



Towards an integrated view of escape decisions in birds: relation between flight initiation distance and distance fled

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ARTICLE INFO

Article history:

Received 3 May 2017

Initial acceptance 1 June 2017

Final acceptance 9 November 2017

MS. number: 17-00387R

Keywords:

antipredator behaviour
birds
body size
distance fled
escape behaviour
flight initiation distance
starting distance
urbanization

Rapid human population growth and increasing habitat fragmentation lead to more frequent direct encounters between humans and animals. Consequently, numerous habitats will become less suitable for some species due to an increase in perceived risk of predation. Studies show that different species vary greatly in their tolerance to human disturbance, but these findings are typically only based on flight initiation distance (FID, the distance at which animals flee when approached by a potential predator including a human). The aim of this study was to broaden the general view of escape behaviour by including distance fled (DF) in the analyses. We measured FID and DF in 699 birds belonging to 17 species in Estonian urban and rural settlements. We calculated the relationships between two types of escape decisions and behavioural, environmental and morphological parameters. There was a positive relationship between FID and DF for heavier species, but not for lighter species suggesting mass-dependent differences in the cost of escape. Flock size and starting distance in rural habitats were important predictors of FID while distance to refuge was only positively correlated with DF. Birds in rural habitats escaped earlier and further and exhibited a positive relationship between starting distance and FID, whereas no such trend was seen in urban birds, possibly due to a narrow zone of awareness. Our findings suggest that DF represents an independent and informative additional measure of antipredator behaviour that together with FID provides a more integrated view of the costs of escape. This, in turn, facilitates finding effective ways for mitigating effects of anthropogenic disturbance on wild animals.

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The human population is projected to increase to 9.7 billion by 2050 and 11.2 billion by 2100 (United Nations, 2015). This population growth implies that more land will be transformed to suit human needs (Luck, 2007), especially near biodiversity hotspots where the human growth rate is higher than the global average (Cincotta, Wisniewski, & Engelman, 2000). As a result, some natural habitats will be lost, and the remaining habitats will become smaller and more fragmented, which all leads to a decrease in biodiversity (Haddad et al., 2015). Surprisingly, direct anthropogenic disturbance (pedestrians, moving vehicles, noise pollution, domestic animals) can have even more adverse effects on animal communities than changes in vegetation structure and composition (Papouchis, Singer, & Sloan, 2001; Parris & Schneider, 2008; Schlesinger, Manley, & Holyoak, 2008). Evidence suggests that animals perceive human-caused disturbance as predation risk and

that the costs of avoidance and escape, either energetic or loss of opportunities, have similar indirect effects on fitness and population dynamics (Frid & Dill, 2002). Even the abundance of urbanized birds is negatively associated with the number of pedestrians because heightened vigilance reduces time spent foraging (Fernández-Juricic & Tellería, 2000). Thus, finding ways to mitigate the increasing pressure from human-caused disturbance is becoming more important than ever as our population keeps growing.

There has been an increasing amount of literature on escape behaviour over the last 30 years (reviewed by Lima & Dill, 1990; Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2015; Stankowich & Blumstein, 2005). This increase in popularity can be traced to a paper by Ydenberg and Dill (1986) that introduced optimal escape theory, which helped explain the decision-making process behind typical predator–prey encounters. The underlying premise behind optimal escape theory is that when a prey is approached by a predator, in addition to the cost of remaining, that is, the increasing risk of being captured, the prey is also faced with a cost of fleeing. The latter is generally described as a reduction in

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fitness when the animal has to abandon foraging grounds or discontinue interactions with conspecifics (i.e. courting and territorial defence) and from the energetic costs of fleeing itself. Ydenberg and Dill (1986) stated that prey should flee when the cost of fleeing becomes equal to the cost of remaining. Numerous studies have investigated this simple theory by altering these two costs, for example by providing supplementary food to increase the cost of fleeing (Lagos et al., 2009) or by manipulating approach speed to change the perceived risk of predation (Cooper, 2006).

Probably the most important practical implications of research on escape behaviour are comparison of the impact of potential stressors on wildlife (Lord, Waas, Innes, & Whittingham, 2001), and setting species-specific buffer zones between a habitat and a source of disturbance for conservation purposes (e.g. Fernández-Juricic, Venier, Renison, & Blumstein, 2005; Rodgers & Smith, 1995). Such assessments are usually done by measuring the species' flight initiation distance (FID), the distance at which animals flee when approached by a potential predator or other stressor. According to Weston, McLeod, Blumstein, and Guay (2012) the usage of FIDs by wildlife managers is not very common, mainly due to limited data and poor accessibility. Recently, Livezey, Fernández-Juricic, and Blumstein (2016) tried to address these issues by publishing a substantial collection of mean FID and alert distance (AD, the distance at which animals show first signs of alertness when approached by a potential predator) values for birds from across the world.

