when sensing a high risk of predation, chooses to quickly maximize the distance. The lack of the described relationship in the Eurasian jackdaw and the hooded crow could be due to a more relaxed attitude towards humans, as indicated by shorter FID (Livezey et al. 2016) and shorter escape durations (this study). A possible explanation, for why the rook is more cautious, is that its preferred foraging technique is deep probing, rather than surface picking as in the other two species (Waite, 1984). Deep probing probably requires more attention on the ground that can negatively affect antipredator vigilance (Lima & Bednekoff 1999). Still, a quick maximization of the distance from a human could be an unpopular option in highly urbanized birds. A further study comparing urban-rural differences in that matter could help to validate that hypothesis.

#### ***4.4 Escape duration in relation to FID and starting distance***

Escape duration was longer for earlier escapes (as measured by FID-phi, the distance approached in relation to starting distance) but only for approach type “halt” (Fig. A5). This result is in accordance with a previous study examining the relationship between FID and distance fled (Tätte et al. 2018). A most likely explanation for the lack of a similar relationship for approach type “chase” is that even bold prey need to spend time on escape when being chased. The lack of a relationship between FID-phi and angular change during fleeing could be an

indication that late escapes did not suffer from worse initial escape angles. As a reminder, escape duration was the longest for birds trying to escape terrestrially when being chased, but the shortest when the predator stops (Fig. 4).

Therefore, it could be that boldness is an effective way to reduce costs of escape if the predator is unwilling to pursue prey, although otherwise, boldness can be costly. For example, Namibian rock agamas (*Agama planiceps*) with consistently shorter FIDs, i.e. a bolder personality type, spent more time basking, eating and moving around than shyer individuals, but at the same time suffered higher rates of tail loss – an indication of higher predation risk (Carter et al. 2010).

An interesting side-result was that starting distance, i.e. the distance at which the observer started his approach, was in a positive relationship with escape duration for the rook but not for the other two species (Fig. A4). While the positive – and variously interpreted – relationship between starting distance and FID is frequently shown in numerous taxa (Blumstein 2003), a relationship between starting distance and distance fled has not been found (e.g. Tätté et al. 2018; Kalb et al. 2019). The latter is not surprising if it is a species-specific trait as seen in our study. We do not know the exact reason for why only the rook increased escape duration when approached at a longer starting distance, but it could once again be related to wariness of the species (as discussed in chapter 4.3). For example, Tätté et al. (2018) hypothesized that the relationship between starting distance and FID was positive in rural but not in urban habitat because urban birds need to lower their zone of awareness for not to be

distracted too frequently. Starting distance did not relate to the choice of escape angle or angular change during escape.

#### ***4.5 Difference in the perception of approach types***

The finding, that at least the hooded crow perceives approach type “forward” more threatening than approach type “halt” (Fig. 3; Table 1) has implications for future studies of escape behaviour. Researchers need to acknowledge that there could be a difference between approach type “halt” and “forward” when conducting their studies. Most certainly, studies using type “halt” and “chase” intermittently (e.g. Collier & Hogdson 2017) are in danger of producing skewed results. Whenever distance fled, escape duration, or hiding time are to be measured, one needs to decide beforehand which approach to choose in order to have all measurements taken under similar perceived risk of predation. It is up to debate whether the hooded crow, being able to differentiate between approach types “halt” and “forward”, is better at DRA than the other two species, or whether it more often incorrectly translates continued approach as pursuit. After all, a predator that continues to move along the same trajectory while prey escapes in another direction could be an indication that it was not interested in the prey to begin with. However, making detailed assessment about the trajectory of the predator in mid-flight is probably not an easy task, which is why some species could rely on simple cues, i.e. whether the predator stops or not. Furthermore, we noticed that sometimes birds terminate escape, only to continue escaping just moments later. Such behaviour indicates that even corvids are not always capable of correctly assessing risk during escape.

#### **4.6 Escape angle**

We found no statistically reliable predictors for escape angle. That is not surprising as escape trajectories usually have a high variability to provide unpredictability (Domenici et al. 2011). However, since distance to closest refuge was positively related to escape duration, it is possible that escape angle could have been partly predictable if we had measured the angles of closest refuges and added these measurements to the models (Eason et al. 2019). Still, ground was the most preferred refuge type. In contrast to the study by Bateman & Fleming (2014), the preference of refuge type did not change with increasing risk of predation. It is also probable that the choice of initial escape angle, including vertical angle, could become more important during high-speed attacks where swift evasion is required (Lind et al. 2002).

#### **4.7 Conclusions**

In general, the results of this research support the idea that birds monitor the intentions of the predator while escaping to dynamically adjust their escape plans. Although the study was done only on three species of corvids, it is probable that similar behaviour exists in a variety of taxa because, in addition to saving time and energy, prey often need to outmanoeuvre the predators that chase them. In terms of studying the impact of human disturbance on wildlife, the findings highlight that if one wishes to measure the true costs of escape, it might be better to simulate a typical pedestrian that does not stop when prey escapes. A further study on non-urbanized animals, or using a model of some other predator, could shed light on whether these behavioural patterns hold up when the perceived risk of predation is considerably higher.

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523 **REFERENCES**

- 524 Bartoň K. 2017. MuMIn: Multi-Model Inference. R package version 1.40.0.  
525 <https://CRAN.R-project.org/package=MuMIn>
- 526 Bateman PW, & Fleming PA. 2014. Switching to Plan B: changes in the escape  
527 tactics of two grasshopper species (*Acrididae: Orthoptera*) in response to  
528 repeated predatory approaches. *Behavioral Ecology and Sociobiology*,  
529 68(3): 457-465.
- 530 Bates D, Maechler M, Bolker B, & Walker S. 2015. Fitting Linear Mixed-Effects  
531 Models Using lme4. *Journal of Statistical Software*, 67(1): 1–48.  
532 doi:10.18637/jss.v067.i01.
- 533 Breheny P, & Burchett W. 2017. visreg: Visualization of Regression Models. R  
534 package version 2.4-1. <https://CRAN.R-project.org/package=visreg>
- 535 Broom M, & Ruxton GD. 2005. You can run—or you can hide: optimal  
536 strategies for cryptic prey against pursuit predators. *Behavioral Ecology*,  
537 16(3): 534-540.
- 538 Blumstein DT. 2003. Flight-initiation distance in birds is dependent on intruder  
539 starting distance. *Journal of Wildlife Management*, 67: 852-857.
- 540 Blumstein DT. 2006. Developing an evolutionary ecology of fear: how life history  
541 and natural history traits affect disturbance tolerance in birds. *Animal*  
542 *Behaviour*, 71(2): 389–399.
- 543 Carter AJ, Goldizen AW, & Tromp SA. 2010. Agamas exhibit behavioral  
544 syndromes: bolder males bask and feed more but may suffer higher  
545 predation. *Behavioral Ecology*, 21(3), 655-661.

546 Collier A, & Hodgson JY. 2017. A Shift in Escape Strategy by Grasshopper Prey  
 547 in Response to Repeated Pursuit. *Southeastern Naturalist*, 16(4): 503-  
 548 516.

549 Collop C, Stillman RA, Garbutt A, Yates MG, Rispin E, & Yates T. 2016.  
 550 Variability in the area, energy and time costs of wintering waders  
 551 responding to disturbance. *Ibis*, 158(4): 711–725.

552 Cooper Jr WE. 1998. Direction of predator turning, a neglected cue to predation  
 553 risk. *Behaviour*, 135(1): 55–64.

554 Cooper Jr WE. 2006a. Dynamic risk assessment: prey rapidly adjust flight  
 555 initiation distance to changes in predator approach speed. *Ethology*,  
 556 112(9), 858-864.

557 Cooper Jr WE. 2006b. Risk factors and escape strategy in the grasshopper  
 558 *Dissosteira carolina*. *Behaviour*, 143(10), 1201-1218.

559 Cooper Jr WE. 2008. Visual monitoring of predators: occurrence, cost and  
 560 benefit for escape. *Animal Behaviour*, 76(4): 1365–1372.

561 Cooper Jr WE, & Blumstein DT (Eds.). 2015. *Escaping from predators: an*  
 562 *integrative view of escape decisions*. Cambridge: Cambridge University  
 563 Press.

564 Cooper Jr WE, Hawlena D, & Pérez-Mellado V. 2009. Interactive effect of  
 565 starting distance and approach speed on escape behavior challenges  
 566 theory. *Behavioral Ecology*, 20(3): 542–546.

