

## Manuscript Details

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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
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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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**Abbreviated title:** Risk assessment during escape

**Declarations of interest:** none.

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## **-Reviewer 2**

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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



1 **ABSTRACT**

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

19

## 20 1. INTRODUCTION

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

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

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

59 Another important parameter of escape is distance fled (Tätte et al. 2018), or –  
60 when measured in time units – escape duration or flight time (Collop et al.  
61 2006).. Distance fled has received little attention in escape models (Cooper &  
62 Blumstein 2015, p. 57) and is often regretfully neglected when the costs of  
63 escape are discussed (Tätte et al. 2018). Cooper & Pérez-Mellado (2004) have  
64 suggested that distance fled could be similarly modelled as FID, with one slope  
65 predicting risk of predation, and the other predicting cost of leaving a resource  
66 (as in Fig. 1). However, it is unclear whether distance fled is decided upon the  
67 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

92 & Fleming (2014) and Collier & Hogdson (2017) found that grasshoppers  
93 change their escape strategies over successive approaches depending on the  
94 perceived risk of predation. While it was shown that risk of predation is quickly  
95 recalculated, it was unclear whether risk was assessed in real time during  
96 escape or just before each escape. If even a momentary delay can be enough  
97 to make new accurate risk assessments, as shown in Lind et al. (2002), then a  
98 methodology using repeat approaches cannot be regarded as a continuous  
99 pursuit. That is, new escape decisions could still have been made before each  
100 escape. The cost of remaining could have increased each time because of the  
101 heightened perception of predation risk from previous escape attempts.

102 Behaviour in these experiments on grasshoppers changed dynamically, but  
103 possibly not in the way originally hypothesized by Cooper (1998, 2006a).

104 While there is plenty of evidence to suggest that prey do indeed monitor  
105 approaching predators before initiating flight (Stankowich & Blumstein 2005;  
106 Cooper & Blumstein 2015), the extent to which they monitor while fleeing is less  
107 clear. For example, some lizards stop shortly after escape, and subsequently  
108 turn their heads to the side to monitor and assess risk (Cooper 2008). While  
109 some species, e.g. the Eurasian woodcock (*Scolopax rusticola*), do have a 360°  
110 view of their surroundings (Martin 1994), most birds tend to have a blind area at  
111 the back of their head (Martin 2007), including corvids (Fernández-Juricic et al.  
112 2010). Furthermore, visual acuity varies in different parts of the visual field,  
113 forcing birds to move their heads or eyes when monitoring their surroundings  
114 (Fernández-Juricic 2012). Thus, DRA during escape would put requirements on  
115 the movement of the head, or on the escape trajectory. Indeed, escape angles

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

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

140 routes. Three relatively similar species of corvids were used in the study: the  
141 hooded crow (*Corvus cornix*), the rook (*Corvus frugilegus*), and the Eurasian  
142 jackdaw (*Coloeus monedula*). We selected corvids because their high cognitive  
143 abilities (Cramp et al. 2004; Emery & Clayton 2004) should favour DRA, and  
144 larger species tend to have longer distance fled (Tätte et al. 2018), which gives  
145 them more time to assess risk. We also examined whether there are any  
146 interspecific differences in how risk is assessed. Studying how animals react to  
147 different stimuli under threat of predation helps to understand how human-  
148 caused disturbances could affect the well-being of wild animals (Frid & Dill  
149 2002).

## 150 **2. MATERIAL AND METHODS**

### 151 **2.1 Study system**

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

160 The hooded crow, the rook, and the Eurasian jackdaw are common species in  
161 Estonian cultural landscapes, but have often been persecuted by humans (Elts  
162 et al. 2018). The hooded crow and the rook are similar in size (44–47 cm in  
163 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<sup>st</sup> quartile 31.3, 3<sup>rd</sup> 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%)



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

### 189 **2.3 Approach type**

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

### 205 **2.4 Flock size**

206 Flock size was estimated as the number of individual corvids in a 15 m radius of  
207 the focal bird (chosen as the one closest to the observer), similarly to e.g. Guay  
208 et al. (2013), Samia et al. (2017) and Tätte et al. (2018). Other individuals from  
209 that flock were not experimentally approached. However, on some occasions,  
210 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 Tatte 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,

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

## 240 **2.6 FID-phi**

241 Instead of ordinary flight initiation distance (FID), we used FID-phi [*note to the*  
242 *Editor: we would like “phi” to be replaced with the corresponding Greek letter in*  
243 *the final version. PDF conversion at the submission site was unable to display*  
244 *the proper symbol.*] that was calculated as the distance approached by the  
245 observer in relation to starting distance at the moment the focal bird began  
246 escaping. The exact equation of FID-phi was:  $1 - (\text{distance approached} /$   
247  $\text{starting distance})$ . The use of phi index was inspired by Samia & Blumstein  
248 (2014), who used it to study the relationship between alert distance and FID, but  
249 we modified the equation so that the values can be interpreted similarly to  
250 ordinary FID, with larger values indicating an earlier escape. The use of a  
251 relative measure was necessary because approach type “chase” did not allow  
252 us to directly measure the remaining distance to the bird (and we could not  
253 simply subtract the walked distance from starting distance because the birds  
254 often moved while foraging). However, due to the almost universal positive  
255 correlation between starting distance and FID (Blumstein 2003), that may partly  
256 be due to mathematical reasons (Dumont et al. 2012), relative measurement of  
257 escape components may provide more informative results (e.g. Samia et al.

258 2017) that are not biased by mathematical constraints (Samia & Blumstein,  
259 2014).

## 260 **2.7 Statistical methods**

261 The main hypotheses were tested with general linear mixed models using the  
262 library lme4 (Bates et al. 2015) in R version 3.5.2 (R Core Team 2018).  
263 Continuous variables (escape duration, distance to refuge, density of trees,  
264 change in escape angle) were  $\log_{10}$ -transformed to make the data conform  
265 more closely to the normal distribution. The sample means from the values of  
266 starting distance, FID-phi, and escape angle were subtracted to reduce  
267 multicollinearity from the included interaction terms. Escape angle was scaled  
268 by dividing by two times its standard deviation to put it on a similar scale of units  
269 with other predictors (Gelman, 2008). The relationship between escape angle  
270 and other variables could be non-linear, because angles below  $90^\circ$  indicate an  
271 escape towards the predator and over  $90^\circ$  indicates escape away from the  
272 predator, but we have too few observations below  $90^\circ$  to convincingly model  
273 such non-linearity. City district was used as a random factor in all models to  
274 account for potential site and population specific variation. Function dredge from  
275 the library MuMIn (Bartoń 2017) was used to generate all combinations of  
276 predictors from the global model. Using the same library, these combinations  
277 were then ranked by Akaike information criterion (AIC) values and then model  
278 averaging was done on a set of models where  $\Delta AIC < 4$ . Uninformative  
279 parameters were removed from the top model set according to the criteria  
280 suggested by Leroux (2019). The natural average method was used for model  
281 averaging. Estimates of predictors were considered to have support for an

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

287 Circular statistics and figures were carried out with Oriana 4 software (Kovach  
288 2011). Escape angle data were divided into twenty 18° bins centered at 0°.  
289 Escapes to the left and right side were pooled after finding no statistically  
290 significant differences between the distributions of the left and right side for any  
291 of the three species using Watson's  $U^2$  tests (see Fig. A1 for initial escape  
292 directions before pooling). Escape angle of 180° indicates an escape straight  
293 away from the human observer, while an angle of 0° indicates escape towards  
294 the observer.

