

KUNTER TÄTTE

Towards an integrated view  
of escape decisions in birds under  
variable levels of predation risk





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Department of Zoology, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia.

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## LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications denoted in the text by Roman numerals:

- I **Tätte, K.**, Møller, A.P., 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.  
<https://doi.org/10.1016/j.anbehav.2017.12.008>
- II **Tätte, K.**, Ibáñez-Álamo, J. D., Markó, G., Mänd, R., & Møller, A. P. (2019). Antipredator function of vigilance re-examined: vigilant birds delay escape. *Animal Behaviour*, 156, 97–110.  
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- III Samia, D.S.M., Blumstein, D.T., Díaz, M., Grim, T., Ibáñez-Álamo, J.D., Jokimäki, J., **Tätte, K.**, Markó, G., Tryjanowski, P., Møller, A.P. (2017). Rural-Urban Differences in Escape Behavior of European Birds Across a Latitudinal Gradient. *Frontiers in Ecology and Evolution*, 5: 66.  
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- IV Morelli, F., Benedetti, Y., Díaz, M., Grim, T., Ibáñez-Álamo, J., Jokimäki, J., Kisanlahti-Jokimäki, M.L., **Tätte, K.**, Marko, G., Jiang, Y., Tryjanowski, P., Møller, A.P. (2018). Contagious fear: Escape behavior increases with flock size in European gregarious birds. *Ecology and Evolution*, 9(10), 6096–6104. <https://doi.org/10.1002/ece3.5193>
- V **Tätte, K.**, Møller, A.P., Mänd, R. (2020). Corvids exhibit dynamic risk assessment during escape. *Behavioural Processes*, 170, 104017.  
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Author's contribution to the studies (\* denotes a moderate contribution, \*\* a high contribution, \*\*\* a leading role).

	I	II	III	IV	V
Original idea	***	**			***
Study design	***	**		*	***
Data collection	***		**	**	***
Data analysis	***	***			***
Manuscript preparation	***	***	*	*	***

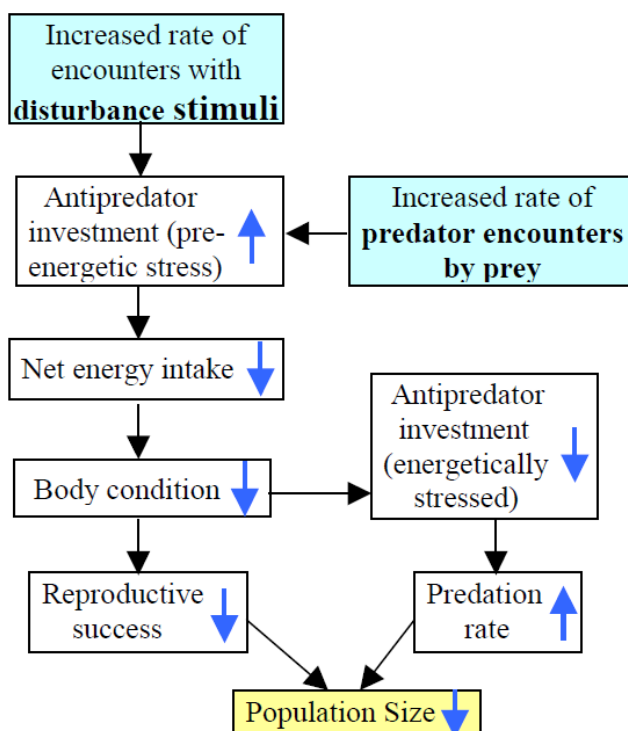
# 1. INTRODUCTION

Animals may greatly increase their fitness if they are well adapted to solve different interspecific interactions – most notably interactions with predators and parasites, as survival is a key aspect of every living organism, and only few species are not part of predator-prey interactions (Abrams, 2000; Lima & Dill, 1990). As such, predation is suggested to have been a strong selective force in the evolutionary diversification of life (Caro, 2005; Wallace, 1877; Lima & Dill, 1990). Furthermore, the selective force of predation works both ways, implying that there is an everlasting predator-prey coevolution involved (Abrams, 2000; Dawkins & Krebs, 1979). A wide array of antipredator defences exists, e.g. morphological and behavioural adaptations to avoid detection, aposematic signals of distastefulness, self-defence related morphological traits (Caro, 2005). However, animals generally resort to escape when an attack from a predator is imminent (Broom & Ruxton, 2005; Caro, 2005; Cooper & Blumstein, 2015). Late escape could have fatal consequences for an individual if it ends with getting caught, but the costs of premature escapes should not be underestimated as these could decrease the time and energy that would otherwise contribute to other fitness-enhancing activities (Ydenberg & Dill, 1986). That same general trade-off is also true for mechanisms of antipredator awareness, e.g. the more time is spent monitoring surroundings for threats, the less time can be allocated to foraging (Beauchamp, 2015; Ciuti et al., 2012; Fortin et al., 2014; Lima & Dill, 1990). Consequently, the perception of risk can have a negative effect on populations by itself because increased investment in antipredator effort can require animals to invest less in other important tasks such as foraging and parental care (Fig. 1; Frid & Dill, 2002; Lima & Dill, 1990). In addition, some animals may relocate to habitats of inferior quality under the threat of predation (Caro, 2005; Frid & Dill, 2002; Laundré, Hernández, & Ripple, 2010; Lima & Dill, 1990). Therefore, a correct assessment of the predation risk posed by potential threats is an integral part of deciding on optimal investment in antipredator behaviours (Cooper & Blumstein, 2015; Lima & Bednekoff, 1999; Lima & Dill, 1990; Ydenberg & Dill, 1986).

In general, antipredator defences of animals should be well adjusted to their habitats and to the predators found there (Caro, 2005). However, numerous ecosystems have been substantially altered since humans began colonizing the world (Dirzo et al., 2014). Chapter 2.1. of the current thesis describes how humans and human activities modify the perceived risk of predation in animals, how the perception of heightened predation risk affects behaviour, and how that difference could cause further changes in the ecosystem. In order to understand or predict the effects that human-caused disturbances have on animal populations, it is often necessary to measure the perceived risk of predation across different contexts (Chapter 2.2.). For example, comparing animal populations between different situations or habitat contrasts, such as inside versus outside protected areas, can be helpful for deciding which species are most threatened by human



disturbances (Samia et al., 2015). Some measures of predation risk, especially vigilance (Chapter 2.2.2.), can simultaneously indicate energetic or opportunity costs induced by higher levels of predation risk (e.g. Ciuti et al., 2012).



**Figure 1.** The conceptual model by Frid & Dill (2002) shows how human-caused disturbances and encounters with natural predators can similarly lead to a decline in population size via behavioural mechanisms. Arrows inside boxes indicate whether the response is negative (downward-facing arrows) or positive (upward-facing arrows). Figure reproduced from Fig. 1 in Frid & Dill (2002), licenced under the CC BY-NC 4.0 licence.

