Corvids exhibit dynamic risk assessment during escape

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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 120º 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.

Keywords	antipredator behaviour; birds; Corvidae; escape behaviour; escape duration; risk assessment

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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]

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Fig. 1. Ydenberg Dill graphical model with addition from Blumstein.pdf [Figure]

Fig. 2. Schematic illustration of different approach types_v3.pdf [Figure]

Fig. 3. Escape duration - Approach type x Species.pdf [Figure]

Fig. 4. Escape duration - Approach type x Escape type.pdf [Figure]

Fig. 5. Initial escapes angles of Eurasian jackdaw, hooded crow, rook.pdf [Figure]

Fig. 6. Change in escape angle - Approach type x Escape type.pdf [Figure]

Fig. A1.jpg [Figure]

Fig. A2. Escape duration x Distance fled by Escape type_new_visuals.pdf [Figure]

Fig. A3. Escape duration x Escape angle by Species.pdf [Figure]

Fig. A4. Starting distance x Escape duration x Species.pdf [Figure]

Fig. A5. Escape duration x FID-phi by Approach type.pdf [Figure]

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Electronic Supplementary Table S2.xlsx [Table]

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Cover letter

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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

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-**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 120º 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 (Hatle 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 (Rodriguez-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 regretfully 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

68 risk of predation and other costs of escape to decide on the final destination. In
69 addition, the so-called zigzagging escape during chase (characterized by
70 frequent turns) is typically attributed to increasing unpredictability of escape
71 (Domenici & Ruxton 2015, p. 213), and not seen as a series of informed
72 corrections to escape trajectory. The question of dynamic risk assessment
73 (DRA) has been briefly discussed in relation to FID (Cooper 1998; Cooper
74 2006a; Bateman & Fleming 2014), time spent in refuge (Martín & López 2005),
75 and distance fled (Bateman & Fleming 2014; Collier & Hogdson 2017), but there
76 seems to be ambiguity about what is dynamic assessment and what is not.

77 Cooper (1998) was possibly the first to point out that the economic model of
78 escape (Ydenberg & Dill 1986) does not account for rapidly changing risk
79 curves, after studying how lizards react to sudden turns by an approaching
80 human. The first study to have purposefully tried to demonstrate DRA in escape
81 behaviour was by Cooper (2006a), who examined how lizards change their FID
82 in relation to the speed of an approaching predator. More specifically, Cooper
83 (2006a) tested whether switching his walking speed from slow to fast, and from
84 fast to slow during approach have a different effect on FID from not changing
85 speed midway. It was evident that slow and fast-slow speeds resulted in a
86 highly similar short FID, and fast and slow-fast speeds had a similar long FID.
87 Cooper (2006a) concluded that FID depends only on the final approach speed,
88 and that this was strong evidence for his hypothesis that prey continuously
89 assess the predation risk when encountering a predator.

90 Other studies that have attempted to demonstrate DRA in escape have been
91 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 360º 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: 180º to maximize distance from the predator (sometimes followed by a turn towards the predator to fly over it), and 90º 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)

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

173 ***2.2 Starting distance***

174 Upon finding a corvid on the ground, we measured the starting distance (i.e. the
175 distance between the observer and the bird) with Laser Rangefinder
176 PROSTAFF 3i (Nikon Vision Co., Ltd., Tokyo, Japan; measurement range 7.3–
177 590 m, accuracy 0.1 m). We avoided starting distances that were considerably
178 shorter than 30 m because with short starting distances, there is a risk that the
179 bird is already in the zone of maximum risk where prey immediately escape
180 when spotting a predator (Fig. 1; Blumstein 2003). Furthermore, unpublished
181 data from our previous studies indicates that the three selected species of
182 corvids very rarely have FIDs longer than 24 m in Estonian urban areas (6
183 observations out of 486). In the present study, starting distances ranged from
184 28.0 m to 59.4 m and the median was 33.7 m (1^{st} quartile 31.3, 3^{rd} quartile
185 37.4). We also recorded the activity of the focal bird. Out of the total 323
186 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

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

217 ***2.5 Escape duration and its predictors***

218 We noted whether escape was terrestrial, aerial, or both (i.e. the bird switched
219 from terrestrial to aerial escape strategy while fleeing). However, in the
220 statistical models we used a binary escape strategy where terrestrial strategy
221 also includes the strategy “both”, because there were too few observations from
222 the category “both” to make more precise models. Escape duration was
223 measured with a stopwatch from the moment escape was initiated until the bird
224 stopped (even if temporarily) with centisecond (cs) precision. If a bird escaped
225 out of sight (13.3% of cases: N = 15 for approach type ”halt”, N = 14 for type
226 ”forward”, and N = 14 for type ”chase”), counting immediately stopped. Each
227 escape trajectory was drawn onto a circle by visual estimation to measure initial
228 and final escape angle in relation to the observer. Later, the difference between
229 initial and final escape angles was defined as change in escape angle.
230 Whenever possible (93.2% of cases), distance fled was linearly measured in
231 addition to escape duration, as in Tätte et al. (2018), but we preferred to use
232 escape duration as the dependent variable because it is a more precise
233 characteristic when dealing with non-linear escape paths (e.g. zigzag
234 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 – (distance approached / 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 (Bartoñ 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, χ^2 (1, N = 82) = 33.38, $p < 0.001$, and also compared with approach type "forward" (7/46), χ^2 (1, N = 89) = 33.95, $p < 0.001$. There was no significant difference in escape strategies between approach type "halt" and "forward", χ^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", χ^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 ΔAIC < 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” (β = −0.174, SE = 0.051, p < 0.001) and “forward” (β = −0.125, SE = 0.044, p = 0.005), it showed an opposite trend for approach type ”chase” (β = 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

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

356 ***3.4 Change in escape angle***

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

368 **4. DISCUSSION**

369 ***4.1 Overview***

370 The main goal of the current study was to examine whether birds dynamically
371 adjust escape behaviour during escape according to the perceived risk of
372 predation. The most apparent finding to emerge from this study was that corvids
373 can easily differentiate between a predator (in this case, a human observer) that
374 pursues (approach type "chase") and one that immediately stops approaching
375 when the bird initiates escape (approach type "halt"), by increasing time spent
376 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; Tätte 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

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

441 ***4.4 Escape duration in relation to FID and starting distance***

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

449 indication that late escapes did not suffer from worse initial escape angles. As a
450 reminder, escape duration was the longest for birds trying to escape terrestrially
451 when being chased, but the shortest when the predator stops (Fig. 4).
452 Therefore, it could be that boldness is an effective way to reduce costs of
453 escape if the predator is unwilling to pursue prey, although otherwise, boldness
454 can be costly. For example, Namibian rock agamas (*Agama planiceps*) with
455 consistently shorter FIDs, i.e. a bolder personality type, spent more time
456 basking, eating and moving around than shyer individuals, but at the same time
457 suffered higher rates of tail loss – an indication of higher predation risk (Carter
458 et al. 2010).