### 295 **3. RESULTS**

#### 296 ***3.1 Escape strategy and refuge type***

297 During escape, more individuals changed their escape strategy from terrestrial  
298 to aerial for approach type "chase" (34/43) compared with approach type "halt"  
299 (5/39) as indicated by the Chi-square test of independence,  $\chi^2 (1, N = 82) =$   
300  $33.38, p < 0.001$ , and also compared with approach type "forward" (7/46),  $\chi^2 (1,$   
301  $N = 89) = 33.95, p < 0.001$ . There was no significant difference in escape  
302 strategies between approach type "halt" and "forward",  $\chi^2 (1, N = 85) = 0.1, p =$   
303  $1.00$ . Previously listed  $p$ -values were adjusted with the Bonferroni correction.  
304 Preference for refuge types was equally distributed among approach types  
305 "halt", "forward", and "chase",  $\chi^2 (6, N = 323) = 3.58, p = 0.734$ , with ground

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

### 308 **3.2 Escape duration**

309 Escape duration was strongly positively correlated with distance fled,  $r = 0.79$ ,  $N$   
310  $= 301$ ,  $p < 0.001$  (Fig. A2). The global model for escape duration contained the  
311 following predictors and their interactions (indicated by an asterisk): *Approach*  
312 *type \* Species + Approach type \* Escape strategy + Approach type \* FID-phi +*  
313 *Escape angle \* Species + Distance to refuge + Starting distance \* Species +*  
314 *Density of trees + Flock size*. Density of trees and flock size were removed from  
315 the top model set (i.e. models with  $\Delta AIC < 4$ ) as these variables had little  
316 statistical impact, were not directly related to main hypotheses, and could be  
317 classified as uninformative parameters (model selection tables can be found in  
318 the Electronic Supplementary Tables S1-S4) (Leroux, 2019).

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

330 when analysed among all species (Fig. 4; Table 2). While aerial escape  
331 strategy, compared to terrestrial escape strategy, increased escape duration for  
332 approach types “halt” ( $\beta = -0.174$ ,  $SE = 0.051$ ,  $p < 0.001$ ) and “forward” ( $\beta =$   
333  $-0.125$ ,  $SE = 0.044$ ,  $p = 0.005$ ), it showed an opposite trend for approach type  
334 “chase” ( $\beta = 0.100$ ,  $SE = 0.047$ ,  $p = 0.035$ ).

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

### 344 **3.3 Escape angle**

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

350 The mean escape angles (after pooling escapes to the left and right side; see  
351 Material and methods) were as follows: 123.4, 95% CI [118.0, 128.8] for the  
352 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),



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

#### 388 ***4.2 Indicators of dynamic risk assessment***

389 Studies have shown that, when a stationary prey is being approached by a  
390 predator, the prey will assess the costs related to fleeing and not fleeing to  
391 decide on the optimal distance at which to escape (Stankowich & Blumstein  
392 2005; Cooper 2006a). However, very little is known about cost assessment  
393 during escape. Before the present study, research on birds suggested that birds  
394 either maximize distance from the predator by escaping at 180°, or escape at  
395 90° for rapid evasion (Domenici et al. 2011). These peaks do not give an  
396 impression that monitoring predators is important to birds during escape. In our  
397 study, all three species had an average initial escape angle close to 120° with  
398 no distinctive peaks (Fig. 5), which most likely represents a middle ground  
399 between maximizing distance, being unpredictable, and monitoring the predator  
400 (Hall et al. 1986; Domenici & Blake 1993).

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

#### 422 ***4.3 Escape duration in relation to escape angle***

423 Escape duration was also related to initial escape angle but only for the rook.  
424 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. Tätté 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, Tätté 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

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

#### 474 ***4.5 Difference in the perception of approach types***

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

495 **4.6 Escape angle**

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

507 **4.7 Conclusions**

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



707 **TABLES**

708 Table 1. Pairwise comparisons of escape durations for approach types "halt",  
 709 "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

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

712

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.

<b>Escape strategy</b>	<b>Contrast</b>	<b>Estimate</b>	<b>SE</b>	<b>df</b>	<b><i>t</i></b>	<b><i>p</i></b>
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

719 **APPENDIX**

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

<b>Predictor</b>	<b>Estimate</b>	<b>SE</b>	<b>2.5<sup>th</sup></b>	<b>97.5<sup>th</sup></b>	<b>z</b>	<b>w<sub>ip</sub></b>
(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

---

724 The natural average method was used for model averaging (on 13 models with  
725  $\Delta AIC < 4$ , see Electronic Supplementary Table S2). Parameter estimates are  
726 followed by unconditional standard errors (SE) and 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles  
727 (95% CI). Estimates in bold indicate that 95% CI does not include 0.  $W_{ip}$  is the  
728 relative importance of each predictor in the model set. City district was included  
729 as random effect. Some species-related effects are not showing meaningful  
730 comparisons but were needed for more specific post-hoc tests.

731

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>	z	$W_{ip}$
(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).  $W_{ip}$  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	2.5 <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

746 The natural average method was used for model averaging (on 15 models with  
 747  $\Delta AIC < 4$ , see Electronic Supplementary Table S4). Parameter estimates are  
 748 followed by unconditional standard errors (SE) and 2.5<sup>th</sup> and 97.5<sup>th</sup> 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.

<b>Escape strategy</b>	<b>Contrast</b>	<b>Estimate</b>	<b>SE</b>	<b>df</b>	<b><i>t</i></b>	<b><i>p</i></b>
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  $0^\circ$ , and  $180^\circ$   
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  $18^\circ$ .