The focus of this thesis is on escape behaviour as this is one of the most significant behavioural indicators of predation risk (Frid & Dill, 2002). Escape behaviour is typically quantified by a single measure called flight initiation distance (FID) that denotes the distance at which a prey individual escapes from an approaching predator (Chapter 2.2.1.). This thesis, however, also explores how FID is related to behavioural decisions that take place before and after escape. Finer knowledge of the interconnectedness of the predatory sequence (Chapter 2.3.) could reveal how animals make decisions when faced with disturbances. It could also help researchers take on which parameters to include in studies of escape behaviour and to make more accurate assessments of the costs of escape. As FID values can be used for calculating set-back distances to protect wildlife from human disturbances (Guay et al., 2016), and used as a

non-invasive index of hunting pressure (Blumstein, Samia, & Cooper, 2016), the information gained from the present thesis would also benefit wildlife managers more directly. In addition, this thesis compares behavioural responses to the perceived risk of predation on very different ecological scales by looking into situational differences, habitat differences, and geographical differences, while also considering traits related to a species' life history. All five studies were carried out using wild birds under natural conditions.

## 2. LITERATURE OVERVIEW

### 2.1. Human-induced predation risk as a novel ecological threat

Changes in the structure of the habitat, species composition, and predator distribution can fundamentally transform the “landscape of fear” (the spatial distribution of perceived risk of predation) of animal populations (Gaynor et al., 2019). Predation risk can dictate the movement and foraging patterns of prey which, in effect, can elicit further changes in ecosystems (Gaynor et al., 2019; Laundré, Hernández, & Ripple, 2010). For example, it is widely accepted that the reintroduction of wolves (*Canis lupus*) into Yellowstone National Park forced elk (*Cervus elaphus canadensis*) to shift foraging from high risk open areas to safer forest edges, which resulted in an increased growth of aspen (*Populus tremuloides*) and willows (*Salix* sp.) in riparian areas that allowed beavers (*Castor canadensis*) to once again populate Yellowstone (Laundré, Hernández, & Ripple, 2010).

Although behaviours show a high plasticity and should be the first line of defence for habituating to novel conditions (van Buskirk, 2012), a number of studies and historical examples (e.g. the extinctions of insular predator-naïve species) show that phenotypic plasticity is often insufficient to overcome rapid environmental changes, such as ongoing climate change (Both & Visser, 2001; Radchuk et al., 2019; Dunn & Møller, 2019), or that plasticity acts in a maladaptive way (van Buskirk, 2012). In other words, the cues used for estimating predation risk may not lead to optimal decisions if ecological conditions start to change in a different way, or at a higher speed, than these cues (Schlaepfer, Runge, & Sherman, 2002).

In many parts of the world, the presence of humans is still a relatively new occurrence in biological terms implying that animals must rely on general rules of thumbs to decide on how to react to humans and related anthropogenic disturbances, such as cars, airplanes, and various noises (Frid & Dill, 2002). These reactions could be maladaptive not only when animals are predator-naïve to humans, but also when animals perceive humans and traffic noise to be a greater threat than they actually are. For example, the conceptual model by Frid & Dill (2002) demonstrates how increased rates of human disturbance could cause population size to decline when increased antipredator effort reduces energy intake of an individual which in turn affects its body condition and thereby reproductive success (Fig. 1). Indeed, a landscape-scale playback experiment showed that the foraging efficiency of Virginia opossums (*Didelphis virginiana*) was reduced during the playback of human voice, compared to the playback of frog vocalizations (Suraci et al., 2019). Furthermore, even seemingly human-tolerant American kestrels (*Falco sparverius*) were ten times more likely to fail at nesting in highly disturbed areas, compared to areas with low levels of human disturbance (Strasser & Heath, 2013). Alternatively, “the predation risk

allocation hypothesis” states that if encounters with predators are frequent, prey might need to decrease antipredator effort and forage actively even when predators are present (Lima & Bednekoff, 1999). In the latter framework, animals with reduced antipredator effort due to the abundance of non-lethal anthropogenic disturbances could suffer by becoming easier targets for their natural predators (Rodriguez-Prieto et al., 2008). To conclude, a high perceived risk of predation can have more detrimental outcomes for populations via behavioural or physiological consequences than the direct effects of predation (Creel & Christianson, 2008; Cresswell, 2008; Zanette et al., 2011). As previously discussed, such indirect risk effects on one animal could cause behaviourally mediated trophic cascades that, for example, can lead to changes in the plant biomass or community structure (Laundré, Hernández, & Ripple, 2010; Schmitz, Beckerman, & O’Brien, 1997).

Controversially, urban areas – the epitome of anthropogenic disturbance – serve as habitat for a large number of animal populations with higher population densities than their counterparts in more natural areas (Chace & Walsh, 2006). Urban areas can be attractive for animals because of an abundance of resources and cavities for nesting (Chace & Walsh, 2006), and relative safety from natural predators (Díaz et al., 2013; Eötvös, Magura, & Lövei, 2018; Fischer et al., 2012; Møller, 2012; but see Chace & Walsh, 2006). However, most of the local fauna and flora will not thrive in human-altered habitats due to a lack of appropriate adaptations for exploiting novel resources and dealing with risks associated with urbanization (Chace & Walsh, 2006; McKinney, 2002; Lowry, Lill & Wong, 2013; Sol et al., 2014). Animals capable of living in urban areas are often characterised by reduced aggression and reduced fear of humans, but it is unclear whether these behavioural changes are caused by adaptation, phenotypic sorting, or habituation (Lowry, Lill & Wong, 2013). Indirect evidence suggests that microevolutionary adaptations are a more likely explanation than habituation because the difference in fear responses between rural and urban populations increases with the number of generations since the colonization of urban habitats (Møller, 2008). Still, the initial colonization of urban areas is suggested to require a high degree of variation in behavioural plasticity in terms of coping with elevated levels of disturbance (Carrete & Tella, 2009; Møller, 2010; Lowry, Lill & Wong, 2013). Accordingly, Holtmann et al. (2017) found that bold dunnocks (*Prunella modularis*) were more likely to occupy territories with high human disturbance, whereas shy dunnocks settled in territories with low number of pedestrians.