459 An interesting side-result was that starting distance, i.e. the distance at which
460 the observer started his approach, was in a positive relationship with escape
461 duration for the rook but not for the other two species (Fig. A4). While the
462 positive – and variously interpreted – relationship between starting distance and
463 FID is frequently shown in numerous taxa (Blumstein 2003), a relationship
464 between starting distance and distance fled has not been found (e.g. Tätte et al.
465 2018; Kalb et al. 2019). The latter is not surprising if it is a species-specific trait
466 as seen in our study. We do not know the exact reason for why only the rook
467 increased escape duration when approached at a longer starting distance, but it
468 could once again be related to wariness of the species (as discussed in chapter
469 4.3). For example, Tätte et al. (2018) hypothesized that the relationship
470 between starting distance and FID was positive in rural but not in urban habitat
471 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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REFERENCES

Bartoñ K. 2017. MuMIn: Multi-Model Inference. R package version 1.40.0. https://CRAN.R-project.org/package=MuMIn

Bateman PW, & Fleming PA. 2014. Switching to Plan B: changes in the escape tactics of two grasshopper species (*Acrididae: Orthoptera*) in response to repeated predatory approaches. *Behavioral Ecology and Sociobiology*, 68(3): 457-465.

Bates D, Maechler M, Bolker B, & Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1): 1–48. doi:10.18637/jss.v067.i01.

Breheny P, & Burchett W. 2017. visreg: Visualization of Regression Models. R package version 2.4-1. https://CRAN.R-project.org/package=visreg

Broom M, & Ruxton GD. 2005. You can run—or you can hide: optimal strategies for cryptic prey against pursuit predators. *Behavioral Ecology*, 16(3): 534-540.

Blumstein DT. 2003. Flight-initiation distance in birds is dependent on intruder starting distance. *Journal of Wildlife Management*, 67: 852-857.

Blumstein DT. 2006. Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Animal Behaviour*, 71(2): 389–399.

Carter AJ, Goldizen AW, & Tromp SA. 2010. Agamas exhibit behavioral syndromes: bolder males bask and feed more but may suffer higher 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, & Maclennan 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-
619 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.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Ydenberg RC, & Dill LM. 1986. The economics of fleeing from predators. *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 ($D_{optimal}$). 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).

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

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

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	*t*	*p*
Eurasian jackdaw *(Coloeus monedula)*						
	”halt”–“forward”	−0.025	0.050	340	−0.50	0.871
	”halt”–“chase”	**−0.280**	0.051	339	−5.50	< 0.001
	”forward”–“chase”	**−0.255**	0.052	338	−4.91	< 0.001
Hooded crow *(Corvus cornix)*						
	”halt”–“forward”	**−0.144**	0.059	346	−2.45	0.039
	”halt”–“chase”	**−0.259**	0.062	340	−4.19	< 0.001
	”forward”–“chase”	−0.115	0.061	341	−1.89	0.143
Rook *(Corvus frugilegus)*						
	”halt”–“forward”	0.030	0.055	345	0.55	0.849
	”halt”–“chase”	**−0.239**	0.056	347	−4.29	< 0.001
	”forward”–“chase”	**−0.269**	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).

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

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

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

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	2.5th	97.5th	z	w_{ip}
(Intercept)	**2.099**	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”	**0.421**	0.060	0.304	0.538	7.05	1.00
Escape strategy	**0.191**	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	**−0.295**	0.071	−0.434	−0.156	4.15	1.00
Distance to refuge	**0.096**	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)	**0.218**	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)	**0.229**	0.048	0.134	0.323	4.74	1.00
FID-phi	**0.404**	0.202	0.008	0.801	2.00	0.78
Approach type “forward” * FID-phi	**−0.534**	0.229	−0.983	−0.084	2.33	0.68
Approach type “chase” * FID-phi	**−0.531**	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)	**1.109**	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

The natural average method was used for model averaging (on 13 models with ΔAIC < 4, see Electronic Supplementary Table S2). Parameter estimates are followed by unconditional standard errors (SE) and 2.5^{th} and 97.5^{th} 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**	**2.5th**	**97.5th**	***z***	***w$_{ip}$***
(Intercept)	**1.830**	0.066	1.701	1.958	27.85	
FID-phi	**−0.506**	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 ΔAIC < 4, see Electronic Supplementary Table S3). Parameter estimates
737 are followed by unconditional standard errors (SE) and 2.5th and 97.5th
738 percentiles (95% CI). W_{ip} 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

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

Predictor	Estimate	SE	2.5th	97.5th	*z*	w_{ip}
(Intercept)	**−2.919**	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”	**0.342**	0.116	0.114	0.571	2.94	1.00
Escape duration	**1.544**	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)	**−0.203**	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

746 The natural average method was used for model averaging (on 15 models with
747 ΔAIC < 4, see Electronic Supplementary Table S4). Parameter estimates are
748 followed by unconditional standard errors (SE) and 2.5th and 97.5th percentiles
749 (95% CI). W_{ip} is the relative importance of each predictor in the model set.
750 Estimates in bold indicate that 95% CI does not include 0. City district was
751 included as random effect.

752

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	*t*	*p*
Terrestrial escape						
	”halt”–“forward”	−0.153	0.153	339	−1.00	0.577
	”halt”–“chase”	**−0.494**	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