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



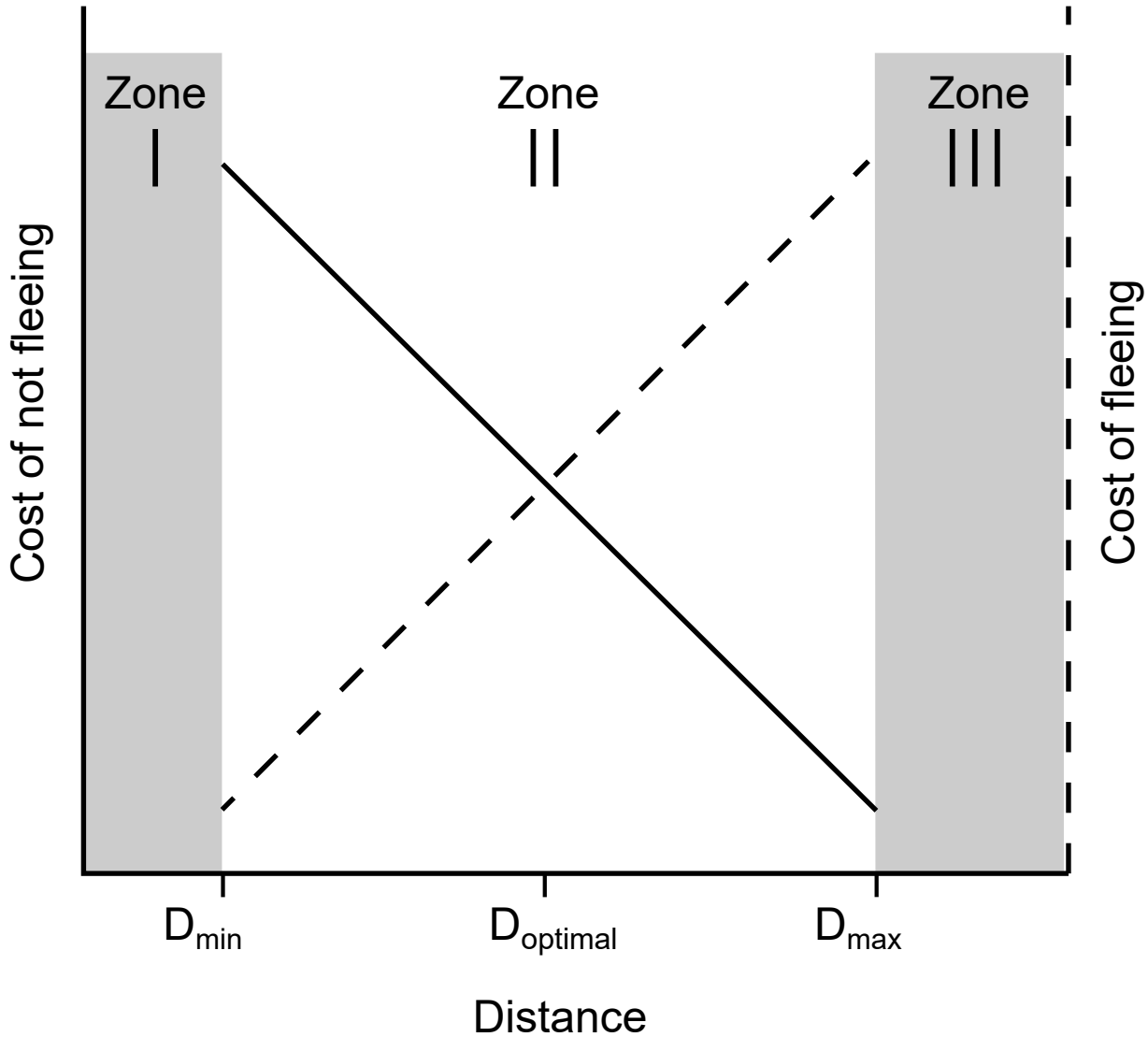
781 **Overview of Electronic Supplementary Material**

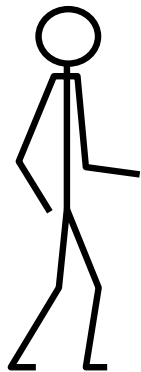
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783 duration.

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

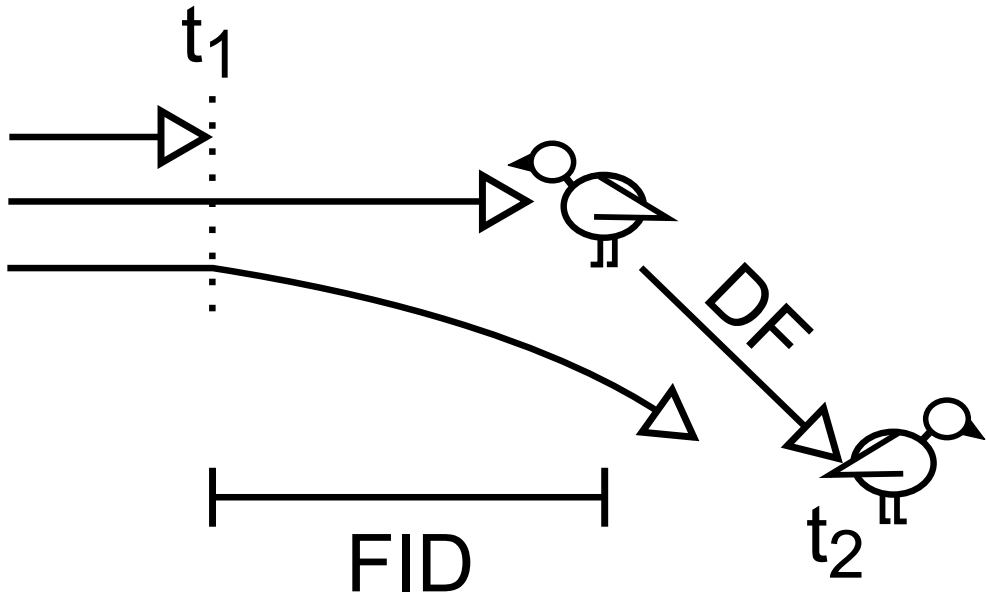
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787 escape angle.