- 567 Cooper Jr WE, & Pérez-Mellado V. 2004. Tradeoffs between escape behavior  
568 and foraging opportunity by the Balearic lizard (*Podarcis lilfordi*).  
569 *Herpetologica*, 60(3): 321–324.
- 570 Cramp S, Simmons KEL, Snow DW, & Perrins CM. 2004. *The birds of the*  
571 *western Palearctic interactive*. UK, Sheffield: BirdGuides.
- 572 Domenici P, Blagburn JM, & Bacon JP. 2011. Animal escapology II: escape  
573 trajectory case studies. *Journal of Experimental Biology*, 214(15): 2474–  
574 2494.
- 575 Domenici P, & Blake R. W. 1993. Escape trajectories in angelfish (*Pterophyllum*  
576 *eimekei*). *Journal of Experimental Biology*, 177: 253–272.
- 577 Domenici P, & Ruxton GD. 2015. Prey behaviors during fleeing. In: Cooper Jr  
578 WE, & Blumstein DT (Eds.). *Escaping from Predators: An Integrative*  
579 *View of Escape Decisions*. Cambridge: Cambridge University Press, pp.  
580 113–151.
- 581 Dumont F, Pasquaretta C, Réale D, Bogliani G, & Hardenberg A. 2012. Flight  
582 initiation distance and starting distance: biological effect or mathematical  
583 artefact? *Ethology*, 118(11): 1051–1062.
- 584 Eason P K, Nason LD, & Alexander JE. 2019. Squirrels do the Math: Flight  
585 Trajectories in Eastern Gray Squirrels (*Sciurus carolinensis*). *Frontiers in*  
586 *Ecology and Evolution*, 7: 66.
- 587 Elts J, Kuus A, & Leibak E. 2018. *Linnuatlas. Eesti haudelindude levik ja*  
588 *arvukus*. Tartu: Estonian Ornithological Society, p. 342–349.

589 Emery NJ, & Clayton NS. 2004. The mentality of crows: convergent evolution of  
590 intelligence in corvids and apes. *Science*, 306(5703): 1903–1907.

591 Fernández-Juricic E. 2012. Sensory basis of vigilance behavior in birds:  
592 synthesis and future prospects. *Behavioural Processes*, 89(2): 143–152.

593 Fernández-Juricic E, O'Rourke C, & Pitlik T. 2010. Visual coverage and  
594 scanning behavior in two corvid species: American crow and Western  
595 scrub jay. *Journal of Comparative Physiology A*, 196(12): 879–888.

596 Frid A, & Dill L. 2002. Human-caused disturbance stimuli as a form of predation  
597 risk. *Conservation Ecology*, 6(1): 11.

598 Gelman, A. 2008. Scaling regression inputs by dividing by two standard  
599 deviations. *Statistics In Medicine*, 27(15), 2865-2873.

600 Guay PJ, Lorenz RD, Robinson RW, Symonds MR, & Weston MA. 2013.  
601 Distance from water, sex and approach direction influence flight  
602 distances among habituated black swans. *Ethology*, 119(7), 552-558.

603 Hall SJ, Wardle CS, & Maclellann DN. 1986. Predator evasion in a fish school:  
604 Test of a model for the fountain effect. *Marine Biology*, 91: 143–148.

605 Hatle JD, Salazar BA, & Whitman DW. 2001. Sluggish movement and  
606 repugnant odor are positively interacting insect defensive traits in  
607 encounters with frogs. *Journal of Insect Behavior*, 14(4): 479–496.

608 Holtmann B, Santos ES, Lara CE, & Nakagawa S. 2017. Personality-matching  
609 habitat choice, rather than behavioural plasticity, is a likely driver of a

610 phenotype–environment covariance. *Proceedings of the Royal Society B:*  
611 *Biological Sciences*, 284(1864), 20170943.

612 Kalb N, Anger F, & Randler C. 2019. Flight initiation distance and escape  
613 behavior in the black redstart (*Phoenicurus ochruros*). *Ethology*, 125(7):  
614 430-438.

615 Kovach WL. 2011. *Oriana – Circular Statistics for Windows, ver. 4*. Pentraeth,  
616 United Kingdom: Kovach Computing Services.

617 Lenth R. 2017. emmeans: Estimated Marginal Means, aka Least-Squares  
618 Means. R package version 0.9.1. [https://CRAN.R-](https://CRAN.R-project.org/package=emmeans)  
619 [project.org/package=emmeans](https://CRAN.R-project.org/package=emmeans)

620 Leroux SJ. 2019. On the prevalence of uninformative parameters in statistical  
621 models applying model selection in applied ecology. *PLoS One*, 14(2),  
622 e0206711.

623 Lima SL, & Bednekoff PA. 1999. Back to the basics of antipredatory vigilance:  
624 can nonvigilant animals detect attack? *Animal Behaviour*, 58(3): 537–  
625 543.

626 Lind J, Kaby U, & Jakobsson S. 2002. Split-second escape decisions in blue tits  
627 (*Parus caeruleus*). *Naturwissenschaften*, 89(9), 420-423.

628 Livezey KB, Fernández-Juricic E, & Blumstein DT. 2016. Database of Bird  
629 Flight Initiation Distances to Assist in Estimating Effects from Human  
630 Disturbance and Delineating Buffer Areas. *Journal of Fish and Wildlife*  
631 *Management*, 7(1): 181–191.

632 López P, & Martín J. 2015. The personality of escape. In: Cooper Jr WE, &  
 633 Blumstein DT (Eds.). *Escaping from Predators: An Integrative View of*  
 634 *Escape Decisions*. Cambridge: Cambridge University Press, pp. 385-  
 635 404.

636 Martin GR. 1994. Visual fields in woodcocks *Scolopax rusticola* (Scolopacidae;  
 637 *Charadriiformes*). *Journal of Comparative Physiology A*, 174(6): 787–  
 638 793.

639 Martin GR. 2007. Visual fields and their functions in birds. *Journal of*  
 640 *Ornithology*, 148(2): 547–562.

641 Martín J, & López P. 2005. Wall lizards modulate refuge use through continuous  
 642 assessment of predation risk level. *Ethology*, 111(2): 207–219.

643 Mikula P. 2014. Pedestrian density influences flight distances of urban birds.  
 644 *Ardea*, 102(1), 53-61.

645 Møller AP. 2008. Flight distance of urban birds, predation, and selection for  
 646 urban life. *Behavioral Ecology and Sociobiology*, 63(1), 63.

647 Polo-Cavia N, López P, & Martín J. 2008. Interspecific differences in responses  
 648 to predation risk may confer competitive advantages to invasive  
 649 freshwater turtle species. *Ethology*, 114(2): 115–123.

650 R Core Team. 2018. R: A language and environment for statistical computing.  
 651 Vienna, Austria: R Foundation for Statistical Computing. URL  
 652 <https://www.R-project.org/>.

653 Rodriguez-Prieto I, Fernández-Juricic E, & Martín J. 2008a. To run or to fly: low  
 654 cost versus low risk escape strategies in blackbirds. *Behaviour*, 145(8),  
 655 1125–1138.

656 Rodriguez-Prieto I, Fernández-Juricic E, Martín J, & Regis Y. 2008b.  
 657 Antipredator behavior in blackbirds: habituation complements risk  
 658 allocation. *Behavioral Ecology*, 20(2), 371-377.

659 Samia DS, & Blumstein DT. 2014. Phi index: a new metric to test the flush early  
 660 and avoid the rush hypothesis. *PLoS One*, 9(11), e113134.

661 Samia DS, Blumstein DT, Díaz M, Grim T, Ibáñez-Álamo JD, Jokimäki J, Tätté  
 662 K, Markó G, Tryjanowski P, & Møller AP. 2017. Rural-urban differences  
 663 in escape behavior of European birds across a Latitudinal Gradient.  
 664 *Frontiers in Ecology and Evolution*, 5: 66.  
 665 <https://doi.org/10.3389/fevo.2017.00066>.

666 Tätté K, Møller AP, & Mänd R. 2018. Towards an integrated view of escape  
 667 decisions in birds: relation between flight initiation distance and distance  
 668 fled. *Animal Behaviour*, 136: 75–86.

669 Waite RK. 1984. Winter habitat selection and foraging behaviour in sympatric  
 670 corvids. *Ornis Scandinavica*, 15: 55–62.

671 Ydenberg RC, & Dill LM. 1986. The economics of fleeing from predators.  
 672 *Advances in the Study of Behavior*, 16(C): 229–249.

## 673 **FIGURE LEGENDS**

674 Figure 1. The graphical model by Ydenberg & Dill (1986) predicted that when  
675 the distance between a prey and an approaching predator decreases  
676 (horizontal axis), cost of not fleeing (solid line) increases, while cost of fleeing  
677 (dashed line) decreases, and that the intersection of these two curves would  
678 predict optimal flight initiation distance ( $D_{\text{optimal}}$ ). The zones indicate whether risk  
679 assessment takes place (zone II) or not (zone I & III) depending on the distance  
680 from the predator (Blumstein 2003). Figure is redrawn from Cooper & Blumstein  
681 (2015) with permission from Cambridge University Press.

682 Figure 2. Schematic illustration of the three approach types compared in this  
683 study.  $T_1$  = time when bird initiated escape,  $t_2$  = time when bird stopped  
684 escaping,  $t_2 - t_1$  = escape duration, FID = flight initiation distance, DF = distance  
685 fled. Arrows indicate movement. Termination of approach is determined by  $t_1$  for  
686 “halt”, and by  $t_2$  for “forward” and “chase”. See Material and Methods for a  
687 detailed explanation.

688 Figure 3. Relationships between approach type and escape duration for (a)  
689 Eurasian jackdaw, (b) hooded crow, and (c) rook. Black circles represent  
690 estimated marginal means and grey rectangles represent confidence intervals  
691 (both are based on predictions from a linear mixed model).

692 Figure 4. Relationships between approach type and escape duration for (a)  
693 terrestrial and (b) aerial escape strategies. Black circles represent estimated  
694 marginal means and grey rectangles represent confidence intervals (both are  
695 based on predictions from a linear mixed model).