## 2.2. Measuring perceived risk of predation

It is difficult to measure direct predation rate as it requires radiotracking or visual observation of the animals of interest (Creel & Christianson, 2008). Susceptibility of different species to predation can also be assessed by calculating the difference between the observed number of prey items minus the expected

number of prey found near the nests of raptors (Møller et al., 2012). However, it is suggested that the perceived risk of predation is a more appropriate measure if the researcher is interested in finding the potential overall effect that predation risk could have on a population, because animals are more likely to respond to changes in local conditions than to per-capita mortality rates (Cresswell, 2008; Schmitz, Beckerman, & O'Brien, 1997). The perceived risk of predation, i.e. fear, can be measured indirectly by hormonal and behavioural indicators (Laundré, Hernández, & Ripple, 2010). Hormonal covariates of predation risk, such as glucocorticoid levels, are better to be measured non-invasively by faecal sampling of cortisol metabolites or contents in feathers to avoid measuring the immediate stress caused by trapping and handling (Mateo, 2007). The perceived risk of predation is, however, more often judged on behavioural patterns measured visually in the field or in the laboratory. Studying predation risk by recording behavioural measurements has probably been a more popular choice because of the ease of use (Tarlow & Blumstein, 2007) and cost-effectiveness, but it can also lead to results that would not emerge from hormonal studies because predation risk can affect behaviour without a visible change in hormone levels (Creel, Winnie, & Christianson, 2009; Tarlow & Blumstein, 2007). Of course, the opposite can be true as well – for example, the heart rate of royal penguins (*Eudyptes schlegeli*) significantly increased when a pedestrian approached, but the penguins did not initiate escape (Holmes, Giese, & Kriwoken, 2005). To make more detailed predictions about how animals behave under risk of predation, it is also possible to experimentally manipulate predation risk or available resources before measuring the behavioural response (e.g. Cooper, Hawlena, & Pérez-Mellado, 2009; Cooper & Pérez-Mellado, 2004).

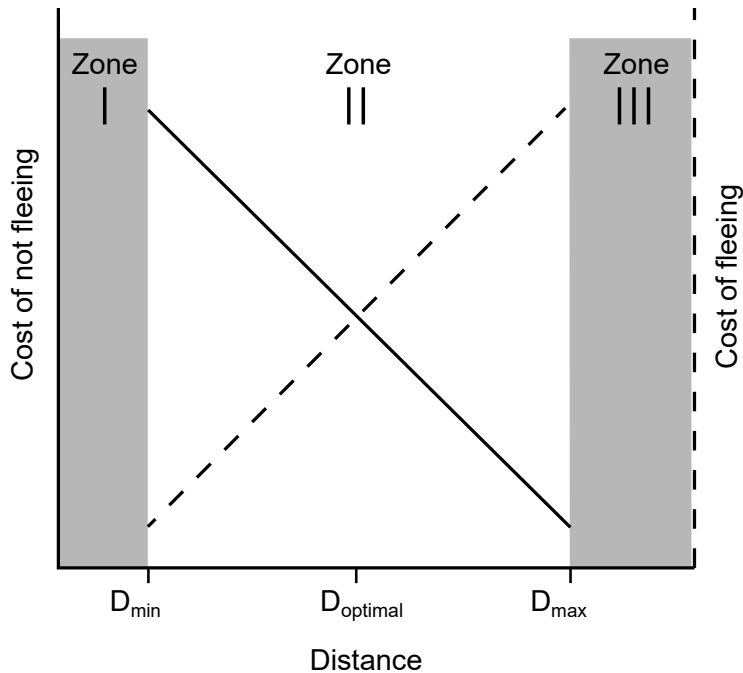
While a variety of behaviours, e.g. foraging rate, group size, and habitat use, could indicate the perceived risk of predation (Gaynor et al., 2019), and there is no single best method to quantify such risks (Tarlow & Blumstein, 2007), one of the most commonly used, and relatively straight-forward, ecological measures of the perceived risk of predation in animals are vigilance and FID (Frid & Dill, 2002). It is important to note that these measures are often not discussed as indicators of predation risk, but rather as responses to disturbances or stressors (Tarlow & Blumstein, 2007), but operating under the predation risk framework proposed by Frid & Dill (2002), this thesis will treat them as such. An ISI Web of Science search conducted on October 22, 2019, while restricting to biologically relevant search categories, found that there are 924 publications that have “flight initiation distance” or any of its synonyms (flush distance, flight distance, escape distance, approach distance) mentioned in the topic. Vigilance, having become popular earlier in the behavioural sciences than FID, was found to be a part of the topic in 1568 publications after searching for the term “vigilance” under the same criteria. The main interpretational difference between the two measures, in the sense of perceived risk of predation, is that vigilance levels should depict a more general wariness towards predators, while FID can be seen as a response to a specific encounter with a predator. Still, responses to different predation events, as measured by FID, can be highly similar due to

“the predation risk allocation hypothesis” (Rodríguez-Prieto et al., 2008). Section 2.2.1 will briefly discuss how FID and vigilance are measured, how they vary under variable levels of predation risk, which ecological patterns these indices have revealed, and the potential weaknesses of these methods.

### 2.2.1. Flight initiation distance

FID is calculated as the distance between prey and an approaching threat when the prey begins its escape (Blumstein & Cooper, 2015). This simple metric has been successfully used in mammals, birds, fish, reptiles, amphibians, and invertebrates (reviewed in Blumstein & Cooper, 2015; Blumstein, Samia, & Cooper, 2016; Samia et al., 2016; Stankowich & Blumstein, 2005; Weston et al., 2012). There is empirical support that FID is related to predation risk. On an individual level, frequent playbacks of predator calls, compared to non-predatory calls, increased the FID of song sparrows (*Melospiza melodia*) (Zanette et al., 2011), while ringed barn swallows (*Hirundo rustica*) captured by predators had significantly shorter FIDs than survivors (Møller, 2014), and Namibian rock agamas (*Agama planiceps*) with shorter FIDs suffered higher rates of tail loss (Carter, Goldizen, & Tromp, 2010). At the population level, ungulates in areas with hunting activity, compared with less and non-hunted areas, generally have longer FIDs (reviewed by Stankowich, 2008; see also Cappa et al., 2017), and FID is shorter in urban populations of birds, and decreases with latitude, paralleling raptor abundance trends (Díaz et al., 2013). At the species level, threatened species in Europe and Australia have longer FIDs, although an inverse trend was found for North American birds (Møller et al., 2014).

The framework for the study of FID is largely based on the economic model by Ydenberg & Dill (1986) that made the prediction that when the distance between a prey and an approaching predator decreases, the cost of not fleeing increases, while the cost of fleeing decreases, and that the optimal distance for escape would be when the cost of fleeing is equal to the cost of remaining (Fig. 2). The costs of fleeing involve a variety of potential opportunity costs, such as foraging, courting, or defence of a territory, and the energetic costs of escape itself. The model has later been refined (e.g. Blumstein, 2003), but the basic premise has remained the same. That economic view of escape decisions sparked a large interest in finding the ecological factors that shape the costs of escape (Cooper & Blumstein, 2015). As a result, FID is not just a tool used for estimating the perceived risk of predation, but rather a source of research questions. The growing body of research has indeed confirmed that the presence of resources, such as food, increases the cost of flight, implying a shorter FID (Cooper & Pérez-Mellado, 2004), while factors related to higher predation risk, e.g. faster approach speed, longer distance to refuge, and eye contact, will increase the cost of remaining and, therefore, increase FID (Cooper & Pérez-Mellado, 2004; Cooper, Hawlena, & Pérez-Mellado, 2009; Bateman & Fleming, 2011; Lagos et al., 2009; Stankowich & Blumstein, 2005).