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

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

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

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

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

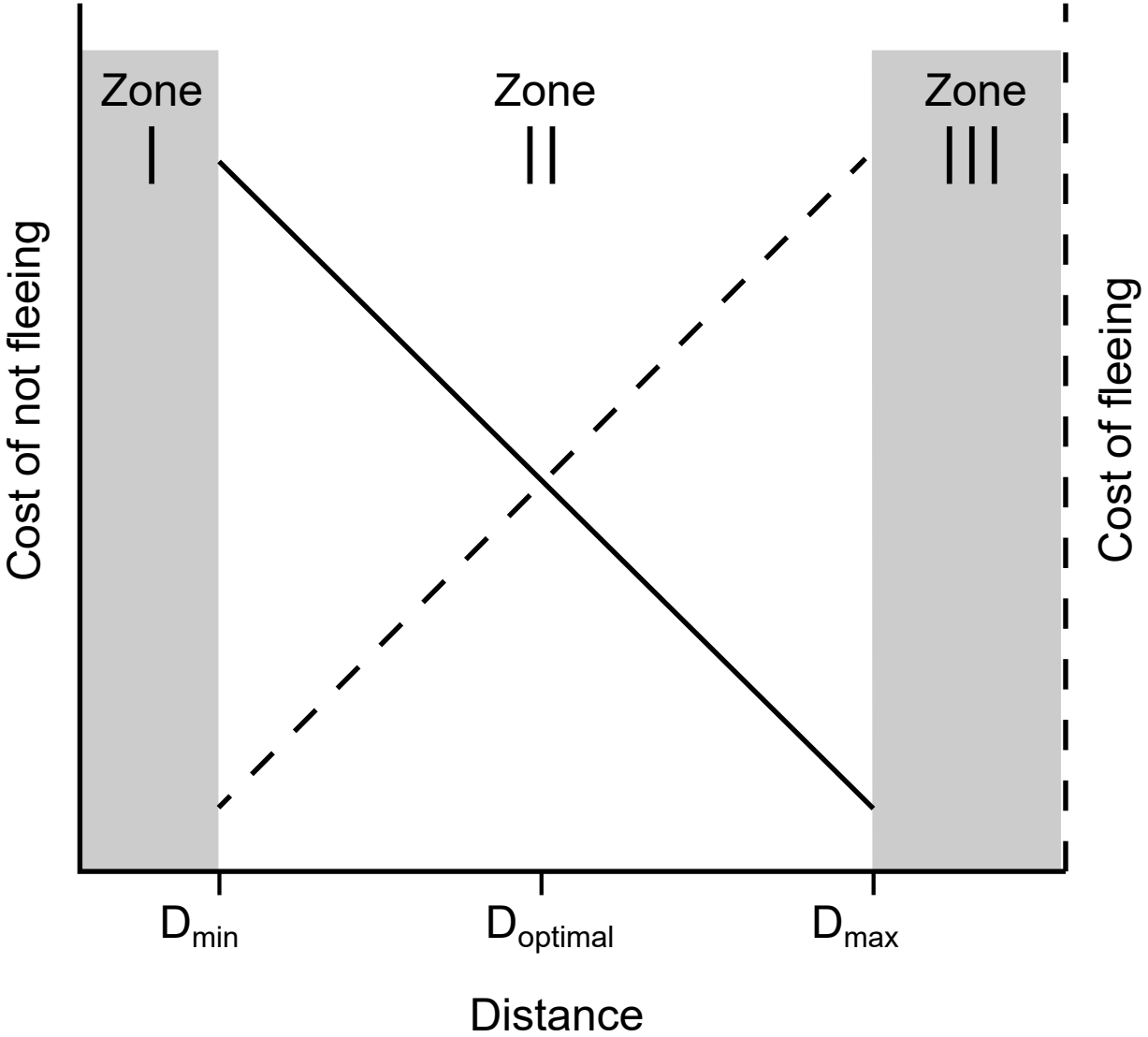
Overview of Electronic Supplementary Material

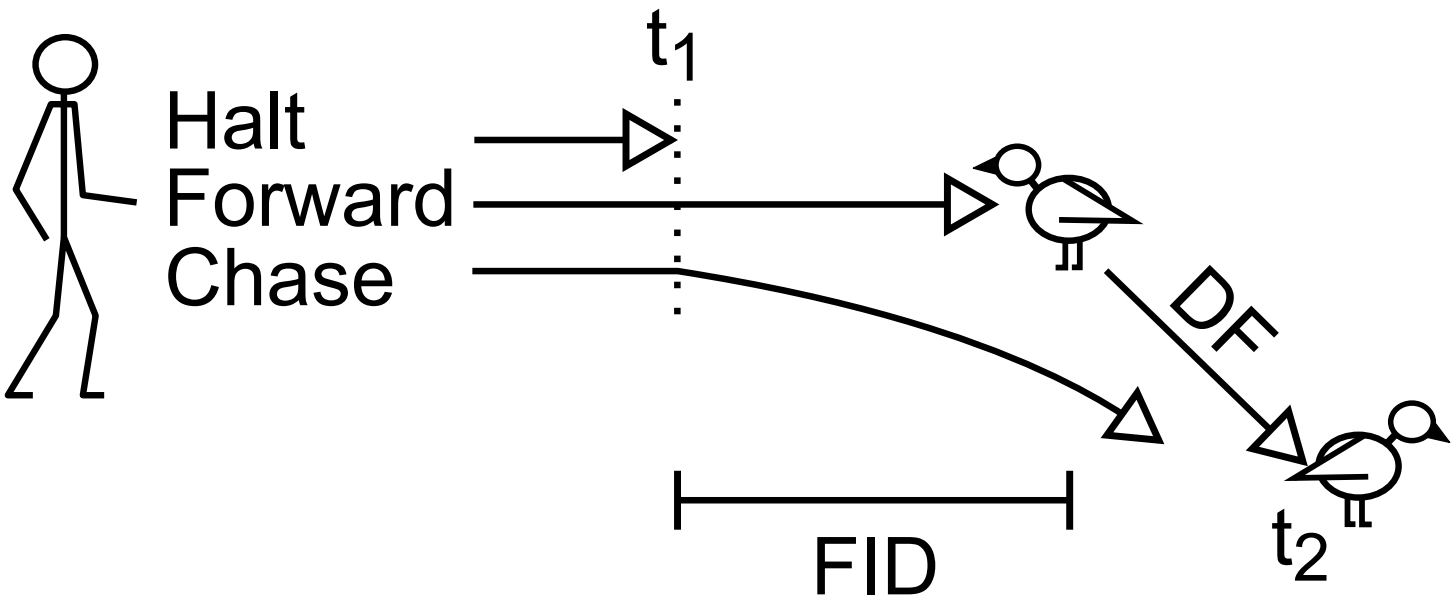
Electronic Supplementary Table S1. Initial top model set predicting escape duration.