696 Figure 5. Distributions of initial escape angles of (a) Eurasian jackdaw, (b)  
697 hooded crow, and (c) rook. Escapes to the left and right are pooled. The human  
698 observer is positioned at 0° and 180° indicates an escape angle directly away  
699 from the human observer. Black line with error bars indicates mean escape  
700 angle with 95% confidence intervals. Numbers inside the circle help to count the  
701 number of escapes in different directions. Bin intervals are 18°.

702 Figure 6. Relationships between approach type and change in escape angle for  
703 (a) terrestrial and (b) aerial escape strategies. Black circles represent estimated  
704 marginal means and grey rectangles represent 95% confidence intervals (both  
705 are based on predictions from a linear mixed model).

706

## TABLES

Table 1. Pairwise comparisons of escape durations for approach types "halt", "forward", and "chase" across species of birds in Estonia.

Species	Contrast	Estimate	SE	df	<i>t</i>	<i>p</i>
Eurasian jackdaw ( <i>Coloeus monedula</i> )						
	"halt"–"forward"	–0.025	0.050	340	–0.50	0.871
	"halt"–"chase"	<b>–0.280</b>	0.051	339	–5.50	< 0.001
	"forward"–"chase"	<b>–0.255</b>	0.052	338	–4.91	< 0.001
Hooded crow ( <i>Corvus cornix</i> )						
	"halt"–"forward"	<b>–0.144</b>	0.059	346	–2.45	0.039
	"halt"–"chase"	<b>–0.259</b>	0.062	340	–4.19	< 0.001
	"forward"–"chase"	–0.115	0.061	341	–1.89	0.143
Rook ( <i>Corvus frugilegus</i> )						
	"halt"–"forward"	0.030	0.055	345	0.55	0.849
	"halt"–"chase"	<b>–0.239</b>	0.056	347	–4.29	< 0.001
	"forward"–"chase"	<b>–0.269</b>	0.054	342	–5.01	< 0.001

Tukey method was used for *p*-value adjustment. Estimates in bold indicate *p*-values below significance threshold level (0.05).

713 Table 2. Pairwise comparisons of escape durations for approach types “halt”,  
 714 “forward”, and “chase” across terrestrial and aerial escape strategies in birds in  
 715 Estonia.

Escape strategy	Contrast	Estimate	SE	df	<i>t</i>	<i>p</i>
Terrestrial escape						
	"halt"–"forward"	–0.071	0.051	347	–1.38	0.351
	"halt"–"chase"	<b>–0.396</b>	0.053	346	–7.41	< 0.001
	"forward"–"chase"	<b>–0.325</b>	0.049	345	–6.64	< 0.001
Aerial escape						
	"halt"–"forward"	–0.022	0.040	340	–0.55	0.848
	"halt"–"chase"	<b>–0.123</b>	0.040	341	–3.06	0.007
	"forward"–"chase"	<b>–0.101</b>	0.040	341	–2.51	0.034

716 Tukey method was used for *p*-value adjustment. Estimates in bold indicate *p*-  
 717 values below significance threshold level (0.05).

718

## APPENDIX

Table A1. Model averaged estimate values predicting changes in escape duration of 324 birds belonging to three species. Reference levels: approach type "halt", terrestrial escape for escape strategy, and Eurasian jackdaw for species.

Predictor	Estimate	SE	2.5 <sup>th</sup>	97.5 <sup>th</sup>	z	w <sub>ip</sub>
(Intercept)	<b>2.099</b>	0.052	1.996	2.202	39.97	
Approach type "forward"	0.069	0.058	-0.046	0.183	1.17	1.00
Approach type "chase"	<b>0.421</b>	0.060	0.304	0.538	7.05	1.00
Escape strategy	<b>0.191</b>	0.053	0.086	0.295	3.59	1.00
Approach type "forward" * Escape strategy	-0.066	0.069	-0.201	0.070	0.95	1.00
Approach type "chase" * Escape strategy	<b>-0.295</b>	0.071	-0.434	-0.156	4.15	1.00
Distance to refuge	<b>0.096</b>	0.033	0.031	0.161	2.89	1.00
Escape angle	-0.048	0.041	-0.127	0.032	1.17	1.00
Escape angle * Species (hooded crow)	0.045	0.063	-0.078	0.169	0.72	1.00
Escape angle * Species (rook)	<b>0.218</b>	0.057	0.106	0.329	3.81	1.00
Species (hooded crow)	0.034	0.047	-0.059	0.127	0.72	1.00
Species (rook)	<b>0.229</b>	0.048	0.134	0.323	4.74	1.00
FID-phi	<b>0.404</b>	0.202	0.008	0.801	2.00	0.78
Approach type "forward" * FID-phi	<b>-0.534</b>	0.229	-0.983	-0.084	2.33	0.68
Approach type "chase" * FID-phi	<b>-0.531</b>	0.218	-0.960	-0.103	2.43	0.68
Starting distance	-0.411	0.431	-1.257	0.436	0.95	0.58
Starting distance * Species (hooded crow)	0.047	0.554	-1.043	1.137	0.09	0.47

Starting distance * Species (rook)	<b>1.109</b>	0.526	0.073	2.145	2.10	0.47
Approach type “forward” * Species (hooded crow)	0.109	0.076	-0.040	0.258	1.44	0.47
Approach type “chase” * Species (hooded crow)	-0.039	0.080	-0.196	0.118	0.49	0.47
Approach type “forward” * Species (rook)	-0.073	0.075	-0.220	0.073	0.98	0.47
Approach type “chase” * Species (rook)	-0.070	0.076	-0.218	0.079	0.92	0.47

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The natural average method was used for model averaging (on 13 models with  $\Delta AIC < 4$ , see Electronic Supplementary Table S2). Parameter estimates are followed by unconditional standard errors (SE) and 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles (95% CI). Estimates in bold indicate that 95% CI does not include 0.  $W_{ip}$  is the relative importance of each predictor in the model set. City district was included as random effect. Some species-related effects are not showing meaningful comparisons but were needed for more specific post-hoc tests.

732 Table A2. Model averaged estimate values predicting changes in escape angle  
 733 of 324 birds belonging to three species. Reference levels: terrestrial escape for  
 734 escape strategy and Eurasian jackdaw for species.

Predictor	Estimate	SE	2.5 <sup>th</sup>	97.5 <sup>th</sup>	<i>z</i>	<i>w<sub>ip</sub></i>
(Intercept)	<b>1.830</b>	0.066	1.701	1.958	27.85	
FID-phi	<b>-0.506</b>	0.190	-0.879	-0.133	2.66	1.00
Distance to refuge	-0.093	0.075	-0.240	0.054	1.24	0.41
Escape strategy	-0.008	0.059	-0.123	0.108	0.13	0.24
Starting distance	-0.064	0.466	-0.981	0.854	0.14	0.24
Species (hooded crow)	-0.006	0.073	-0.150	0.138	0.08	0.04
Species (rook)	-0.022	0.069	-0.160	0.115	0.32	0.04

735 The natural average method was used for model averaging (on eight models  
 736 with  $\Delta AIC < 4$ , see Electronic Supplementary Table S3). Parameter estimates  
 737 are followed by unconditional standard errors (SE) and 2.5<sup>th</sup> and 97.5<sup>th</sup>  
 738 percentiles (95% CI). *w<sub>ip</sub>* is the relative importance of each predictor in the  
 739 model set. Estimates in bold indicate that 95% CI does not include 0. City  
 740 district was included as random effect.

741

Table A3. Model averaged estimate values predicting angular change during escape of 324 birds belonging to three species. Reference levels: Approach type “halt” for approach type, terrestrial escape for escape strategy, and Eurasian jackdaw for species.

Predictor	Estimate	SE	2.5 <sup>th</sup>	97.5 <sup>th</sup>	z	$w_{ip}$
(Intercept)	<b>-2.919</b>	0.366	-3.634	-2.200	7.95	
Approach type “forward”	0.101	0.099	-0.095	0.296	1.01	1.00
Approach type “chase”	<b>0.342</b>	0.116	0.114	0.571	2.94	1.00
Escape duration	<b>1.544</b>	0.160	1.229	1.858	9.63	1.00
Escape strategy	-0.178	0.092	-0.359	0.004	1.91	0.95
Species (hooded crow)	-0.162	0.099	-0.356	0.032	1.63	0.59
Species (rook)	<b>-0.203</b>	0.097	-0.394	-0.011	2.07	0.59
FID-phi	-0.303	0.291	-0.874	0.269	1.04	0.36
Starting distance	0.645	0.732	-0.795	2.084	0.88	0.34
Approach type “forward” * Escape strategy	0.015	0.188	-0.354	0.385	0.08	0.14
Approach type “chase” * Escape strategy	-0.183	0.194	-0.566	0.200	0.94	0.14
Starting distance * Species (hooded crow)	-1.173	1.696	-4.510	2.164	0.69	0.03
Starting distance * Species (rook)	0.102	1.625	-3.094	3.299	0.06	0.03

The natural average method was used for model averaging (on 15 models with  $\Delta AIC < 4$ , see Electronic Supplementary Table S4). Parameter estimates are followed by unconditional standard errors (SE) and 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles (95% CI).  $w_{ip}$  is the relative importance of each predictor in the model set. Estimates in bold indicate that 95% CI does not include 0. City district was included as random effect.