**Figure 2.** The economic model of escape predicts that when the distance between a prey and an approaching predator decreases (horizontal axis), cost of not fleeing (solid line) increases, while cost of fleeing (dashed line) decreases, and that the optimal moment of escape would be at the intersection of these two curves ( $D_{optimal}$ ) (Ydenberg & Dill, 1986). Risk assessment occurs only between  $D_{min}$  and  $D_{max}$ , i.e. in zone II (Blumstein, 2003). Figure is reproduced from study V (with the permission of Elsevier), where it was redrawn from Cooper & Blumstein (2015) with permission from Cambridge University Press.

Besides assessing the impact of different stressors on wildlife, the values of FID are also proposed to help with creating set-back distances (also called buffer zones) between a habitat and a source of disturbance to reduce the negative effects of human-caused disturbances (Rodgers & Smith, 1995). For example, researchers have created an online tool called AvianBuffer that, based on the published data on FID, calculates set-back distance for a given set of species (Guay et al., 2016). The premise of using FIDs for set-back distances is supported by the findings that FID tends to be a species-specific trait (Blumstein et al., 2003; Guay et al., 2016). Present set-back distances are not always evidence based, and, therefore, they are not sufficient for some of the species that these buffer zones are meant to protect (Glover et al., 2011). However, using just the mean values of FID is also insufficient for development of reliable set-back distances (Fernández-Juricic et al., 2005). In addition, as FIDs can be longer for individuals in better condition, it might be wrong to assume that the most responsive populations are the most vulnerable ones (Beale & Monaghan, 2004).

A meta-analysis by Stankowich & Blumstein (2005) concluded that the variation in FID is influenced by predatory, environmental, conditional and experiential factors; all with about medium effect sizes ( $r \sim 0.30$ ). A more recent meta-analysis on birds highlighted urbanization as the factor with the largest effect size ( $r = 0.62$ ) in explaining variation in escape responses, followed by species body mass ( $r = 0.39$ ), predation ( $r = 0.37$ ), and range size ( $r = 0.35$ ) (Møller, 2015). It is well established that heavier, i.e. larger, bird species escape earlier (Blumstein, 2006; Møller, 2015; Samia et al., 2015; Weston et al., 2012), and that in fishes FID also increases with the length of an individual (Gotanda, Turgeon, & Kramer, 2009). With urbanization, the strength of the relationship between body mass and FID should be weaker as larger birds have reduced their escape responses the most in response to human disturbance (Samia et al., 2015). The interspecific variation in FID of birds has also been linked to various physiological and morphological measures, such as basal metabolic rate, haematocrit levels, wing area and aspect ratio, brain mass, and eye size (Møller, 2009; Møller & Erritzøe, 2014; Møller, Vagasi, & Pap, 2013).

While there have been some minor differences in how FIDs are measured (Weston et al., 2012), the main controversy surrounding analyses on FIDs is focused on the positive correlation between FID and starting distance – the distance at which the observer starts to approach prey in order to evoke an escape response. After Blumstein (2003) found that 64 of 68 bird species showed a positive relationship between starting distance and FID, similar evidence from mammals, lizards, and invertebrates has surfaced (Blumstein, 2010). Yet, a study on Balearic lizards (*Podarcis lilfordi*) found that the relationship only existed when the observer approached rapidly (Cooper, Hawlena, & Pérez-Mellado, 2009). The main ecological explanation for the relationship between starting distance and FID is that longer starting distance can potentially result in an earlier detection of the predator by prey, which means that the prey will need to allocate some of its finite attention to monitoring the approaching predator and, hence, the benefit of remaining decreases (Blumstein, 2003; Blumstein, 2010). Alternatively, early escape could be viewed as visual signal to the predator that it has been detected (Caro, 2005). Dumont et al. (2012) also brought attention to the issue that starting distance can only be smaller or equal to FID, meaning that there is a possibility that the positive relationship between starting distance and FID is simply a mathematical artefact due to heteroscedasticity. Still, several studies have used statistical methods that are free of the mentioned mathematical constraints (these are quantile regression and  $\Phi$ -index) and shown that animals are more likely to escape early than late after becoming alert of the predator (Chamaillé-Jammes & Blumstein, 2012; Samia & Blumstein, 2015). If there were no costs to monitoring predators, the economic model of escape (Ydenberg & Dill, 1986) would not predict such early escape. Also, it is unlikely that the prevailing relationship between starting distance and FID is caused by an increase in falsely recording spontaneous vigilance and locomotion as an antipredator reaction at longer starting distances (Williams et al., 2014). Currently, the standard recommendation is to include



alert distance or starting distance as a covariate in the models of FID, but the debate on how to analyse and interpret the relationship between starting distance and FID continues (Blumstein et al., 2015).

Unlike vigilance, measuring FID usually requires direct intervention with the focal animal, because natural predation events are rare and difficult to measure. That circumstance makes FID less ideal for use in densely vegetated habitats and on endangered populations as it could be unethical to purposefully disturb animals in risk of extinction. Consequently, studies using FID, compared to vigilance, could be more biased by selecting species that are coping well with human-caused disturbances. For example, Samia et al. (2015) found that larger birds have reduced FID the most in response to human disturbance, and suggested that larger bird species are therefore better at tolerating ecotourism. However, by knowing that only a small number of bird species occupy areas with high human disturbance, i.e. cities (McKinney, 2002; Lowry, Lill & Wong, 2013; Sol et al., 2014), one could also deduce that larger species are worse off because of greater behavioural change needed to occupy areas with high disturbance levels. The implications of these “filtering processes”, that exclude species which do not coexist with humans, are not well understood (Blumstein, Samia, & Cooper, 2016).

### **2.2.2. Vigilance**

The definition for vigilance – the other widely used ecological measure of perceived risk of predation – is not as clear-cut as the definition for FID. Vigilance is generally described as a state of alertness involving the act of scanning surroundings to detect and monitor relevant stimuli, e.g. predators and competitors (reviewed by Beauchamp, 2015; Quenette, 1990). Vigilance is typically quantified by visually measuring the occurrence of head-up posture of an animal, i.e. proportion of time spent vigilant, or number of vigilance bouts per time unit, or average duration of vigilance bouts (Allan & Hill, 2018; Beauchamp, 2015). However, one could also use other indicators, such as heart rate, hormonal levels, or pupil dilation, to study vigilance in the broader definition (Beauchamp, 2017).

The study of vigilance gained popularity after Pulliam (1973) published a short mathematical model describing how flocking behaviour is beneficial because it increases the probability of detecting an approaching predator by increasing the collective vigilance of the group. Interestingly, the odds of detecting a predator in groups may not be enhanced only by greater overall time spent on monitoring, but also due to a greater field of view covered (Shackleton, Alves, & Ratnieks, 2018). As a result, individual vigilance can be significantly reduced in larger animal groups while still gaining an advantage in the detection of predators (Pulliam, 1973). However, alternative explanations exist – for example, individual vigilance in groups could also decrease due to the “dilution effect”, which states that an individual has a smaller risk of being attacked in larger groups (Roberts, 1996). In addition, birds of prey are often more

successful at attacking small than large flocks (Cresswell, 1996), indicating that predation risk is lower in larger groups through confusion effects (Caro, 2005). Anyhow, the initial focus on the benefit of vigilance on group living has resulted in group size being the main interest of most research on vigilance (Beauchamp, 2015, p. 117).