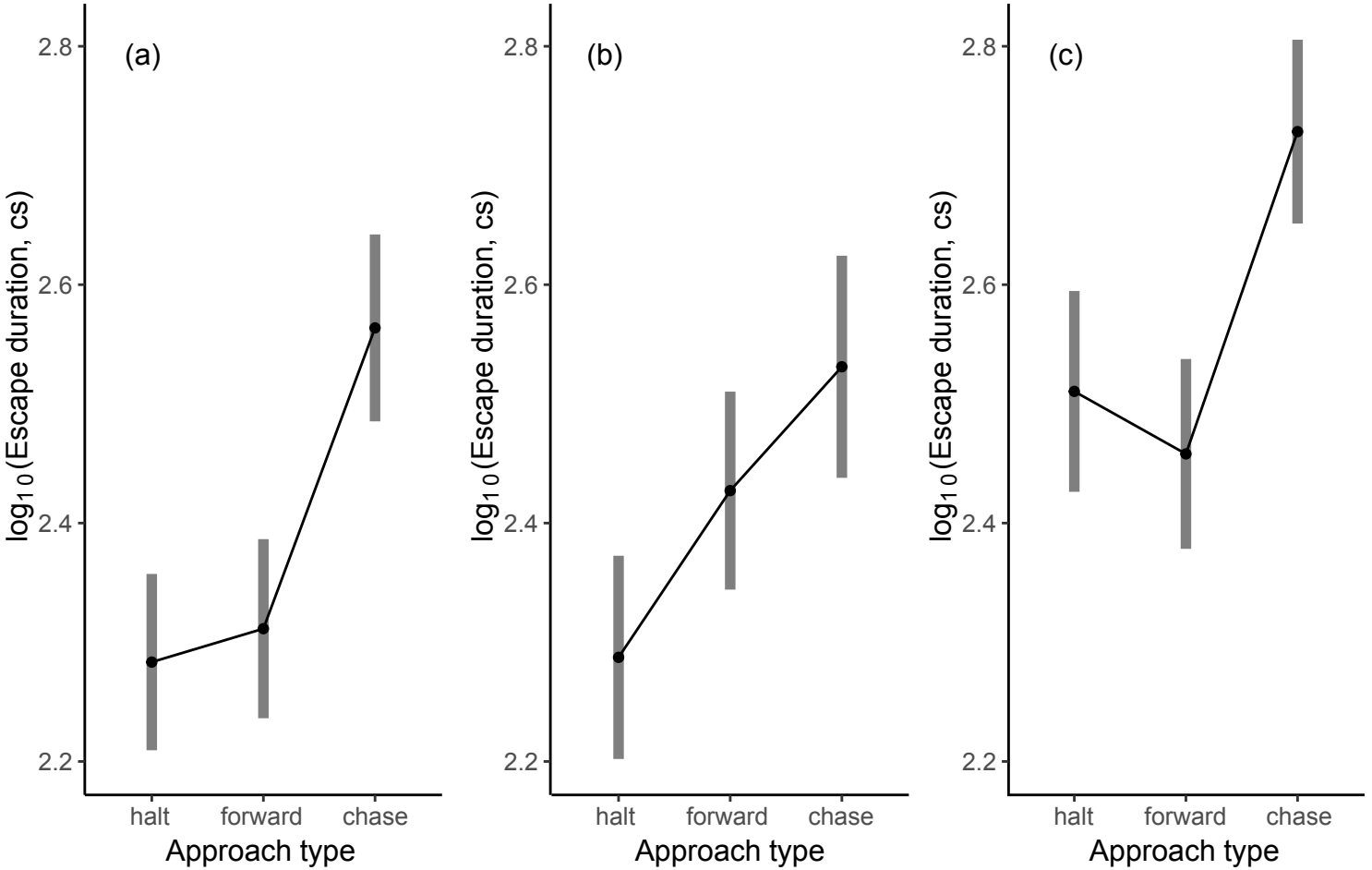
Electronic Supplementary Table S2. Top model set used for model averaging escape duration after removing uninformative parameters.

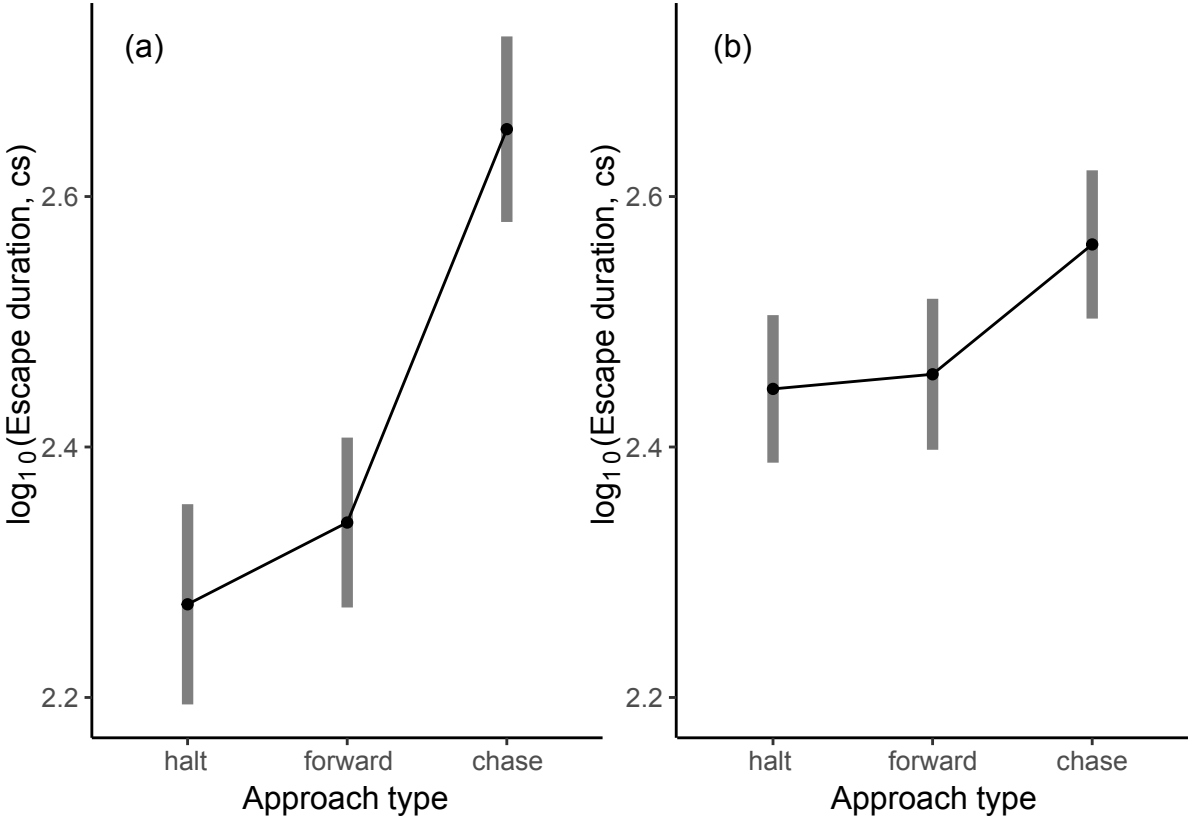
Electronic Supplementary Table S3. Top model set used for model averaging escape angle.