753 Table A4. Pairwise comparisons of angular change for approach types "halt",  
 754 "forward", and "chase" across terrestrial and aerial escape strategies.

Escape strategy	Contrast	Estimate	SE	df	<i>t</i>	<i>p</i>
Terrestrial escape						
	"halt"–"forward"	–0.153	0.153	339	–1.00	0.577
	"halt"–"chase"	<b>–0.494</b>	0.175	334	–2.82	0.014
	"forward"–"chase"	–0.341	0.158	336	–2.15	0.082
Aerial escape						
	"halt"–"forward"	–0.111	0.119	334	–0.94	0.619
	"halt"–"chase"	–0.272	0.121	332	–2.25	0.065
	"forward"–"chase"	–0.161	0.123	334	–1.32	0.388

755 Tukey method was used for *p*-value adjustment. Estimates in bold indicate *p*-  
 756 values below significance threshold level (0.05).

757



758 Figure A1. Distributions of initial escape angles of (a) Eurasian jackdaw, (b)  
759 hooded crow, and (c) rook. The human observer is positioned at 0°, and 180°  
760 indicates an escape angle directly away from the human observer. Numbers  
761 inside the circle help to count the number of escapes in different directions. Bin  
762 intervals are 18°.

763 Figure A2. Relationships between escape duration and linearly measured  
764 distance fled by escape strategy. Blue rectangles and solid line correspond to  
765 aerial escapes, red circles with dashed line correspond to terrestrial escapes,  
766 and green triangles with semi-dashed line depict terrestrial escapes that  
767 changed into aerial escapes midway. Model estimates (black line; linear  
768 regression) are shown with 95% confidence intervals (coloured area). Only the  
769 observations that contain data on distance fled are presented.

770 Figure A3. Relationships between initial escape angle and escape duration of  
771 (a) Eurasian jackdaw, (b) hooded crow, and (c) rook. Predicted model estimates  
772 (black line) are shown with 95% confidence intervals (grey area).

773 Figure A4. Relationships between starting distance and escape duration of (a)  
774 Eurasian jackdaw, (b) hooded crow, and (c) rook. Predicted model estimates  
775 (black line) are shown with 95% confidence intervals (grey area).

776 Figure A5. Relationships between FID-phi and escape duration for approach  
777 types (a) “halt”, (b) “forward”, and (c) “chase”. Larger values of FID-phi indicate  
778 earlier escapes. Predicted model estimates (black line) are shown with 95%  
779 confidence intervals (grey area).

780

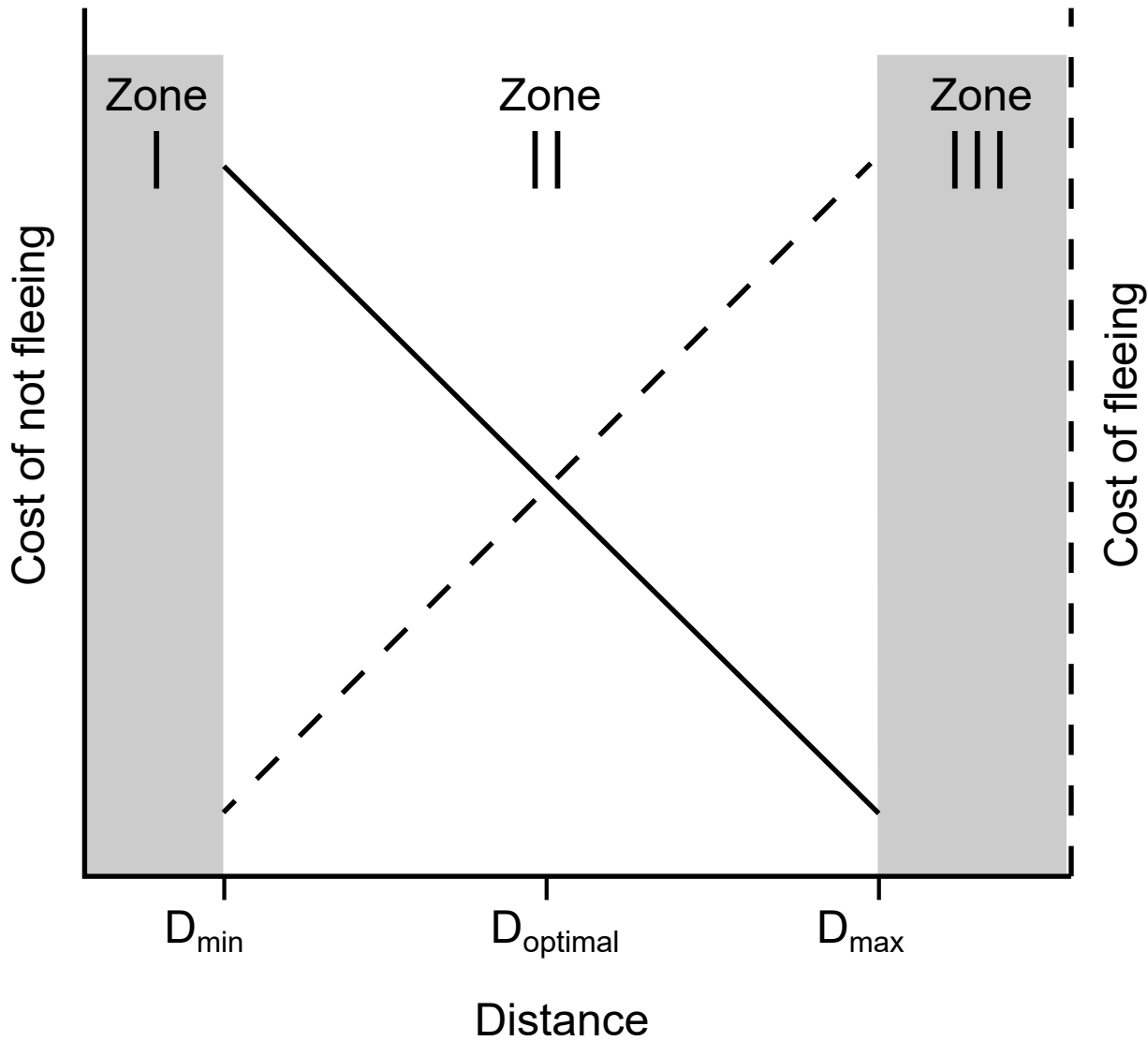
781    **Overview of Electronic Supplementary Material**

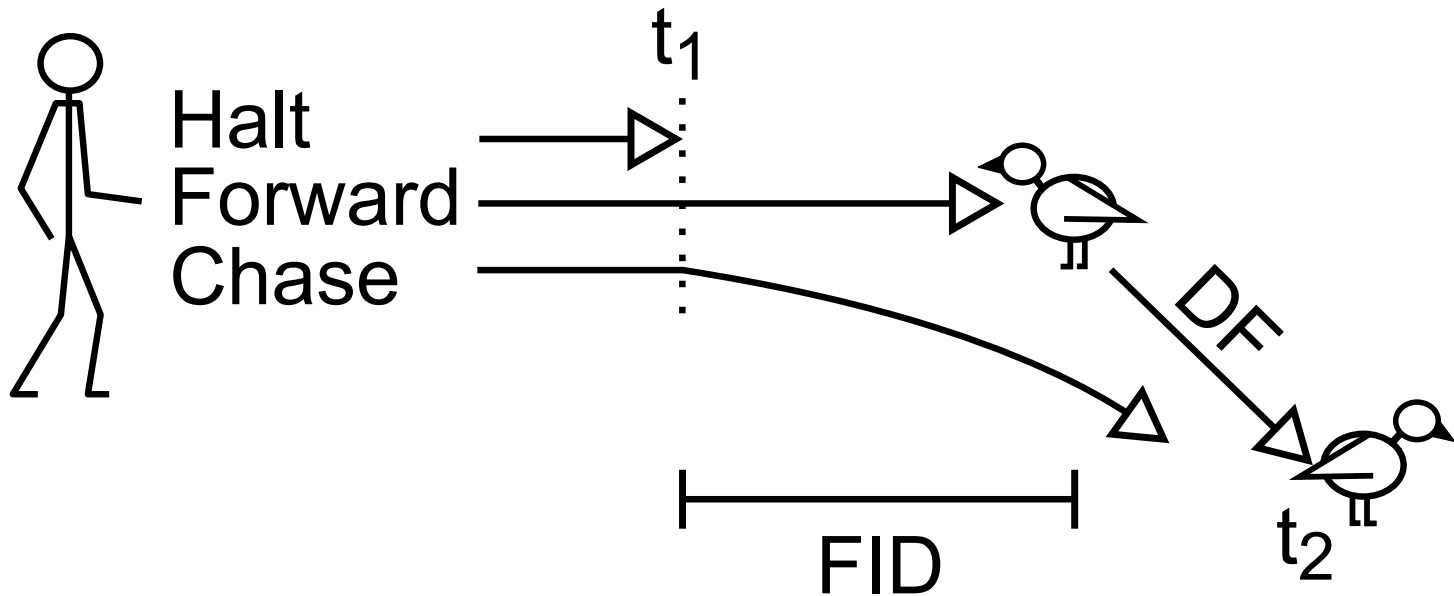
782    Electronic Supplementary Table S1. Initial top model set predicting escape  
783    duration.