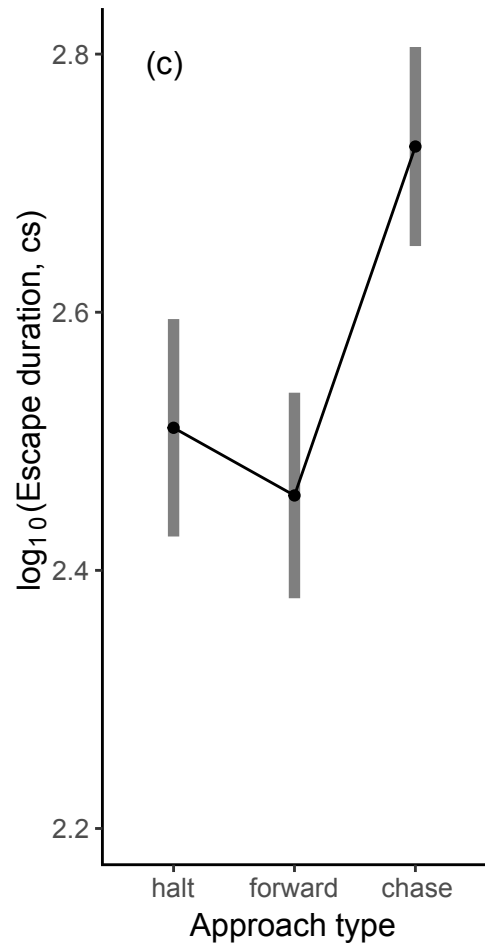
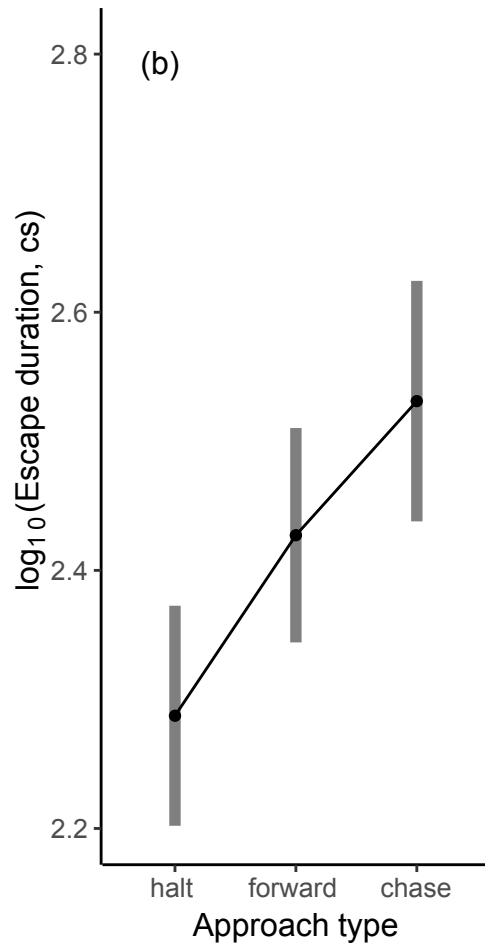
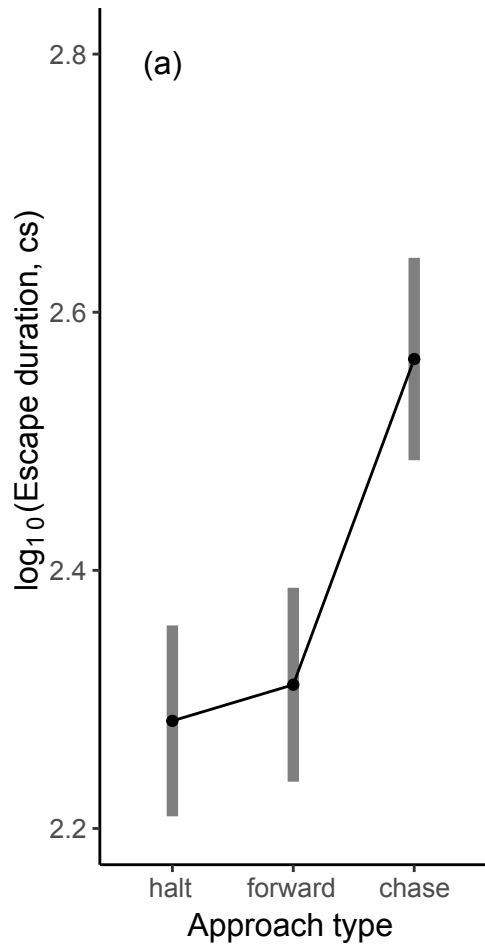
788 Electronic Supplementary Table S4. Top model set used for model averaging  
789 angular change during escape.

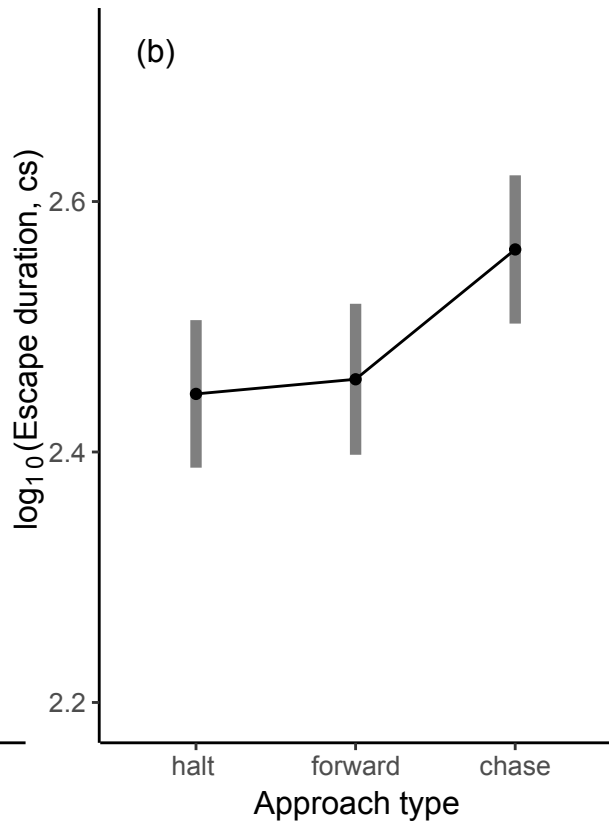
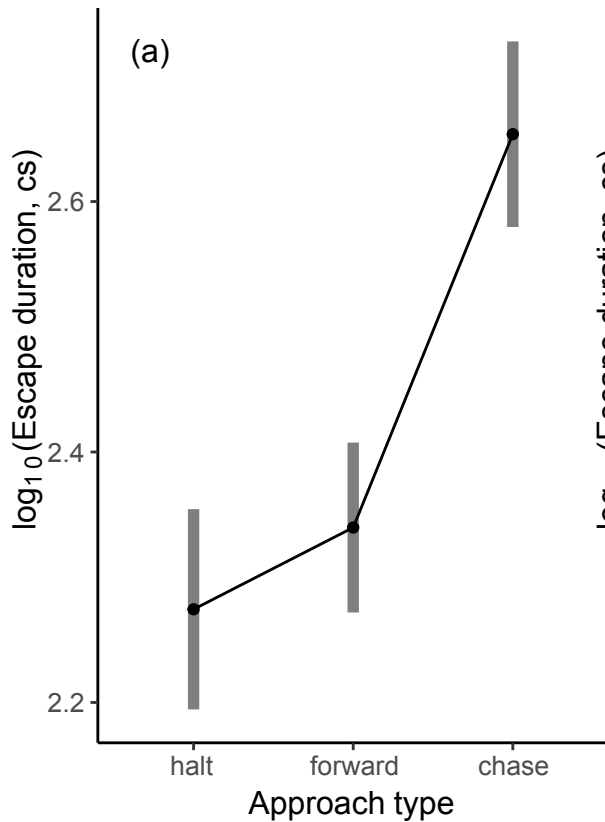