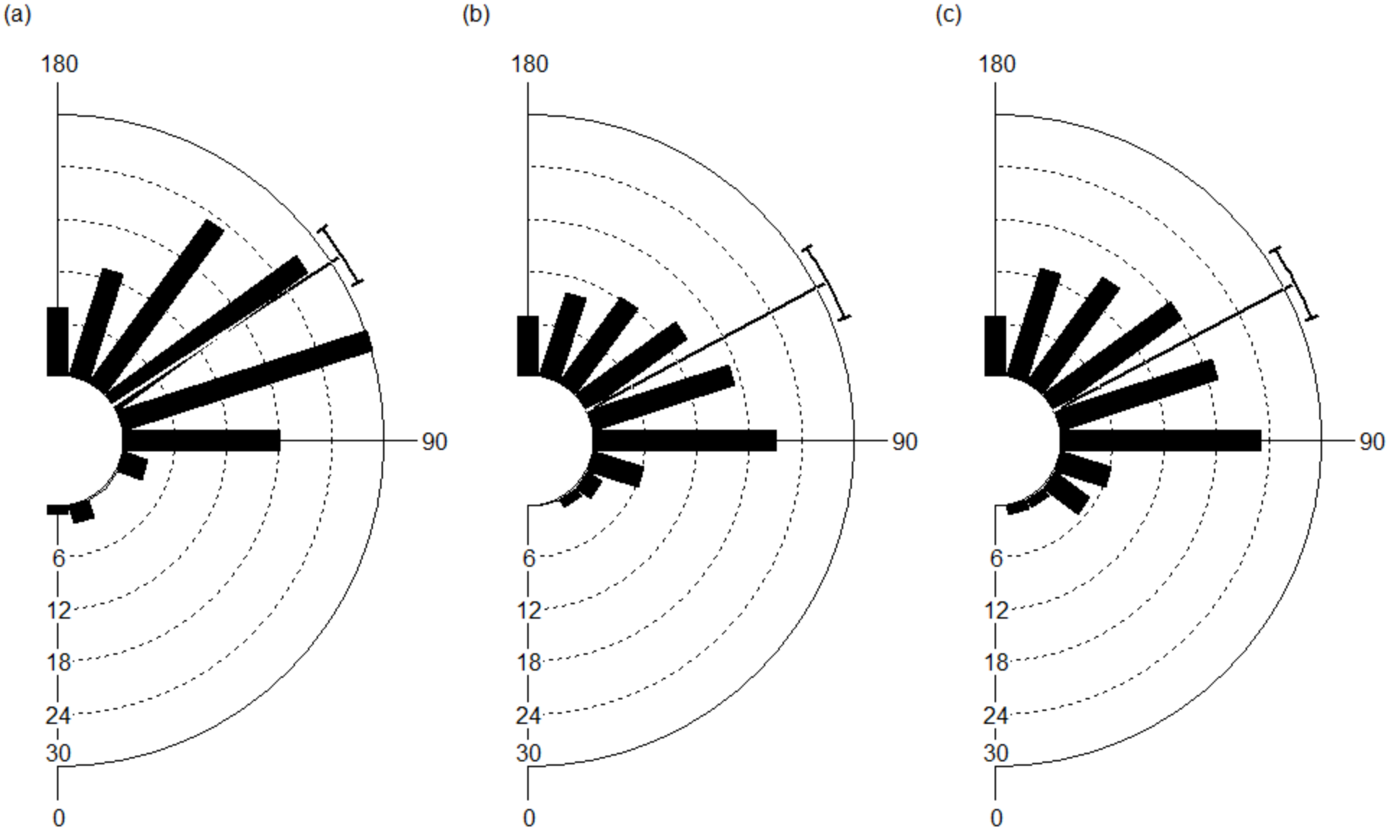
Electronic Supplementary Table S4. Top model set used for model averaging angular change during escape.

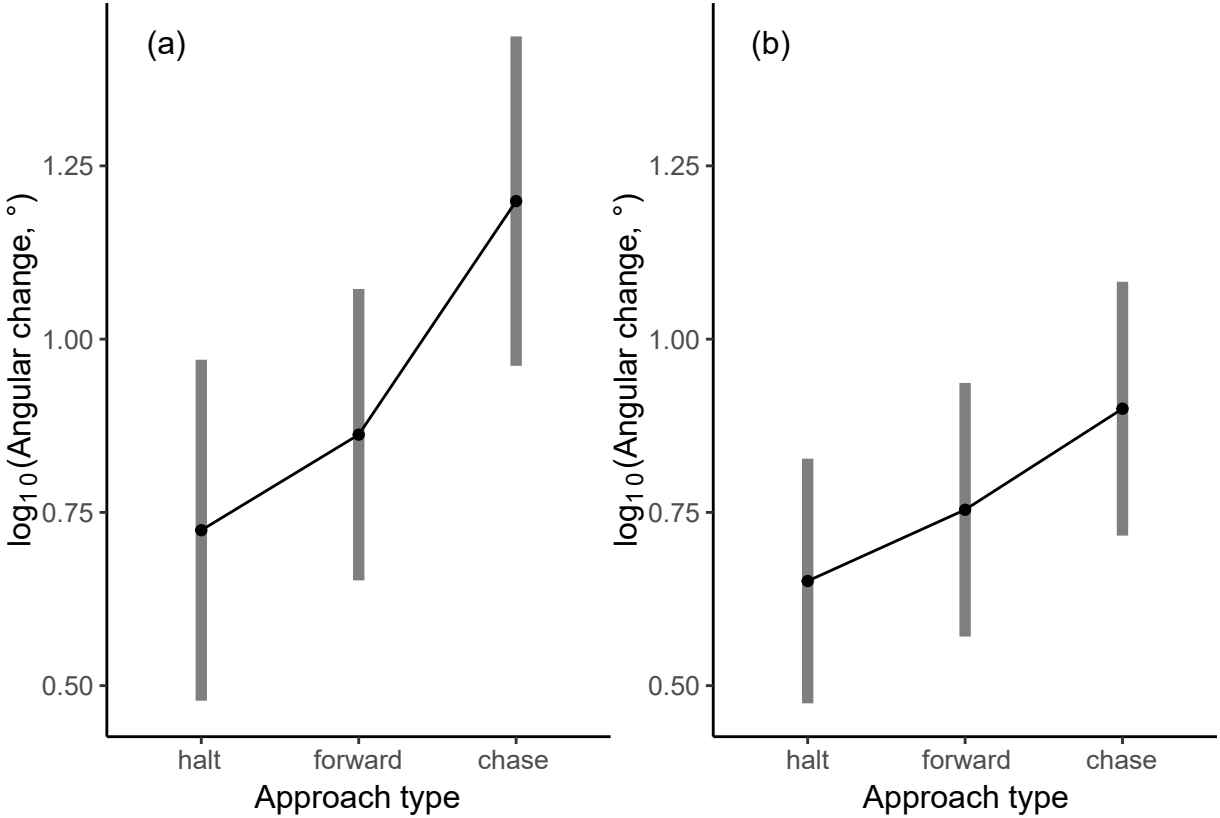

Zone I
Zone II
Zone III
Cost of not fleeing
Cost of fleeing
D_{min}
$D_{optimal}$
D_{max}
Distance