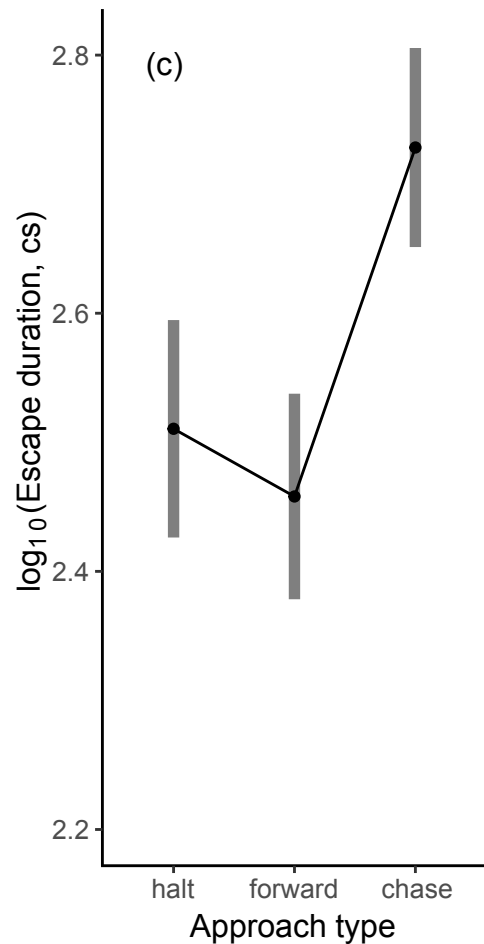
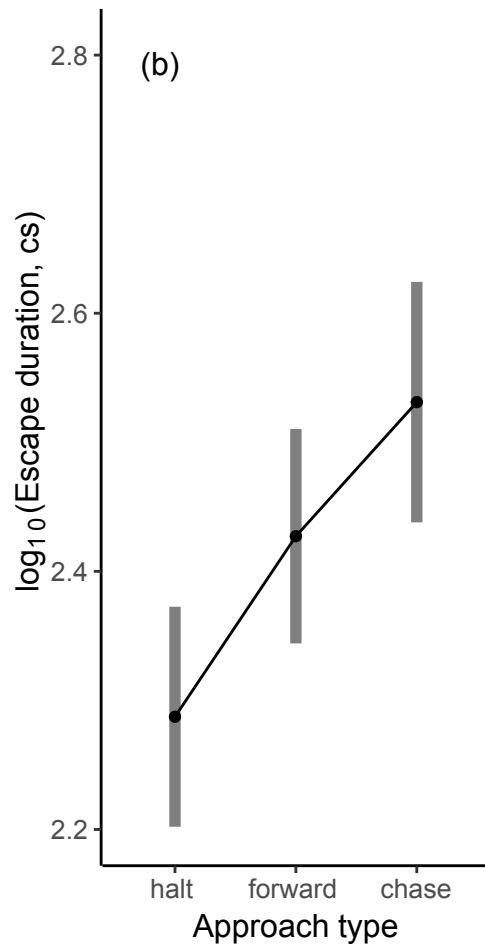
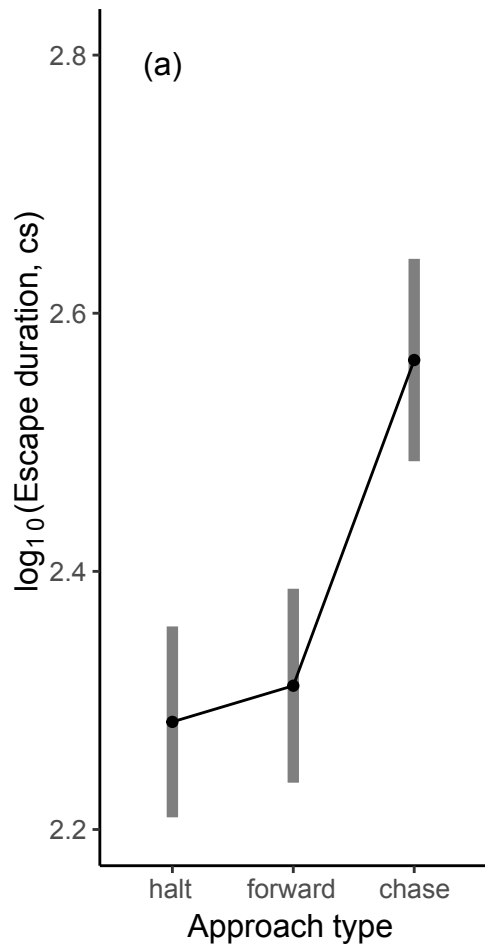
784    Electronic Supplementary Table S2. Top model set used for model averaging  
785    escape duration after removing uninformative parameters.

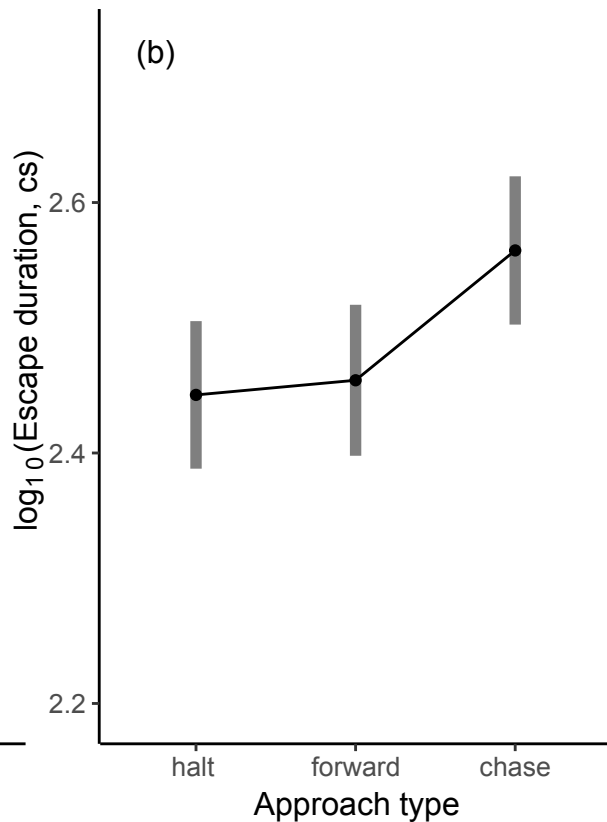
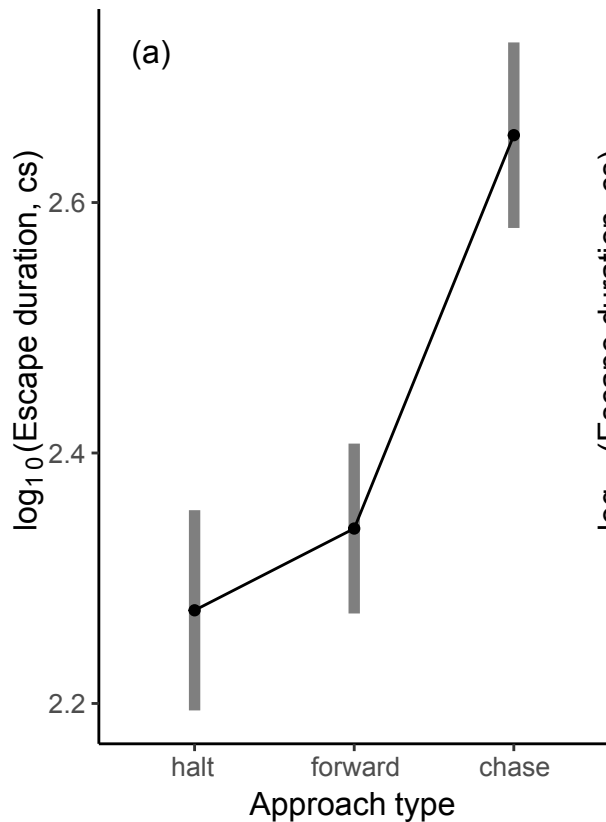
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787    escape angle.