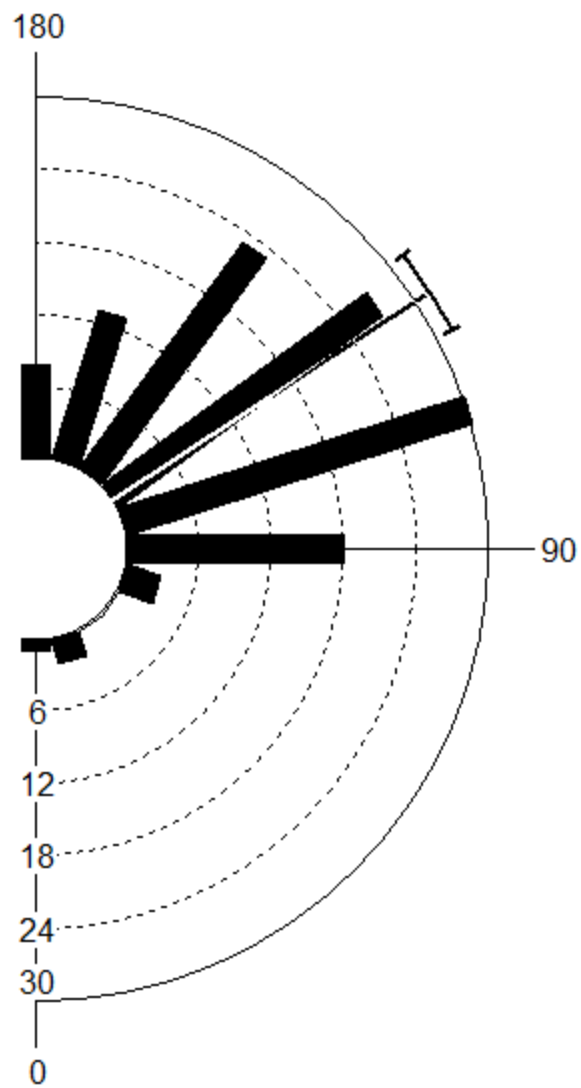
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Forward  
Chase



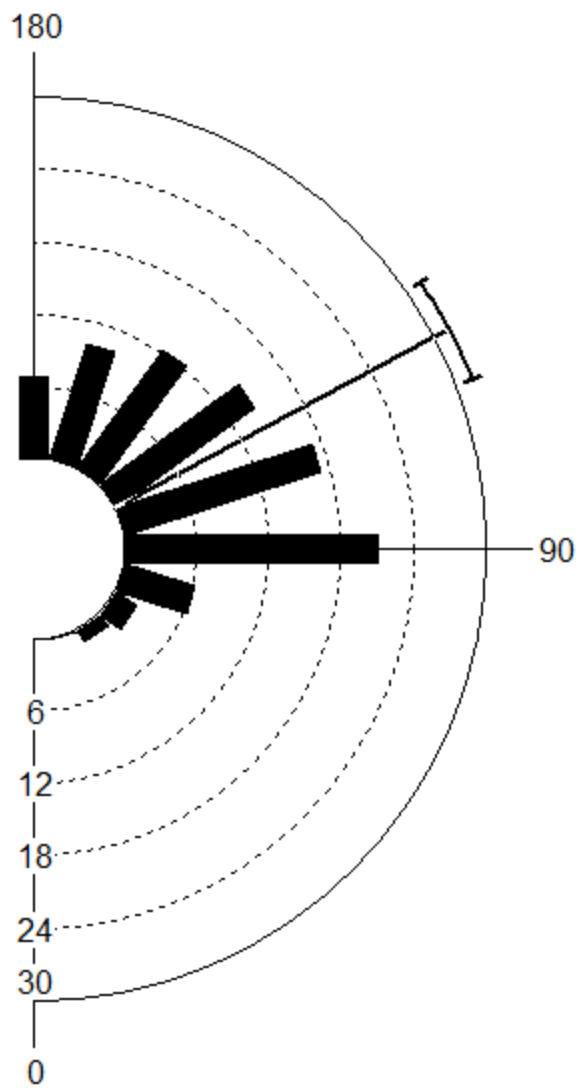




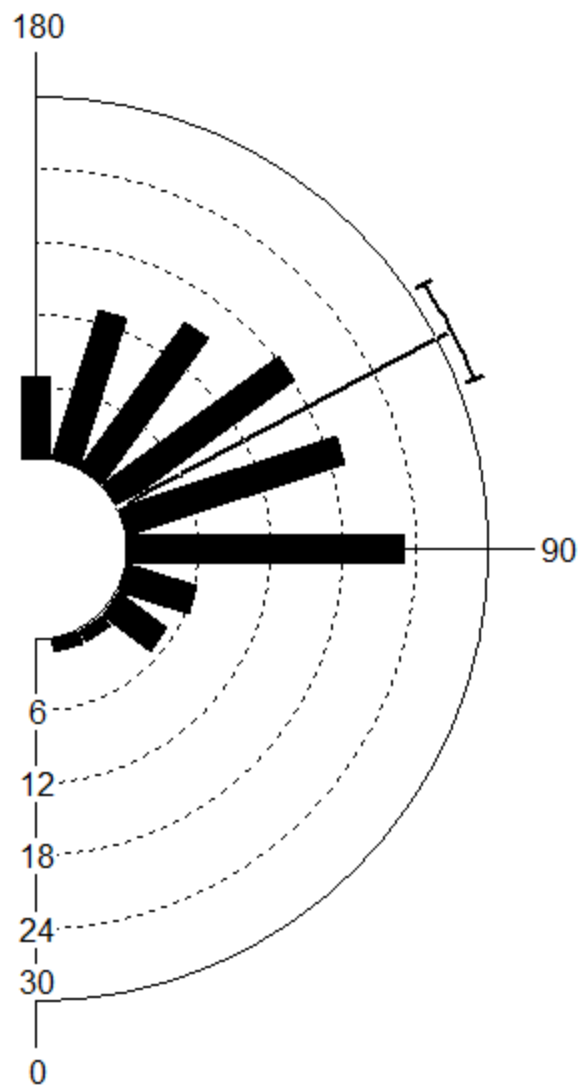
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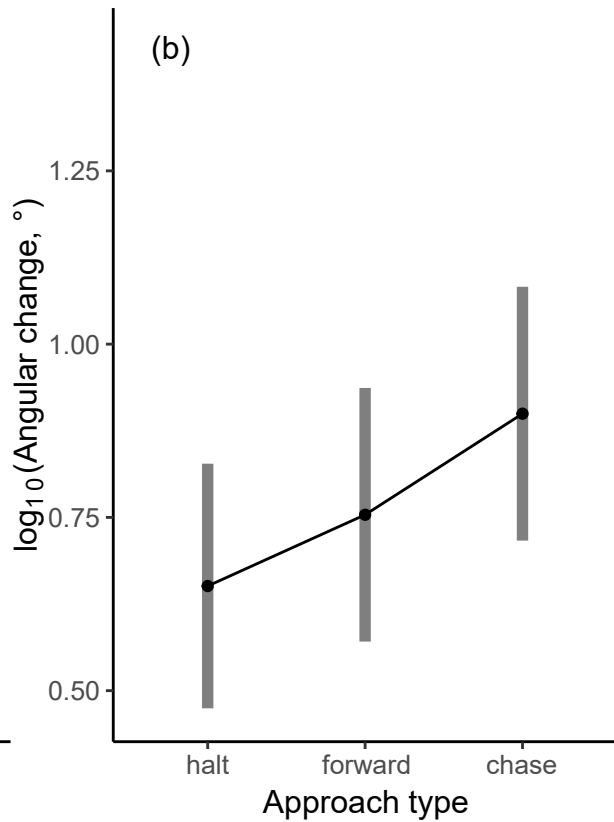
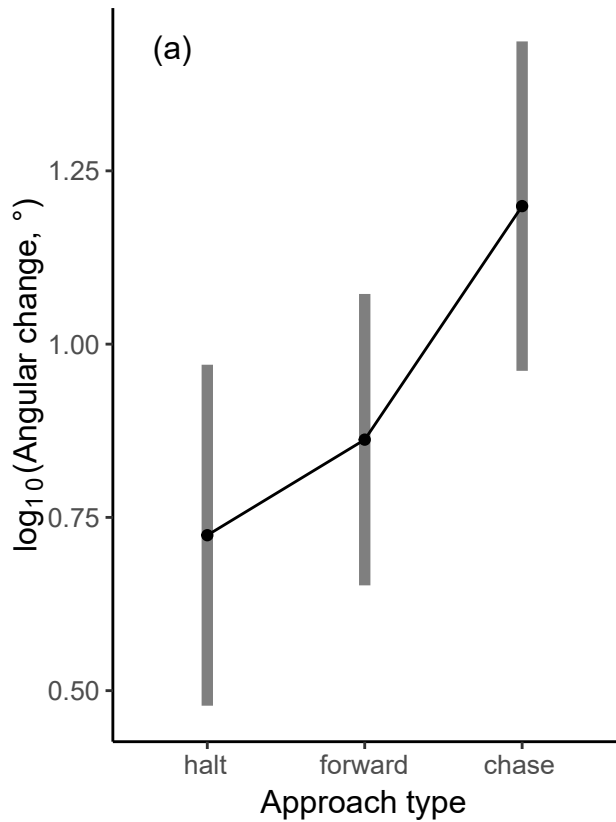