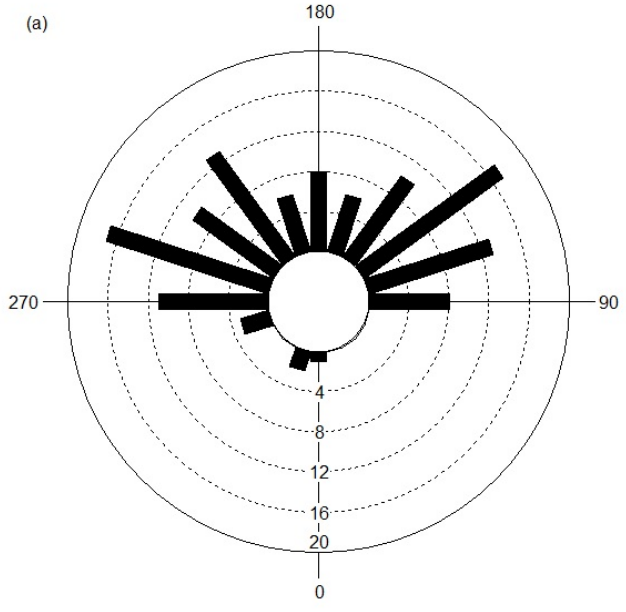

t1
Halt
Forward
Chase
DF
FID
t2

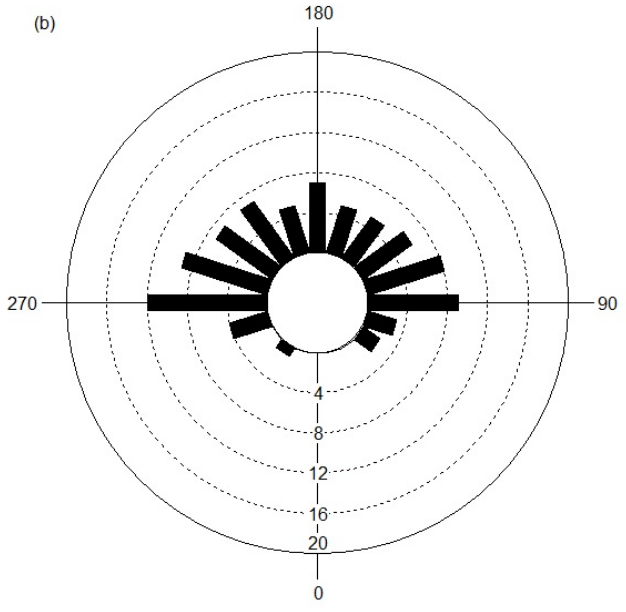

(a)
(b)
(c)
2.8
2.6
2.4
2.2
log10(Escape duration, cs)
halt
forward
chase
Approach type