Vigilance is commonly suggested to trade against other fitness-enhancing activities because the act of vigilance, i.e. head-up scanning, comes at the expense of competing activities that require other postures or a lot of attention (Caro, 2005; Fortin et al., 2004). Indeed, it is common to see a negative relationship between vigilance and foraging (Beauchamp, 2015; Ciuti et al., 2012; Fortin et al., 2014). For example, large mammals grazing with their heads lowered in grass can be effectively blind to threats and need to lift their heads to look around (Underwood, 1982). This trade-off with foraging makes vigilance a useful measure of predation risk because it simultaneously portrays the reduction of time allocated to foraging. However, recent evidence on various taxa clearly shows that vigilance is not necessarily mutually exclusive with other activities (Beauchamp, 2015, p. 42). For example, scanning and handling of food in upright feeders, e.g. many mammalian herbivores, can partly overlap and, therefore, greatly reduce the cost of vigilance (Fortin et al., 2004; Teichroeb & Sicotte, 2012). However, foraging efficiency can still be reduced during vigilance (Fortin et al., 2004), and especially when foraging on foods that require extensive manipulation (Teichroeb & Sicotte, 2012). Furthermore, in some species, vigilance is often clearly incompatible with feeding; for example, the greater flamingo (*Phoenicopterus ruber ruber*) commonly filters food with its head submerged in water (Beauchamp, 2006).

Vigilance is suggested to be an effective tool against predators. Laboratory experiments show that head-up vigilance significantly increases the ability to detect an approaching predator (Lima & Bednekoff, 1999). Accordingly, cow elk are more vigilant when wolves are present in the habitat (Winnie & Creel, 2007). In addition, vigilant guppies (*Poecilia reticulata*) and Thomson's gazelles (*Eudorcas thomsonii*) are less likely to be preyed upon, suggesting that predators have learnt to target less wary prey (FitzGibbon, 1989; Krause & Godin, 1996). As discussed previously in Chapter 2.1., animals use antipredator responses, such as vigilance, to deal with disturbance stimuli (Frid & Dill, 2002). Indeed, vigilance generally increases when human-caused disturbances are more frequent and closer (Beauchamp, 2015, p. 182). Even more, a study by Ciuti et al. (2012) found that elk showed the highest levels of vigilance in response to human-caused disturbances, not to natural predators, and that these higher levels of vigilance also translated into lower foraging rate. Similarly, Clinchy et al. (2016) demonstrated that audio playback of human voices increased vigilance, decreased foraging time, delayed the initiation of foraging, and reduced the number of visits to food patches for badgers (*Meles meles*) more than the sounds of sheep, wolf, dog, and bear (*Ursus arctos*). One emerging exception is that vigilance levels often decrease with urbanization, suggesting that animals are less threatened in urban sites due to a lower density

of natural predators, or that they habituate to these ever-present disturbances (Magle & Angeloni, 2011; Ramirez & Keller, 2010; Valcarcel & Fernández-Juricic, 2009).

Similar to FID, vigilance patterns show consistent inter-individual differences across different ecological conditions, suggesting that vigilance depends on individual personality types (Couchoux & Cresswell, 2011). Still, considerable intra- and interspecific variation in vigilance could be attributed to changes in predation risk, social risk (i.e. threats posed by conspecifics), the availability of food, and environmental factors (Beauchamp, 2015; Quenette, 1990). So far, no meta-analysis has been done on the drivers of vigilance, but according to the review by Beauchamp (2015), the main patterns of the changes in vigilance in relation to drivers related to predation risk are the following: (a) higher vigilance in the periphery of the group where it is more dangerous, (b) higher vigilance when predators (or cues that signal the presence of predators) are more abundant or when predators are close, (c) increased vigilance in more visually obstructed habitats, (d) decreased vigilance when closer to cover, (e) higher vigilance in females due to the caring for the offspring, (f) lower vigilance with increasing age, (g) increased vigilance when further away from neighbours, and (h) increased vigilance during windy weather or dim light levels. However, a number of these drivers are interconnected in a way that makes it difficult to pinpoint the exact cause for many of these general patterns (Beauchamp, 2015). For example, vigilance also decreases with body mass, both intra- and interspecifically, because larger animals are suggested to have a lower probability of being depredated (Caro, 2005; Brivio et al., 2014; Lank & Ydenberg, 2003; Underwood, 1982). However, an alternative explanation would be that heavier, hence older, males have a lower residual reproductive value that makes them more prone to take risks (Beauchamp, 2015, p. 93).

In some animal taxa, e.g. fish, amphibians and invertebrates, it is difficult to measure postural differences that would indicate vigilance (Fleming & Bateman, 2015). Therefore, vigilance is less universal than FID when it comes to the range of taxa that can be used. On the other hand, vigilance does not need direct intervention with the focal animal and can be therefore easily used on endangered populations, or in situations where direct approach towards an individual is restricted, e.g. densely vegetated forests.

The biggest challenge in working with vigilance data is that vigilance, by its definition and typical mode of measurement, is not an indicator of a single behavioural trait. Some mammal researchers have tried to disentangle anti-predator vigilance and vigilance related to social monitoring by differentiating between the targets of vigilance (e.g. Favreau, Goldizen & Pays, 2010; Gosselin-Ildari & Koenig, 2012), but a recent review on primate vigilance encouraged against such practice, claiming it to be unachievable (Allan & Hill, 2018). In birds, it is even more difficult to identify the targets of vigilance because the eyes of birds are typically laterally positioned covering a wide field of view, and have a high degree of heterogeneity in visual performance around the head (Fernández-Juricic, 2012). Currently, it is unclear whether social

vigilance disturbs antipredator vigilance, or whether simply happening to look in the correct direction is enough (Allan & Hill, 2018).

### 2.3. The predatory sequence

According to Endler (1991), a successful predation event follows a sequence of six stages: encounter, detection, identification, approach, subjugation and consumption. In reality, however, the interactions between prey and predators are much more complex – defences and counter-defences can be applied at any stage (Caro, 2005; Endler, 1991). In addition, Endler (1991) predicted that it is in the best interest of prey to interrupt the predatory sequence as soon as possible in order to maximize the chance of escape and use energy most efficiently. Yet, mathematical modelling has shown that early defence is not always the best solution (Bateman, Vos & Anholt, 2014). Furthermore, the economic escape model by Ydenberg & Dill (1986) predicts that the moment of escape is delayed when the cost of remaining is low and the cost of fleeing is high. Still, real world data shows that in birds, at least, predation events are usually short (< 5 s) and about 90% of attacks end in prey successfully escaping the predator (Cresswell, 1996). An analysis of escape responses by 178 bird species showed that birds tend to escape sooner rather than later – possibly to minimize the costs incurred by monitoring the predator (Samia & Blumstein, 2015). Birds generally do not have the morphological or physiological adaptations, such as armour, venom, spikes, and horns, to defend themselves or counter-attack the predator, but the ability to fly gives birds a major advantage when escaping from terrestrial predators (Caro, 2005; Videler, 2006). A surprise attack, on the other hand, could return some edge back to predators (Cresswell, 1996). Therefore, when trying to formalize a general understanding of antipredator responses in birds, it is important to focus on the mechanisms that are linked to the detection of predators and the subsequent decision-making processes that lead to escape.