788    Electronic Supplementary Table S4. Top model set used for model averaging  
789    angular change during escape.

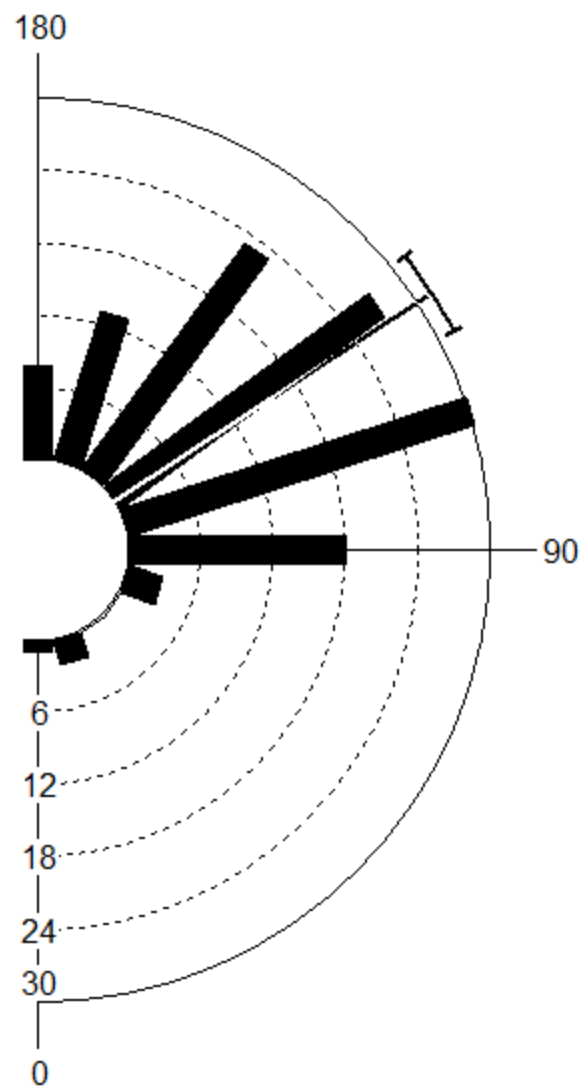




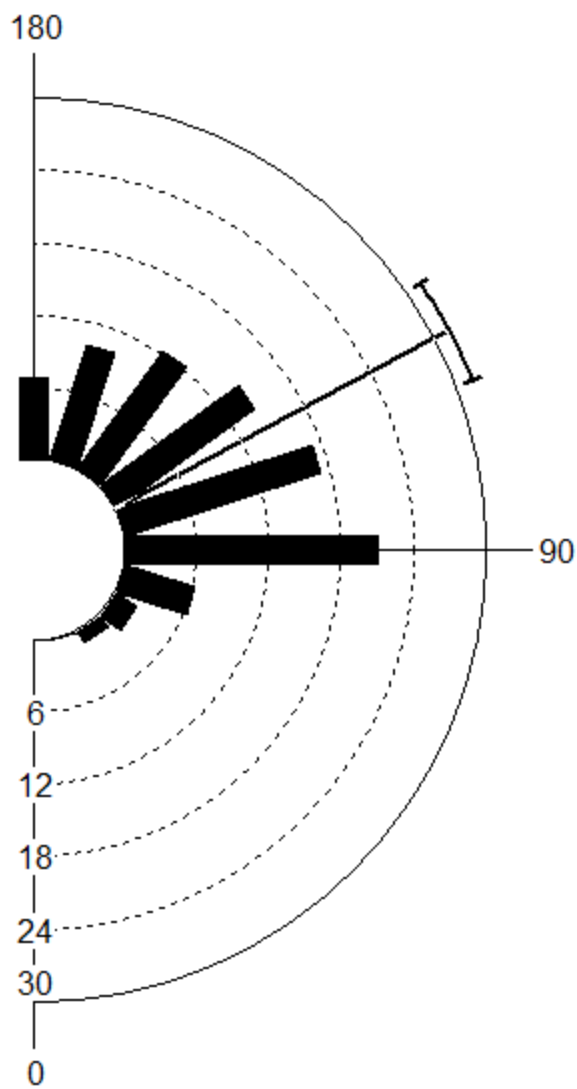




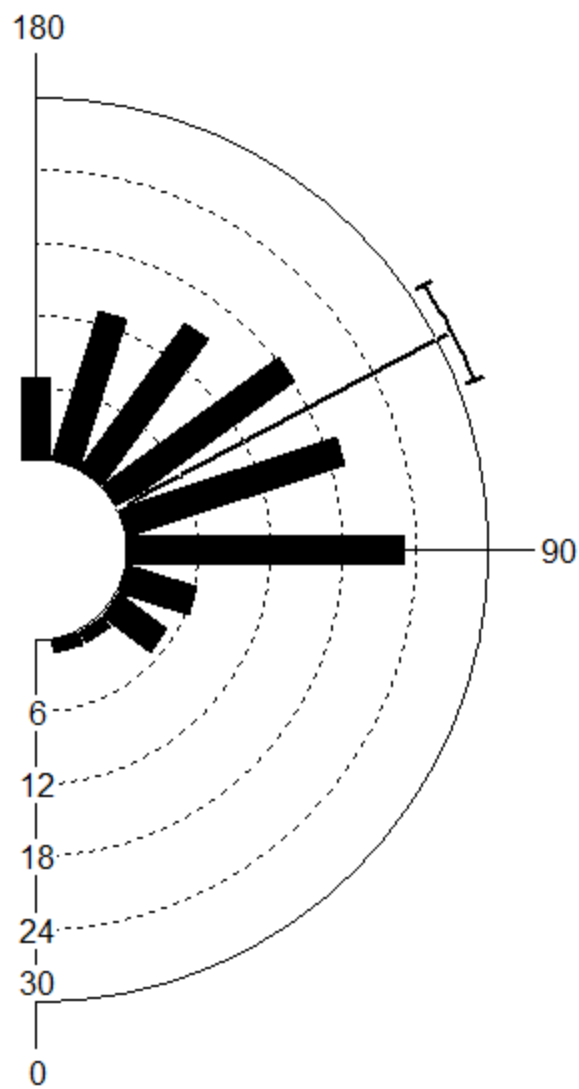
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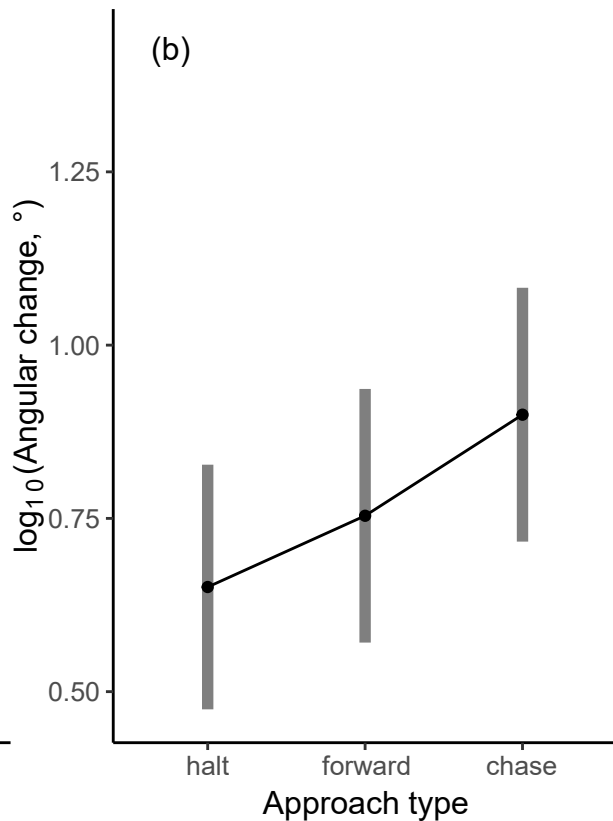
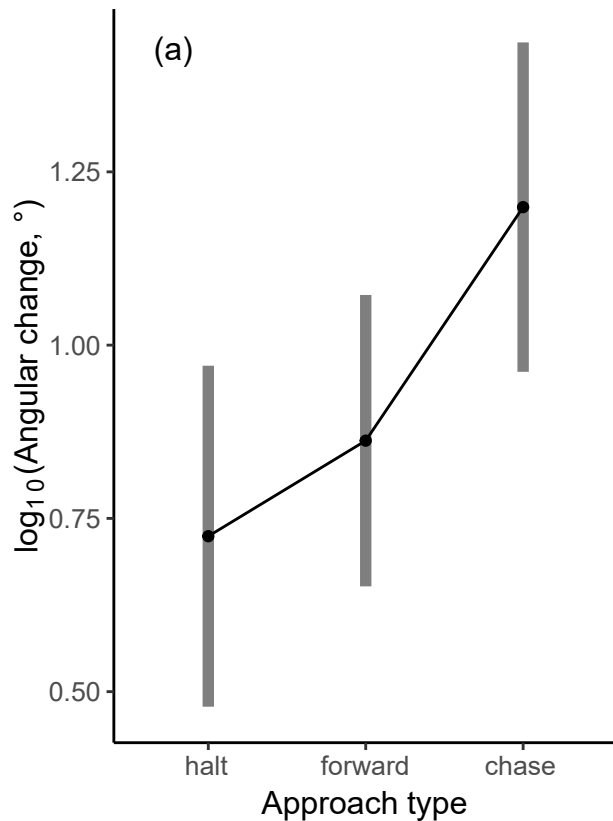