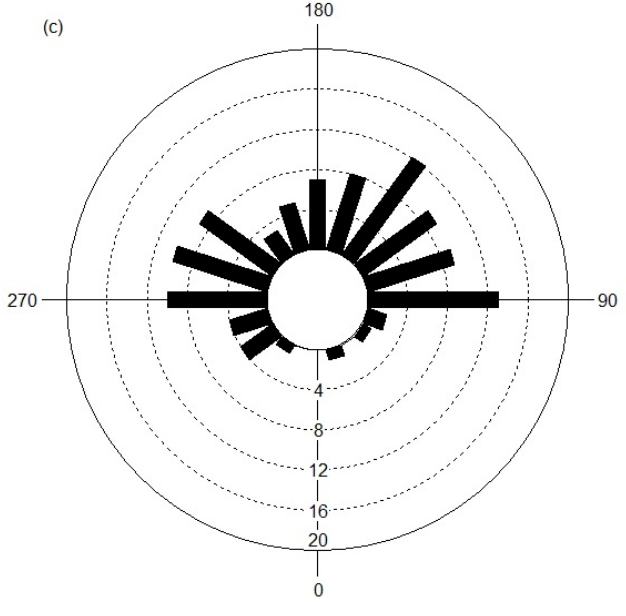

(a)
(b)
log10(Escape duration, cs)
2.6
2.4
2.2
halt
forward
chase
Approach type

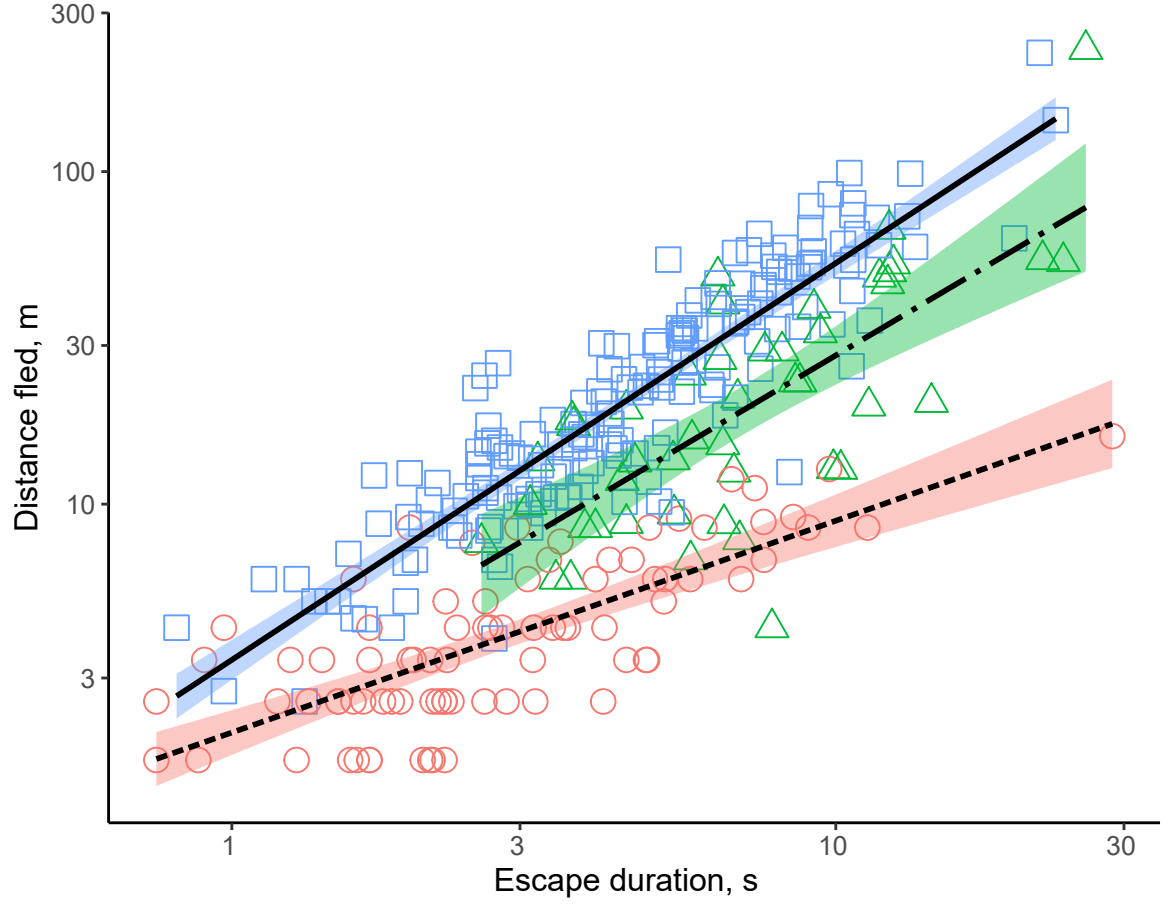

(a)
(b)
(c)
180
90
0
6
12
18
24
30

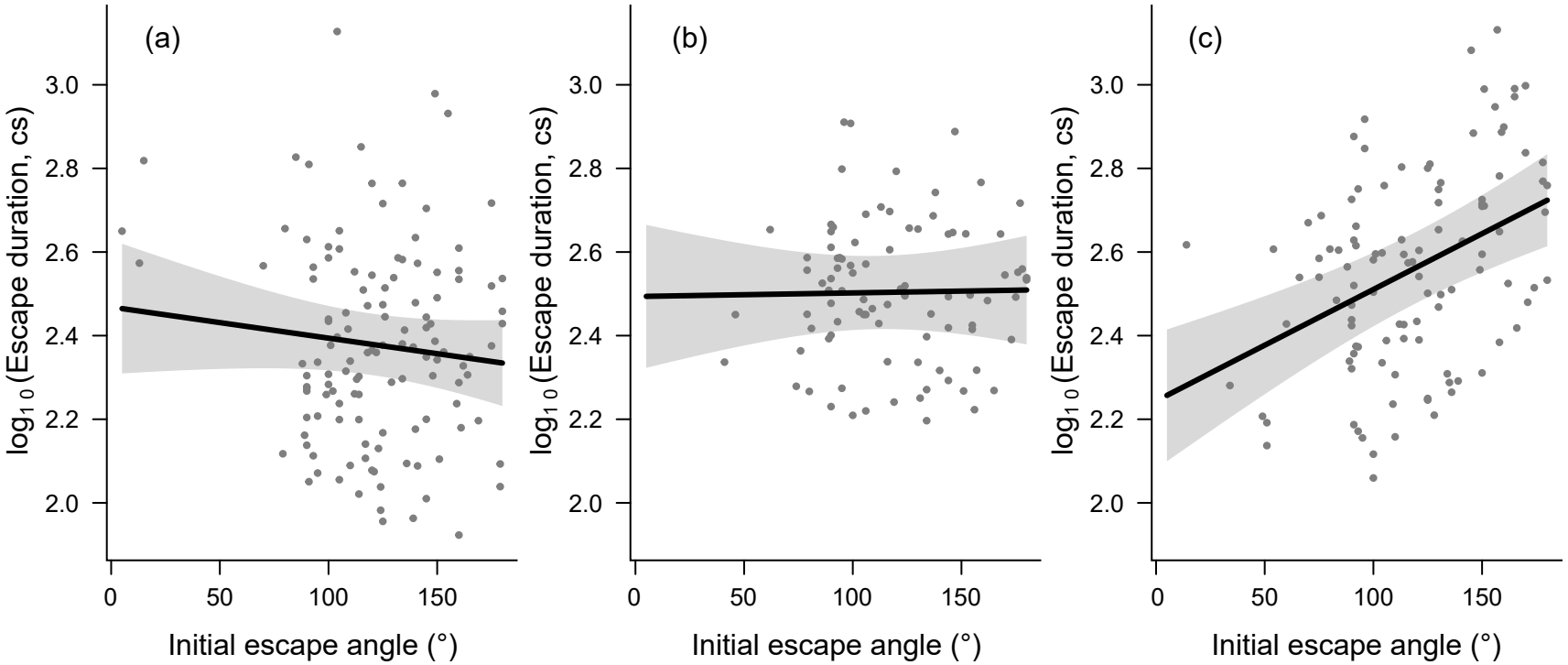

(a)
(b)
1.25
1.00
0.75
0.50
log10(Angular change, °)
halt
forward
chase
Approach type