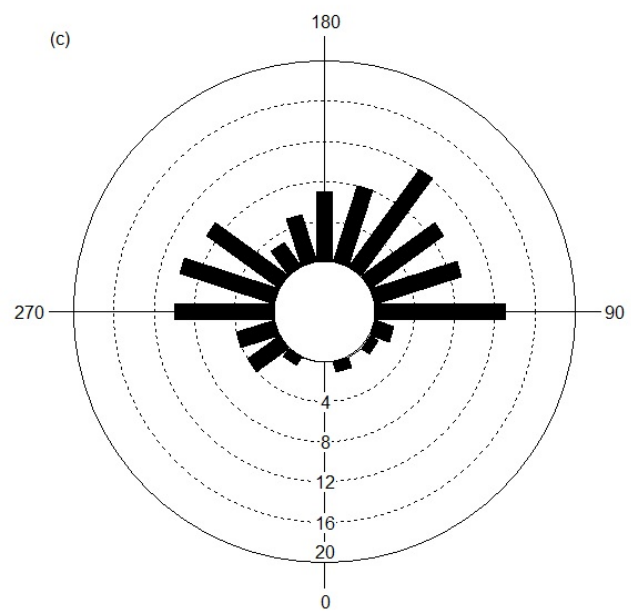
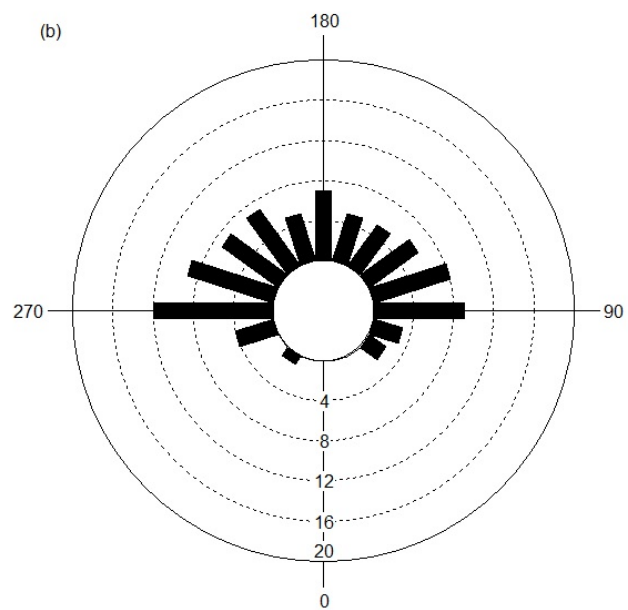
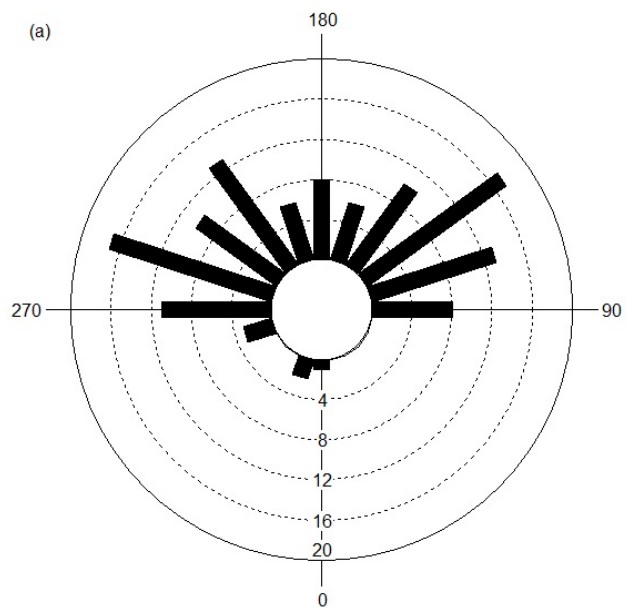
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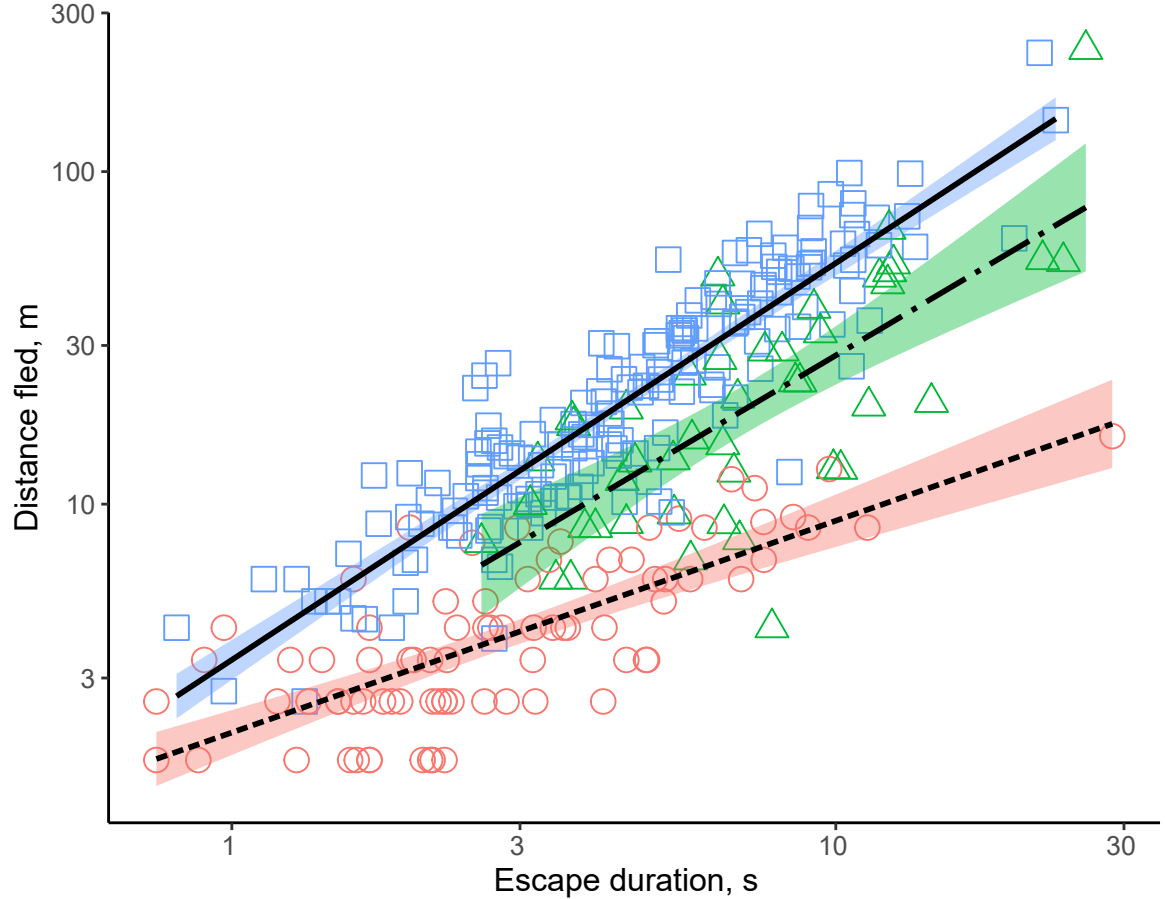
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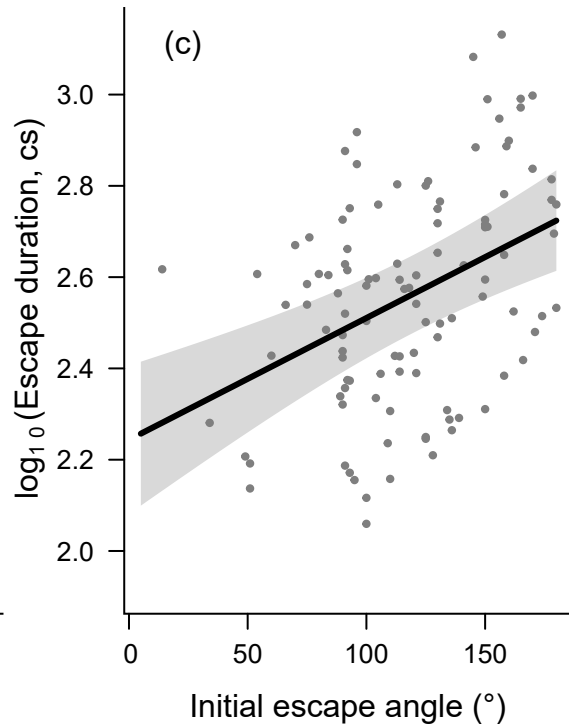
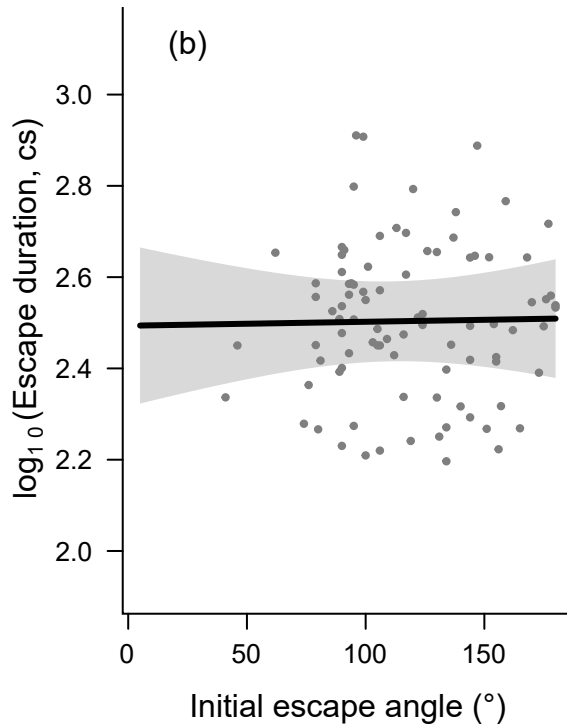
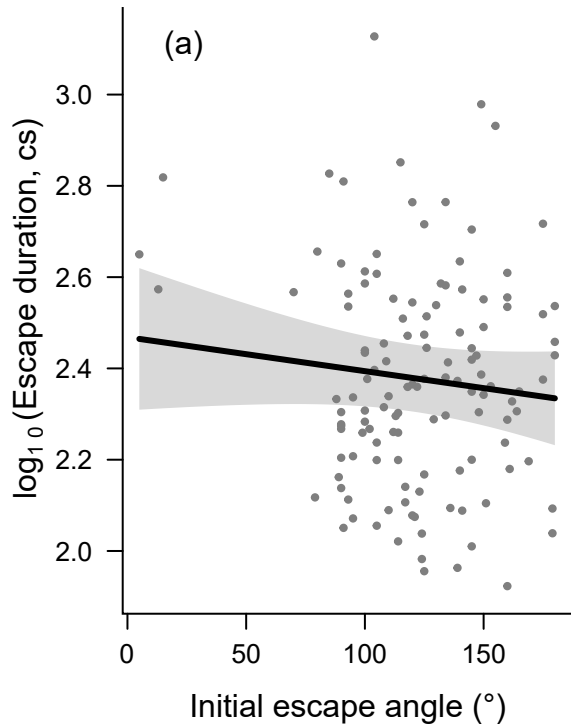