If early escape is beneficial for birds, as discussed above, then we should see a strong relationship between FID and the preceding action patterns. Indeed, the distance at which birds become alert to the approaching predator is one the main drivers of FID (Samia & Blumstein, 2015). Accordingly, the distance at which a predator is detected can be expected to positively correlate with alert distance, the distance at which the prey shows outward signs of alertness, e.g. discontinuing current behaviour, orienting towards the observer, lifting its head up, and freezing (Blumstein, 2010; Stankowich & Coss, 2006). However, as detection distance is difficult to measure (Blumstein, 2010; Weston et al., 2012), and as detection of an approaching object does not imply that it has been categorized as a threat, alert distance is often used as a proxy when assessing the distance at which animals become aware of predators (Cooper & Blumstein, 2014). The idea that early detection results in earlier alert behaviour is indirectly supported by the positive relationships between starting distance and alert distance and,

subsequently, between alert distance and FID (Stankowich & Coss, 2006) as it would be otherwise difficult to economically explain why a predator further from prey would need a stronger antipredator reaction. However, as predicted by Blumstein (2003), the positive relationship between starting distance and alert distance is not infinite because at very long distances prey either fail to detect predators or do not perceive them as object needing to be monitored (zone III in Fig. 2; Stankowich & Coss, 2006).

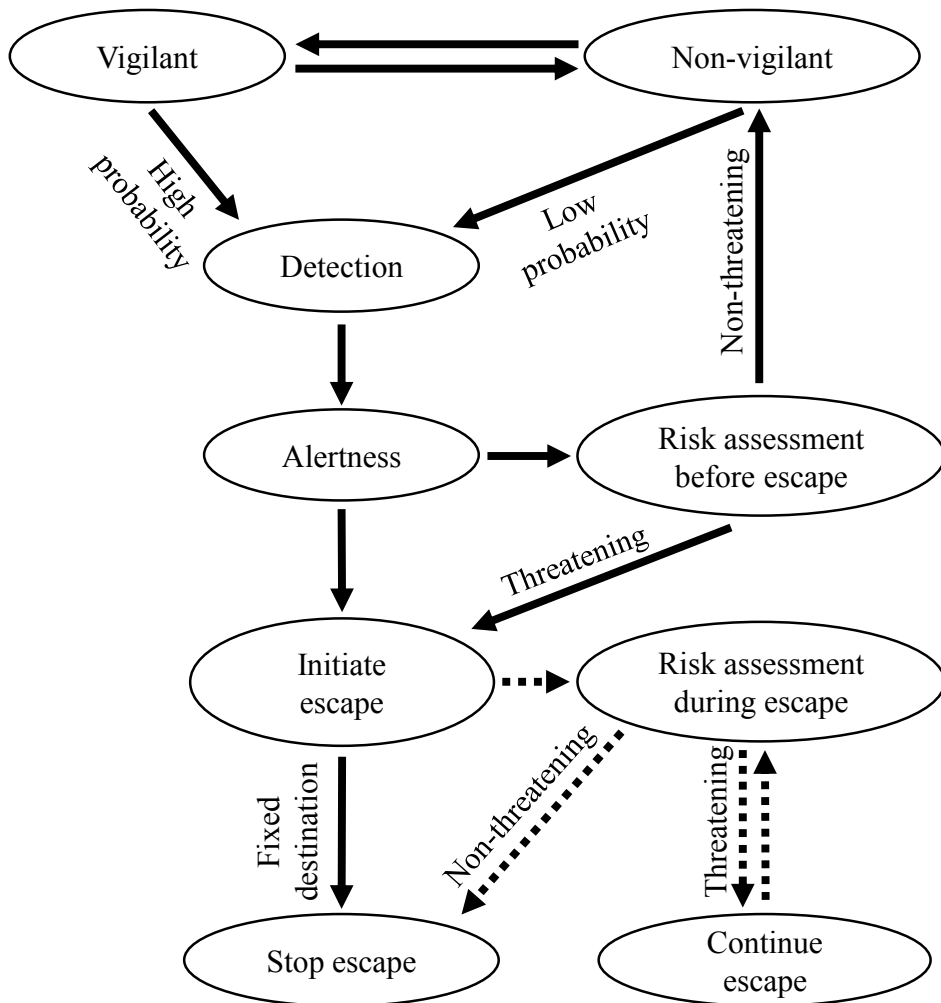
Head-up vigilance is shown to significantly increase the probability that prey will detect a predator, but a bird in head-down posture is also able to detect approaching threats (Lima & Bednekoff, 1999). Therefore, it can be expected that the more time an animal allocates to vigilance, the earlier it is able to detect predators and react (Beauchamp, 2015). Indeed, the reaction times of chaffinches (*Fringilla coelebs*) to approaching predator were dependent on their head-up rate (Cresswell et al., 2003). However, there are surprisingly few studies to document this and some of these studies offer conflicting results (e.g. Jones, Krebs, & Whittingham, 2009; Reimers, Lund, & Ergon, 2011).

Based on these findings and hypotheses, I envision that the escape-centred predatory sequence in birds will follow the basic principles shown in Figure 3. Here I have highlighted that becoming alert does not necessarily imply that escape is imminent, hence the first risk assessment phase can result in either escape or non-vigilance. If active monitoring would always end with prey escaping, then an immediate escape would be more beneficial (Broom & Ruxton, 2005). Prey, however, do actively monitor approaching predators before fleeing (Fernández-Juricic, Jimenez, & Lucas, 2002; Stankowich & Coss, 2006). Besides evaluating the costs of escape, taking last use of available resources, and deciding on the optimal escape strategy (Ydenberg & Dill, 1986), it is also possible that monitoring an approaching predator can lead to the conclusion that the predator has either not yet detected prey, is currently not searching for prey, or is targeting someone else, in which case it could be best not to move (Broom & Ruxton, 2005).