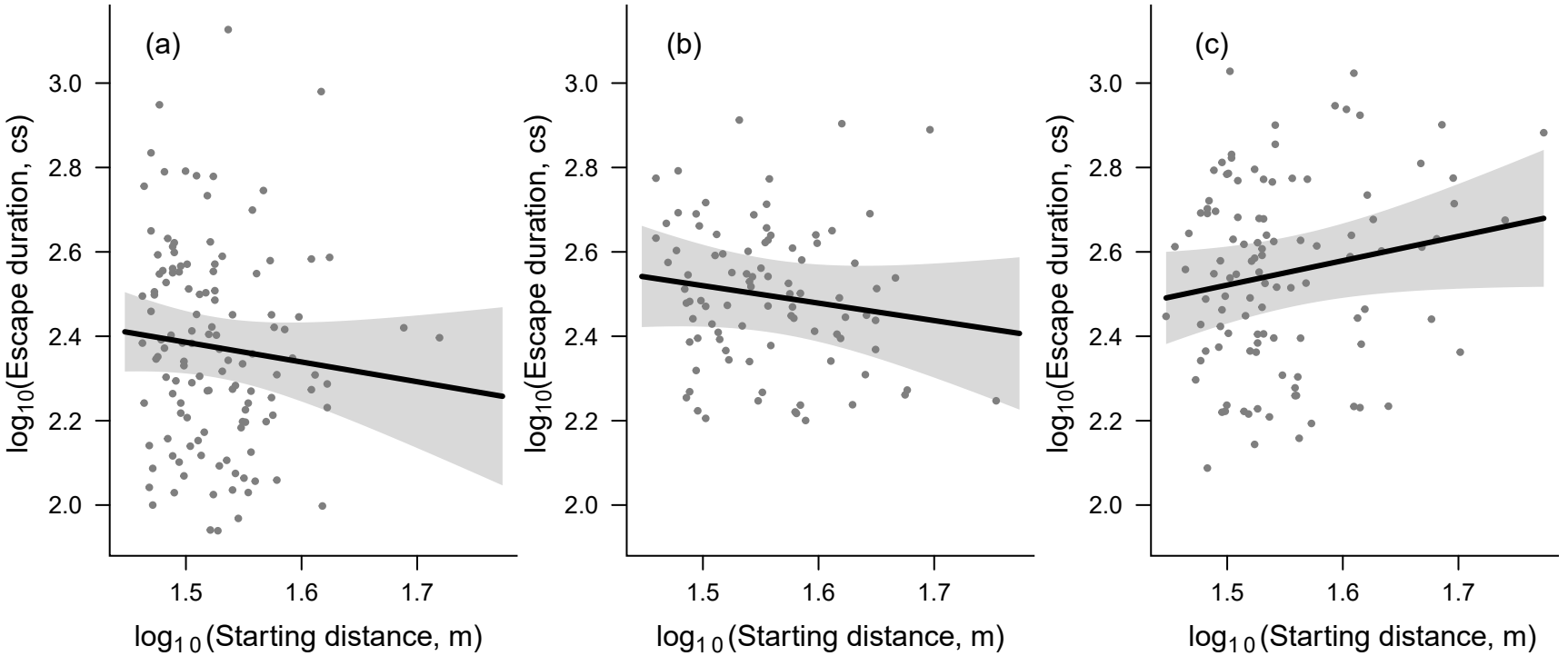

(a)
180
270
90
0
4
8
12
16
20

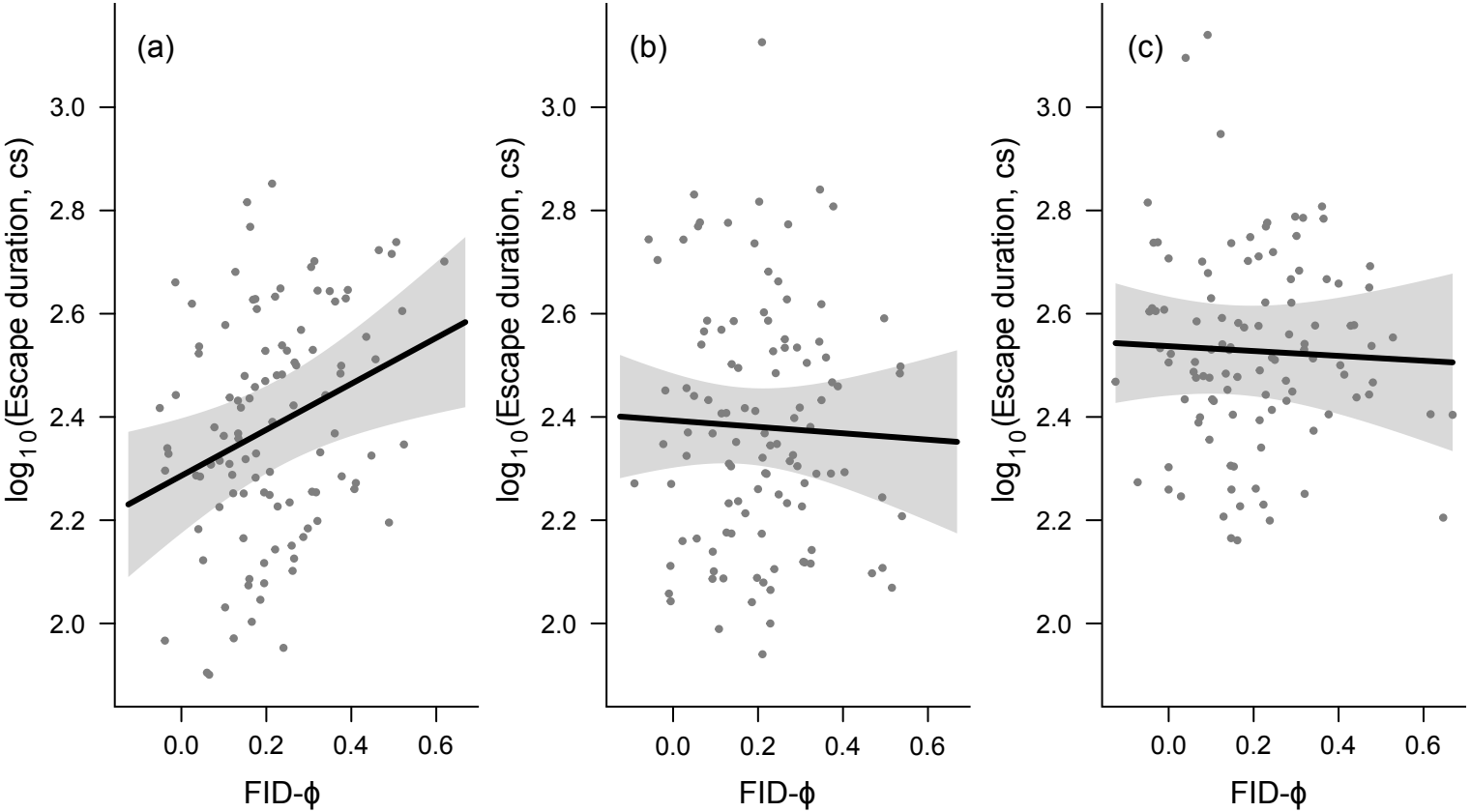

(b)
180
270
90
0
4
8
12
16
20


(c)
180
270
90
0
4
8
12
16
20


300
100
30
10
3
Distance fled, m
1
3
10
30
Escape duration, s


(a)
(b)
(c)
log10(Escape duration, cs)
3.0
2.8
2.6
2.4
2.2
2.0
0
50
100
150
Initial escape angle (°)


(a)
(b)
(c)
log10(Escape duration, cs)
3.0
2.8
2.6
2.4
2.2
2.0
1.5
1.6
1.7
log10(Starting distance, m)


(a)
(b)
(c)
log10(Escape duration, cs)
3.0
2.8
2.6
2.4
2.2
2.0
0.0
0.2
0.4
0.6
FID-ϕ

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