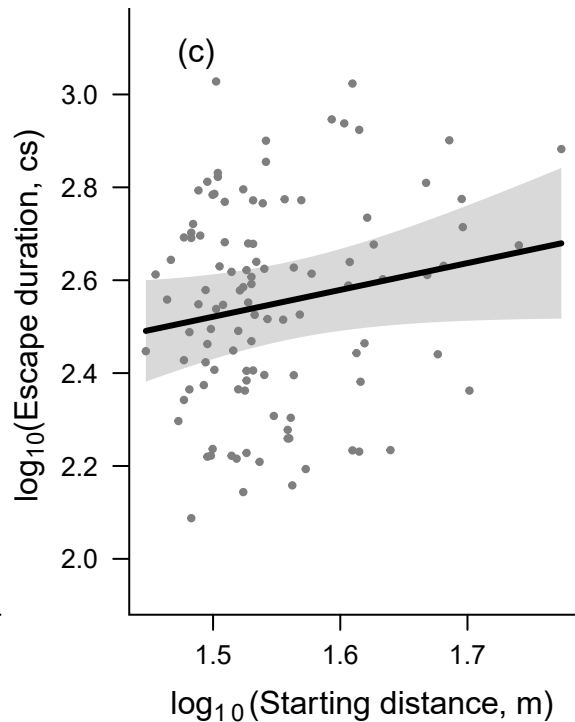
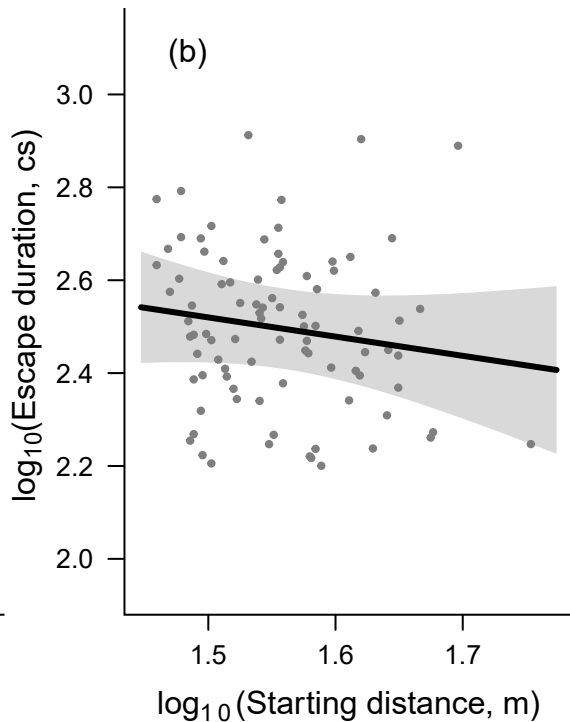
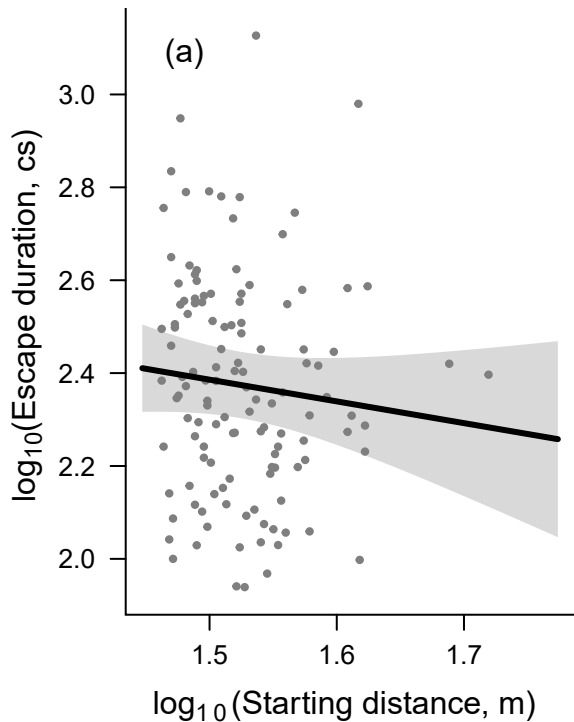