Far too little attention has been paid to whether animals assess risk during fleeing or whether the escape destination is fixed (Fig. 3). If there was a clear relationship between FID and distance fled (DF; the distance moved while fleeing), it would indicate that the perceived risk of predation before escape would orchestrate both variables. Yet, there have been mixed results regarding the question whether earlier escapes lead to longer DF. The relationship between FID and DF (or escape duration) is sometimes positive (Bulova, 1994; Collop et al., 2016; Cooper, 2006; Cooper & Wilson, 2007; Piratelli, Favoretto, & Maximiano, 2015; Stankowich & Coss, 2007), sometimes negative (Andersen, Linnell, & Langvatn, 1996; Vanhooydonck, Herrel, & Irschick, 2007), and often there is no clear relationship (Martín & López, 2000; Rodríguez-Prieto, Fernández-Juricic, & Martín, 2008; Samia et al., 2016). Current research has shown that grasshoppers increase distance fled after successive approaches by the predator (Collier & Hogdson, 2017; Cooper, 2006), but no studies have clearly shown whether predation risk is also assessed during escape. Measuring

DF is difficult because focal animals often flee out of sight (Samia & Blumstein, 2015), which is probably why DF is one of the most neglected variables in models of escape behaviour (Cooper & Blumstein, 2015).

In many species, escape often ends in refuges that restrict access to predators, e.g. rock crevices. Refuge use and subsequent hiding times are mostly studied in lizards (Cooper, 2009; Martín and López, 2015). The economic model used for predicting optimal escape distance (Ydenberg & Dill, 1986) has also been successfully used for explaining variance in the hiding times of lizards: higher costs of emerging (e.g. speed, directedness, and closeness of the predator) increase hiding time and higher costs of staying in refuge (e.g. opportunity costs, low temperature) decrease hiding time (Cooper, 2009). Although hiding time seems to be better studied than DF, little is known about how hiding time is related to preceding phases of escape, such as FID and DF (Martín and López, 2015). A study by Cooper & Sherbrooke (2015) showed that longer starting distances increase FID as well as hiding time, indicating that hiding time could also be interconnected to preceding escape phases. In addition, as previously mentioned, the scope of taxa is very limited (Martín and López, 2015). Birds, for example, are known to perceive a lower risk of predation, indicated by shorter FID, when perched higher (Fernández-Juricic, Vaca, & Schroeder, 2004), but it is likely that the use of higher perches often reduces foraging opportunities, implying a similar cost-benefit trade-off as with more traditional refuges.



**Figure 3.** A schematic overview of the sequential nature of the predator-prey interactions leading to successful escape from the viewpoint of prey. For simplicity, alternative scenarios (e.g. death feigning, intimidation, capture) are left out. Dashed lines indicate uncertainty as it is not clear whether animals continue to assess risk after initiating flight. Relationships are based on the general concepts discussed in Blumstein (2015), Caro (2005) and Cooper & Blumstein (2015).

### 3. AIMS OF THE THESIS

To improve conservation of wildlife populations, it is necessary to know whether the behavioural adaptations for overcoming disturbances, that often cause a rise in the perceived risk of predation, increase or decrease fitness in a human-dominated world full of novel hazards (Buchholz & Hanlon, 2012). Part of a solution is to develop an understanding of the costs involved in antipredator responses, such as energetic and opportunity costs. When attempting to explain variation in behavioural responses to environmental changes, it is also important to understand mechanisms underlying decision-making processes (Sih, 2013).

The current state of evidence on the sequential nature of escape behaviour (Fig. 3; Chapter 2.3.) raises several questions. First, could vigilance be used as a proxy for FID if it is assumed that higher levels of vigilance provide means of early escape (e.g. Beauchamp, 2015)? Or, vice versa, would a longer FID indicate that an animal allocates more time to antipredator vigilance in lieu of foraging? Both vigilance and FID are influenced by numerous ecological drivers of predation risk, e.g. distance to refuge, density of predators, and body size (see Chapters 2.2.1. and 2.2.2.), which indicates their appropriateness as measures of perceived risk of predation, but the impact of overt vigilance on FID in natural conditions remains unclear. Second, is there anything to gain by measuring multiple traits known to be highly correlated due to their interconnectedness? The answer to the second question is “yes” as some studies have shown that interactions with traits like starting distance can reveal interesting patterns related to escape decisions (Cooper, Hawlena, & Pérez-Mellado, 2009), and that measuring the difference between two correlated variables, such as alert distance and FID, offers insight about which factors affect the length of risk assessment (Samia, Møller, & Blumstein, 2015), and provides novel ways to measure tolerance to humans (Fernández-Juricic, Jimenez, & Lucas, 2002). Using interactions and differences between related escape variables could help to explain how animals cope with urbanization or other changes in the perceived risk of predation. The third question is how related is DF to FID? Are they both simultaneously increased by higher perceived risk of predation (e.g. Cooper, 2006), or could there be a trade-off between the two (e.g. Andersen, Linnell, & Langvatn, 1996), or could there be no relationship because the distance to refuge is the most important predictor of DF (e.g. Martín & López, 2000), or because the cues used for estimating predation risk differ before and after escape? If a short FID were to be compensated with a long DF, then that would cause doubts about the appropriateness of recording only FID to measure the perceived risk of predation and the costs of escape.



With the aforementioned questions in mind, the present thesis has the following aims:

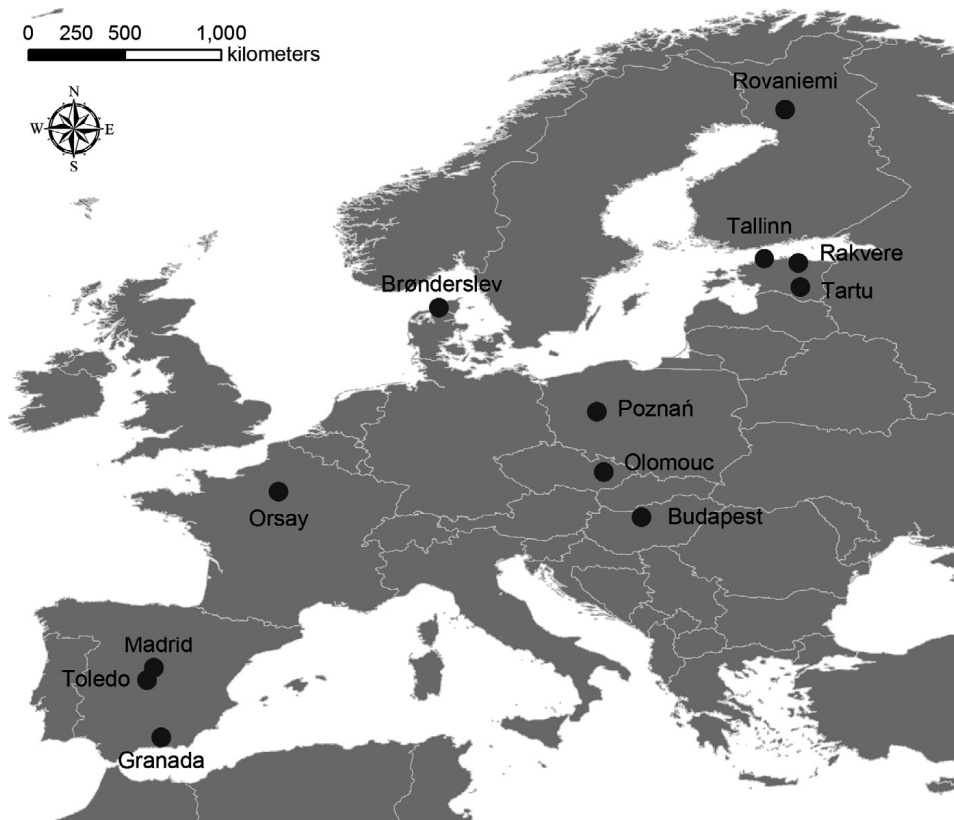
- 1) To provide a greater understanding of the sequential nature of escape behaviour in birds by analysing how different behavioural components are related to each other. For example, if a high level of vigilance increases the possibility of detecting an approaching predator, does it carry-over to earlier escape (study **II**)? Similarly, could difference in escape behaviour between urban and rural populations be explained by the differences in their vigilance levels, pre-detection distances, and risk assessment intervals (studies **II** and **III**)? Finally, does earlier escape indicate longer distance fled (studies **I** and **V**)?
- 2) To study whether birds continue to monitor cues related to predation risk while escaping from a predator (study **V**). Current knowledge on that topic is lacking and, therefore, makes it difficult to do predictions about the predatory sequence (Fig. 3), and hence, the costs of escape.
- 3) To find environmental, behavioural, and morphological factors that covary with the changes in escape related behaviours (studies **I**, **II**, **III**, **IV**, and **V**). Knowledge concerning covariates, such as group size, distance to refuge, and perching height, could help us to understand how birds assess risk, and improve the methodology used for measuring perceived risk of predation.
- 4) To make broad-scale generalizations on escape-related behaviours that could ease the decision making of wildlife managers – a research need highlighted in a recent review by Blumstein, Samia, & Cooper (2016). For that, the thesis contains multi-species studies, sometimes crossing country borders, that compare urban and rural populations (studies **I**, **II**, **III**, and **IV**).