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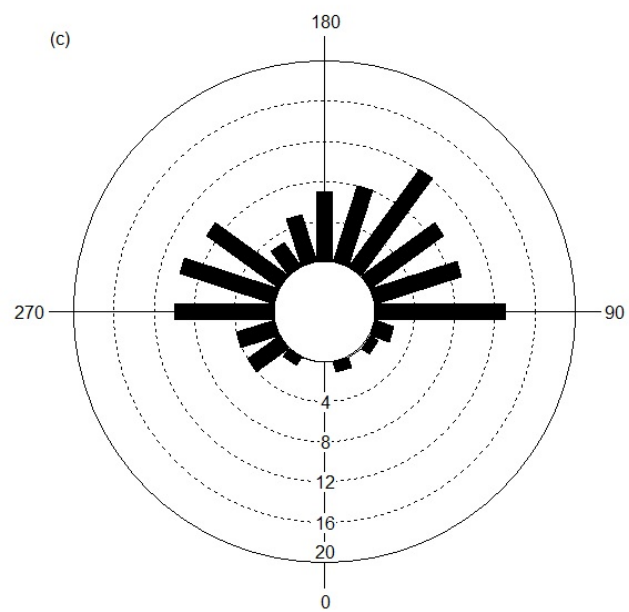
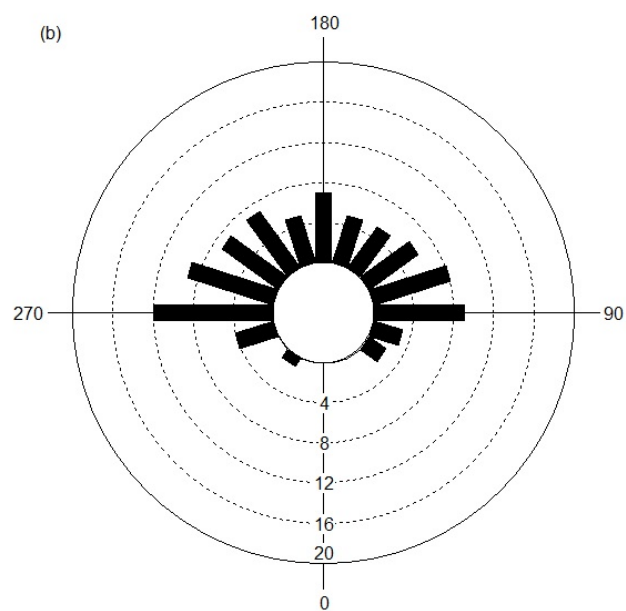
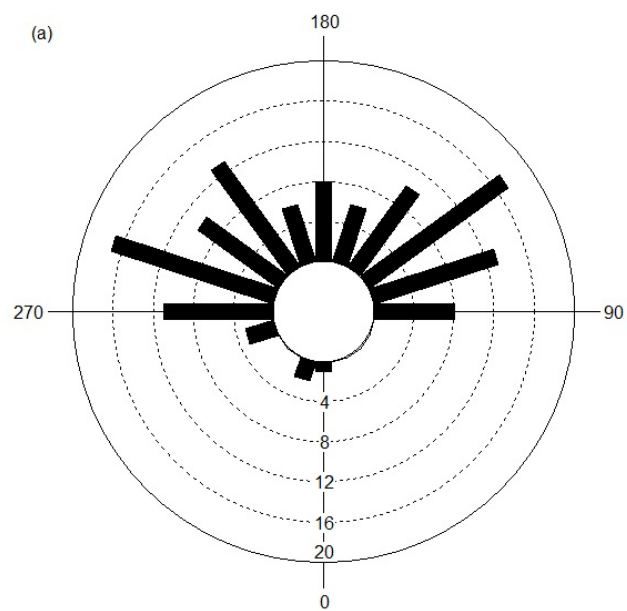


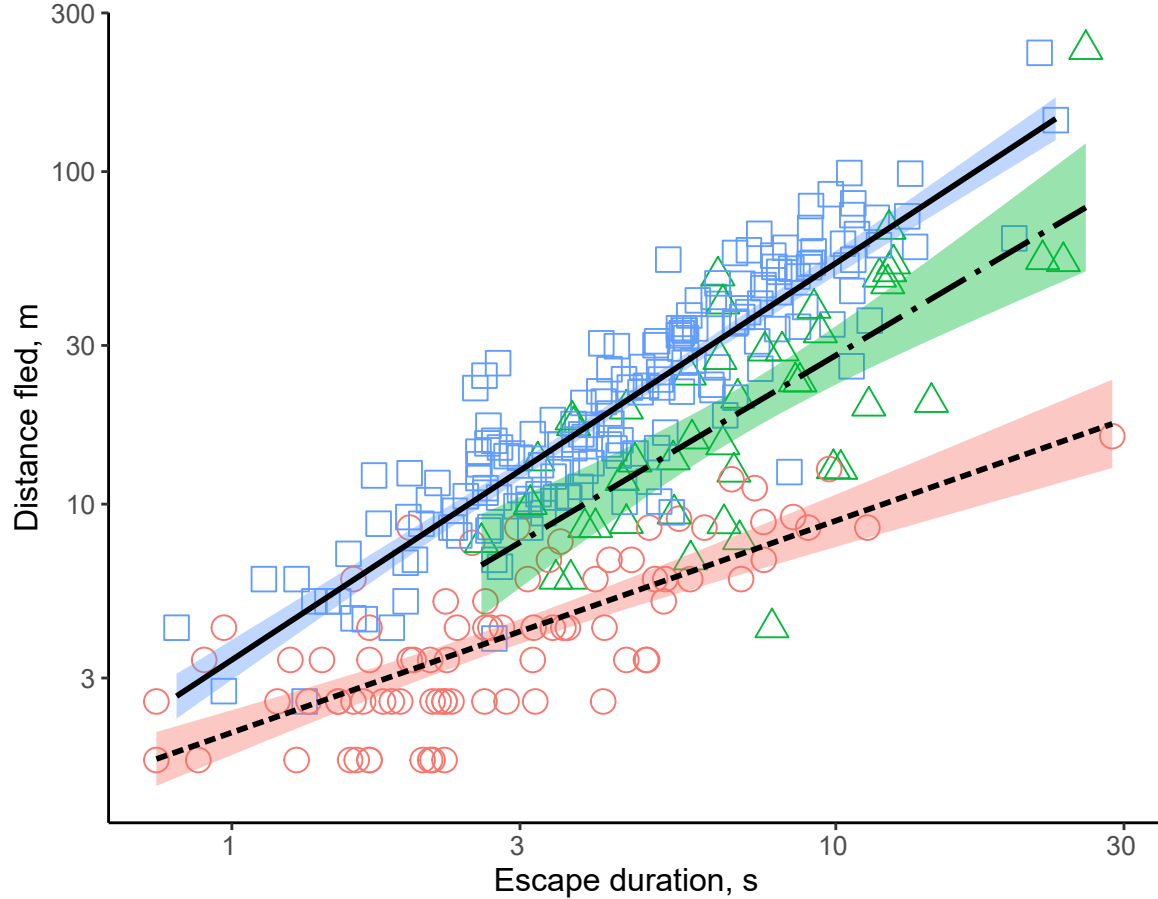
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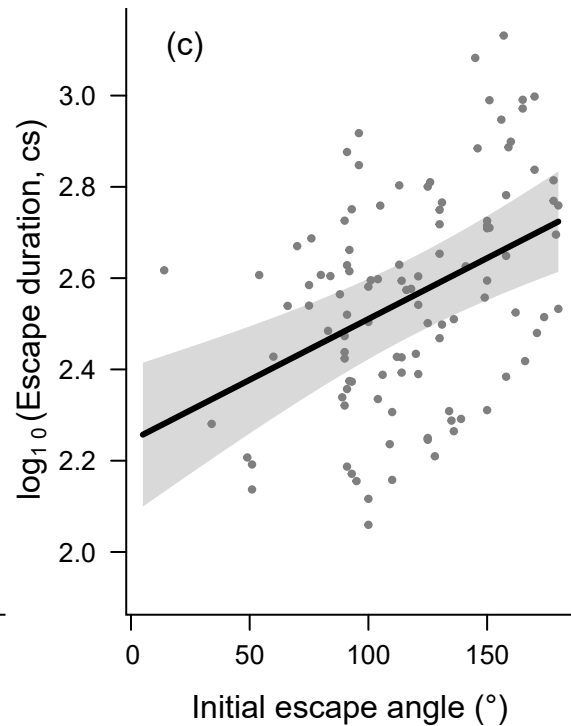
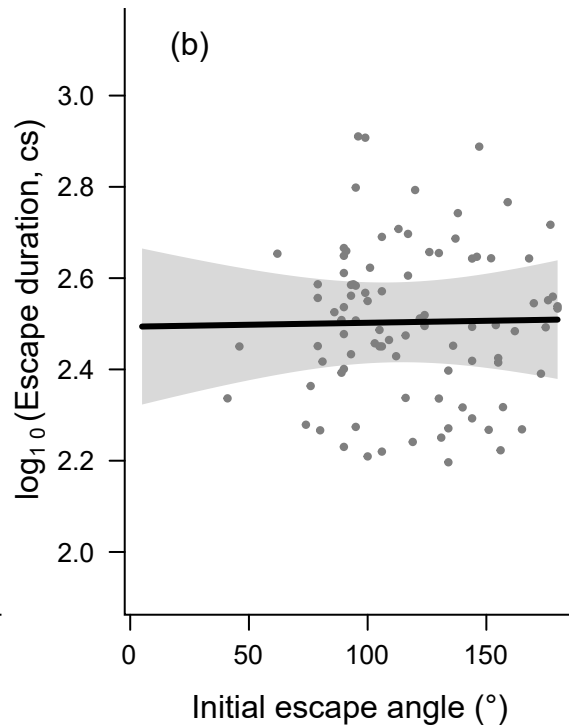
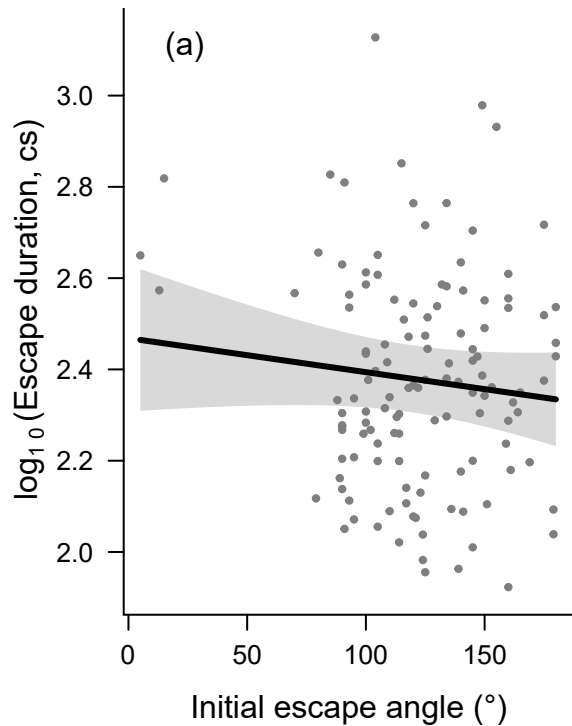