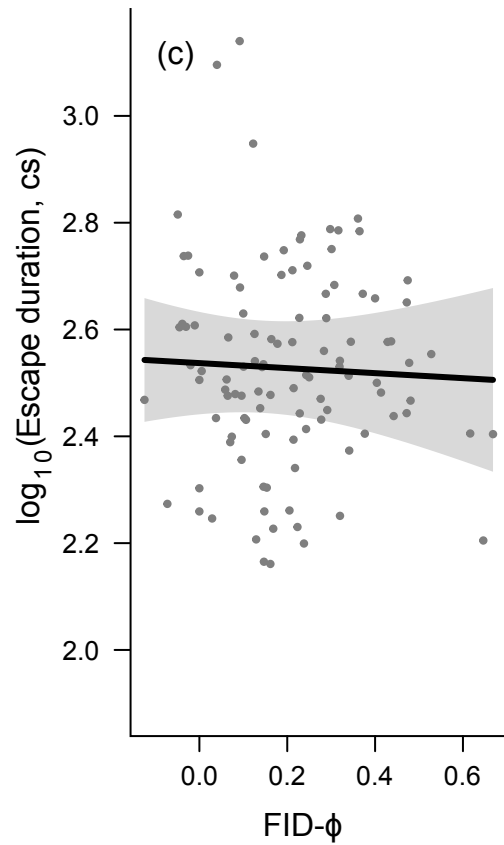
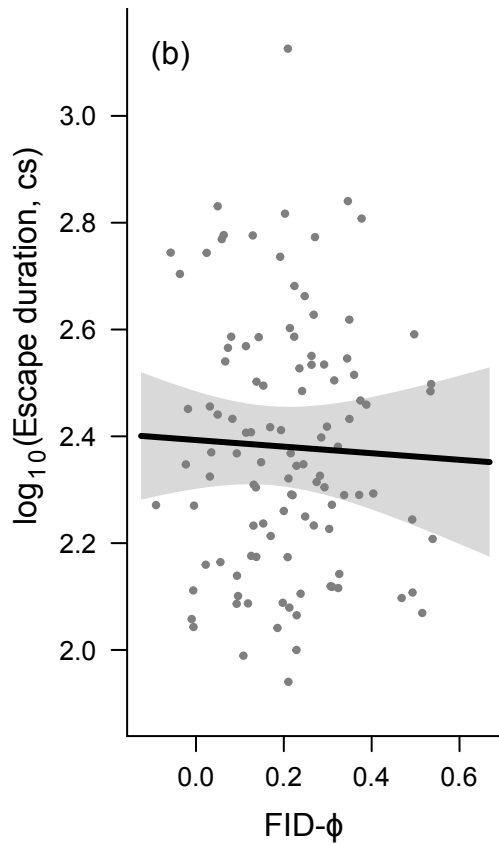
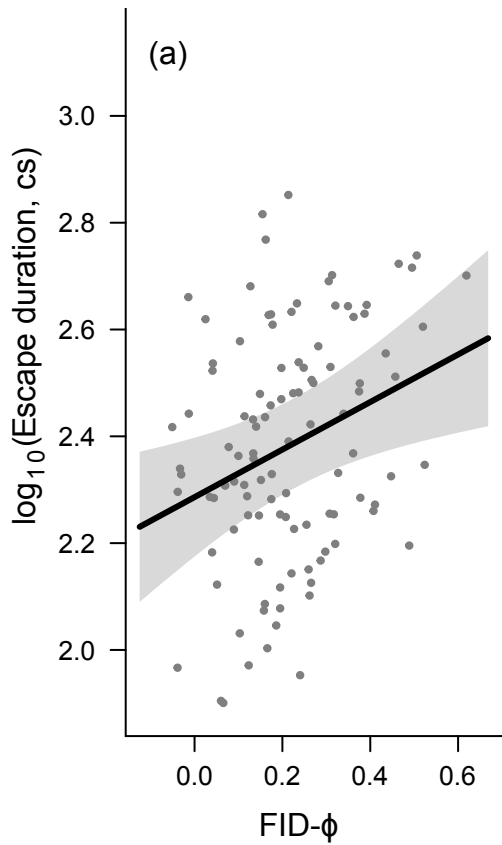












## AUTHOR STATEMENT

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