While numerous factors can alter escape behaviour (Stankowich & Blumstein, 2005; Table 1), the current body of literature has emphasized two prevailing characteristics associated with FID across diverse taxa: body size of prey (Blumstein, 2006; Fernández-Juricic et al., 2006; Gotanda, Turgeon & Kramer, 2009) and starting

distance (SD) of an approaching predator (Blumstein, 2010; Samia & Blumstein, 2015). There are numerous biological explanations for why FID increases with body size: larger eyes provide better means of detection of predators (Møller & Erritzøe, 2014), larger prey are more desirable for predators due to their higher energetic reward (Gill & Hart, 1994), metabolic requirements are relatively higher for smaller animals forcing them to take greater risks (Grant & Noakes, 1987) and larger bird species need more time for take-off (Hedenström & Ålerstam, 1992). In contrast, the positive correlation between SD and FID is not obvious in the context of optimal escape theory. Dumont, Pasquaretta, Réale, Bogliani, and Hardenberg (2012) have argued that this relationship might be a mathematical artefact because FID can only be equal to or smaller than SD. However, after comparing simulated slopes with real data, they acknowledged that the positive relationship between SD and FID also has a biological component for the alpine marmots, *Marmota marmota*, that they studied. One of the likely causes for this relationship is that monitoring the intentions of an approaching predator takes attention away from other activities, and, therefore, it is better to escape soon after catching sight of a predator (Blumstein, 2010). Recent work has provided support for this idea by showing that birds flee relatively soon after becoming alert to a predator (Samia & Blumstein, 2015). In addition, it has been found that urban bird populations take relatively longer to detect an approaching predator than rural populations (Samia et al., 2017), and that the time for roe deer, *Capreolus capreolus*, to detect an approaching threat depends on the perceived level of predation risk and available resources, suggesting that vigilance rate is altered according to external conditions (Bonnot et al., 2017). These findings indicate that the relationship between SD and FID could also depend on the perceived risk of predation.

Table 1
Summary of hypotheses about chosen predictors for flight initiation distance (FID) and distance fled (DF)

Predictor	Dependent variable	Hypothesis
Habitat	FID DF	Urban birds should have shorter FID and DF than rural birds due to lower risk of predation (Møller, 2012), habituation to humans (Blumstein, 2016), innate fearlessness (Carrete & Tella, 2013) and higher abundance of food (Chace & Walsh, 2006)
Body mass	FID DF	Larger birds are expected to escape at longer distances because of better vision (Møller & Erritzøe, 2014), inferior agility (Hedenström & Ålerstam, 1992) and relatively smaller energetic requirements (Bennett & Harvey, 1987). Larger birds are expected to escape further because of differences in flight energetics (Tatner & Bryant, 1986), foraging preferences (Haskell et al., 2002) and fewer possible refuge spots
Flock size	FID DF	Larger flocks have more eyes which should result in earlier detection of approaching predators and, therefore, increase FID (Stankowich & Blumstein, 2005). However, the risk of an individual getting caught decreases in larger flocks which could, alternatively, decrease FID Risk dilution effect should decrease DF
Distance to refuge	FID DF	Short distance to a potential refuge should decrease the risk of predation and, therefore, decrease FID (Stankowich & Blumstein, 2005) Energy-wise, it could be expected that when an animal decides to take refuge, it would choose the closest one (Cooper, 1999). Therefore, the further the closest refuge, the larger DF should be
Starting distance	FID DF	Longer starting distances increase the possibility of early detection of approaching predator by prey. To minimize monitoring costs, prey are expected to escape soon after detecting a predator (Blumstein, 2010), and, therefore, FID is expected to increase with SD Starting distance was included in the model of DF to control whether the relationship between FID and DF is confounded by starting distance, i.e. whether DF increases with longer starting distances
Vegetation cover	FID DF	Larger cover of vegetation should decrease predation risk because it provides more places to take refuge and makes it more difficult for predators to spot prey (Cooper, 2003). Therefore, FID and DF should decrease with increasing vegetation cover
Buffer distance	FID DF	Delaying escape, i.e. longer buffer distance, is expected to decrease FID because it indicates a low risk of predation and/or relatively high value of available resources (Fernández-Juricic et al., 2002) DF should decrease with longer buffer distance for the same reasons as FID, but it is also feasible that when a longer buffer distance results in a suboptimal FID, it is compensated for by longer DF to reduce the high risk of predation (Fernández-Juricic et al., 2002)
Flight initiation distance	DF	It can be expected that DF is controlled by the same principles as FID (balance between risk and cost of escape; Cooper & Pérez-Mellado, 2004) and, therefore, is positively related to FID
Escape method	DF	Most birds can fly and, therefore, have the option to choose between terrestrial and aerial escape. Terrestrial escape is energetically less costly, but also slower and less effective (Butler, 1991). Thus, it is expected that terrestrial escape is used when risk of predation is low, meaning short DF Escape method was not used in the model for FID because the decision on how to flee is presumably not taken until escape has been initiated (Rodríguez-Prieto et al., 2008)

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