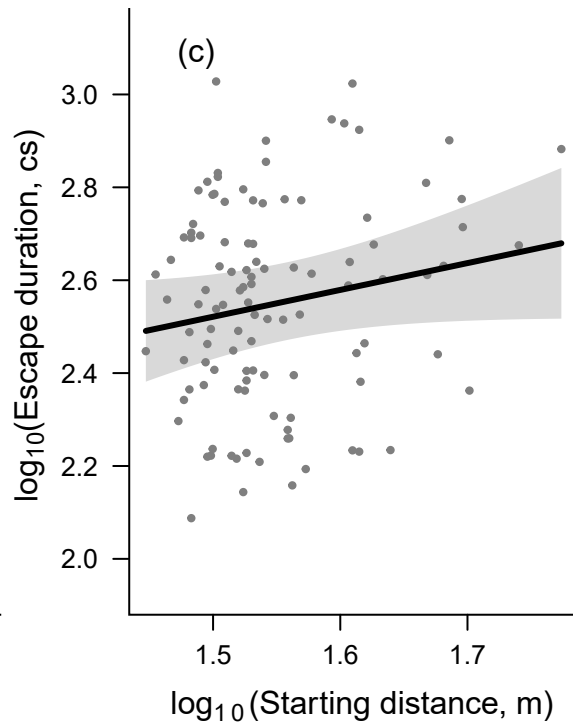
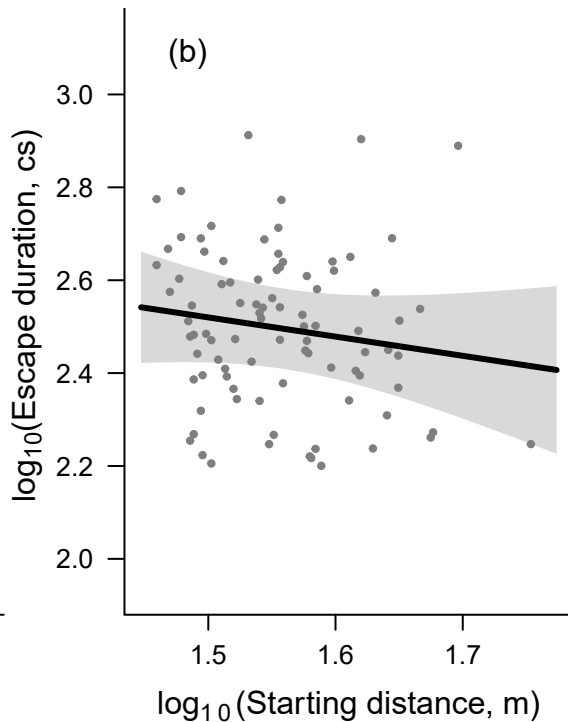
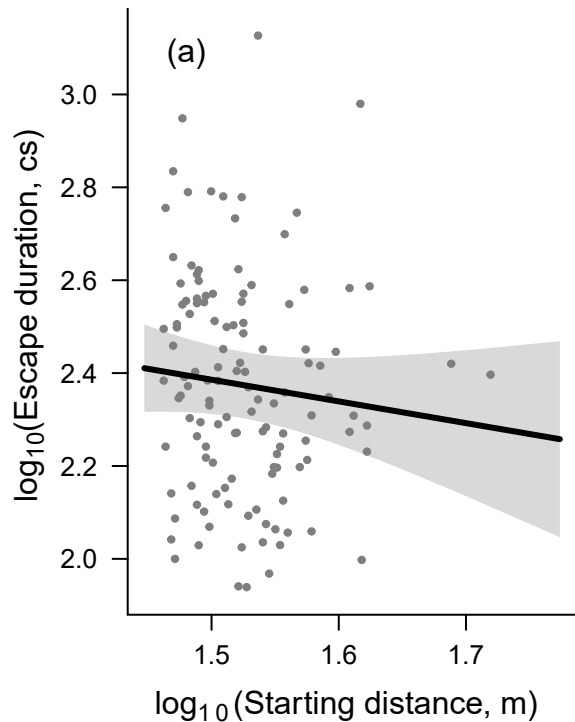


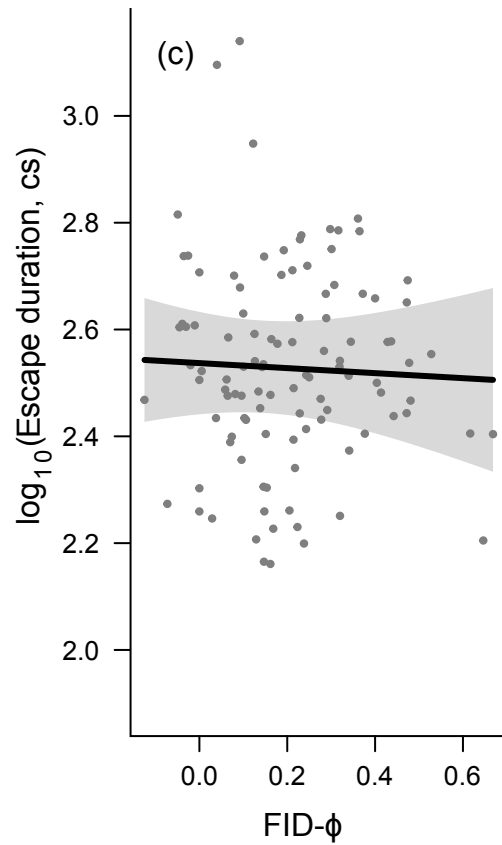
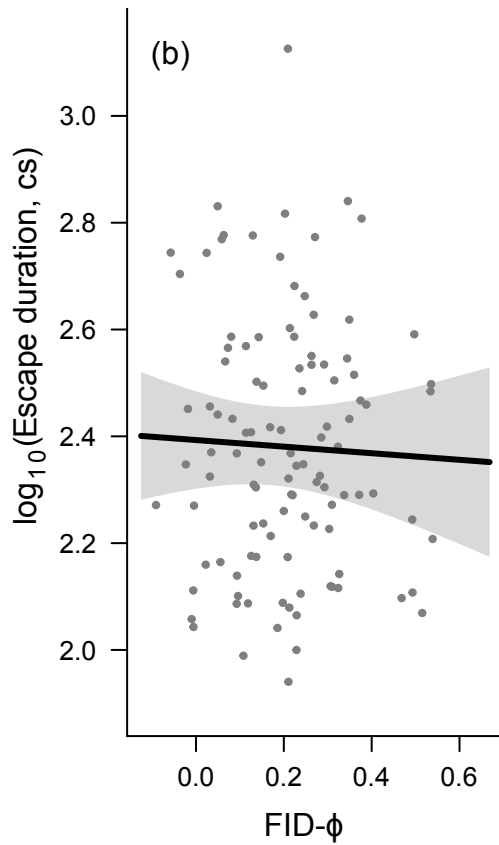
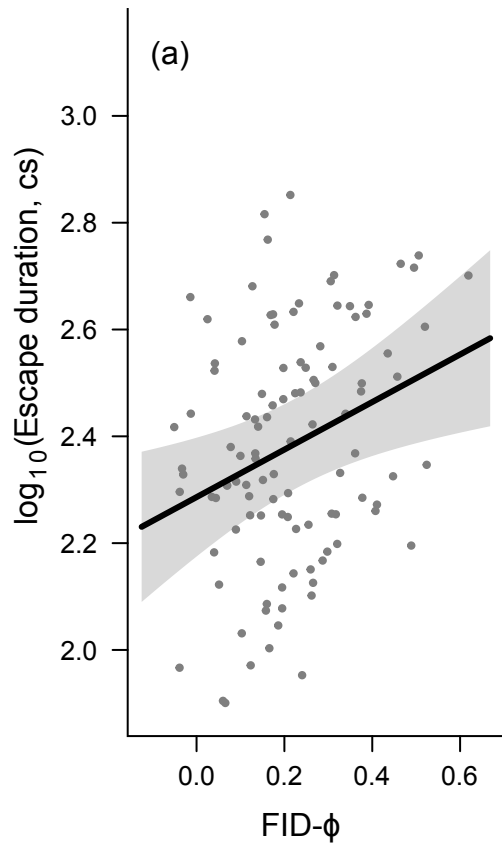












## AUTHOR STATEMENT

**Kunter Tätte:** Conceptualization, Methodology, Investigation, Formal analysis, Writing - Original Draft, Visualization **Anders Pape Møller:** Supervision, Writing - Review & Editing **Raivo Mänd:** Supervision, Writing - Review & Editing.