## 4. MATERIALS AND METHODS

### 4.1. Study system

Four periods of fieldwork were carried out during 2015–2018 to quantify behavioural responses of birds towards human observers (Table 1). Observations for studies **I** and **V** were made in Estonia. Study **II** was carried out in France, Hungary, and Spain. Data for studies **III** and **IV** were collected from Czech Republic, Denmark, Estonia, Finland, France, Hungary, Poland, and Spain to incorporate latitudinal gradient across Europe into the study system (Fig. 4). In all studies except **V**, observations were made intermittently in urban and adjacent rural sites to compare behavioural differences in birds between urban and rural habitats. Habitats were classified based on the guidelines by Marzluff, Bowman, and Donnelly (2001). Urban habitats were characterized by high housing density (>10 buildings/ha), high residential human density (>10 humans/ha) and a high percentage of built-up areas (at least 50%), while rural habitats had lower housing density (<2.5 buildings/ha), lower human density (between 1 and 10 humans/ha), and less built-up areas (5–20%). Functionally, it was assumed that while urban sites have lower levels of predation risk posed by natural predators, there would be higher levels of anthropogenic disturbances (Díaz et al., 2013).

Each location (e.g. street, park) was visited only once during a study to minimize potential resampling of the same individual. In studies **III** and **IV**, visiting the same general area was allowed, but only individuals of different species, sex, or age than those sampled before were tested. Some birds could have flown from one site to another, but it has been shown that pseudoreplication in FID studies is usually not of concern (Runyan & Blumstein, 2004). Study **V** targeted specific set of species (Eurasian jackdaw, *Coloeus monedula*; hooded crow, *Corvus cornix*; and rook, *Corvus frugilegus*), while studies **I**, **II**, **III**, and **IV** did not initially restrict the selection of species during fieldwork. Study **IV**, however, was later restricted to 23 “gregarious” species, i.e. species that have the habit of living or moving together in groups either during breeding or nonbreeding, following the classification by Cramp & Perrins (1994). Studies **III** and **IV** excluded species of which there were less than 16 or 10 observations, respectively, to produce more reliable model estimates. See Table 1 for the number of species and individuals retained in the final data sets used for statistical modelling.



**Figure 4.** Location of 12 study sites across eight European countries, where data for studies III and IV was collected. Figure reproduced from Fig. 1 in study IV, licenced under the CC BY 4.0 licence.

**Table 1.** An overview of the general study designs used in this PhD thesis. Presented values characterise the data and the main response variables used in statistical modelling.

<b>Study no.</b>	<b>Response variables</b>	<b>Field work</b>	<b>Scale</b>	<b>Habitats</b>	<b>No. of species</b>	<b>No. of individuals</b>
I	FID, DF	2016, June-Aug.	2 cities from Estonia	Urban, rural	17	699
II	FID, vigilance, pre-detection distance, assessment interval	2017, Jan.–Mar.	3 cities from 3 countries	Urban, rural	59	1408
III	$\Delta$ Pre-detection distance*, $\Delta$ assessment interval*	2015, Apr.–Sept.	10 cities from 8 countries	Urban, rural	32	5,987
IV	FID	2015, Apr.–Sept.	12 cities from 8 countries	Urban, rural	23	5,753
V	Escape duration, escape angle, angular change	2018, May–July	2 cities from Estonia	Urban	3	324

FID = flight initiation distance, DF = distance fled. Studies III and IV were based on the same initial dataset of 7,302 observations.

\*  $\Delta$  indicates rural-urban difference estimated for a species from a single city.

## 4.2. Behavioural measurements

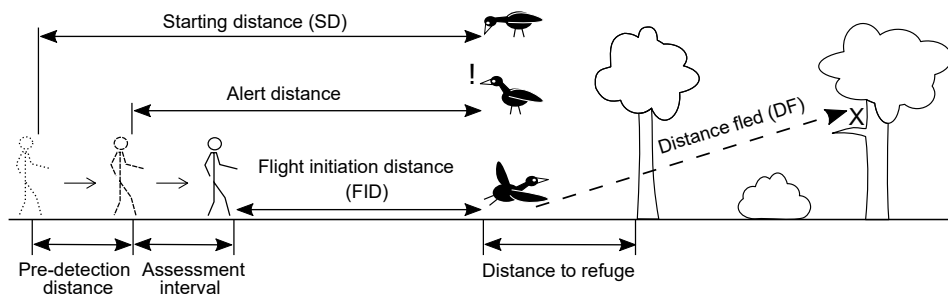
### 4.2.1. Vigilance

In study **II**, when an individual bird was located (when in a flock, chosen as the one closest to the observer), its vigilance was recorded, with a stopwatch, by measuring the time the individual bird kept up its head during two 60 s observation periods in succession. If, for any reason, the view became obstructed, the observation period was ended. The two sequential observations were used to calculate the mean proportion of time spent vigilant.

### 4.2.2. FID and its related parameters

Having located an unalarmed adult bird, i.e. an individual that is foraging, preening, or roosting without signs of alertness towards the observer (i.e. does not discontinue its current behaviour to orient towards the observer and/or freeze),

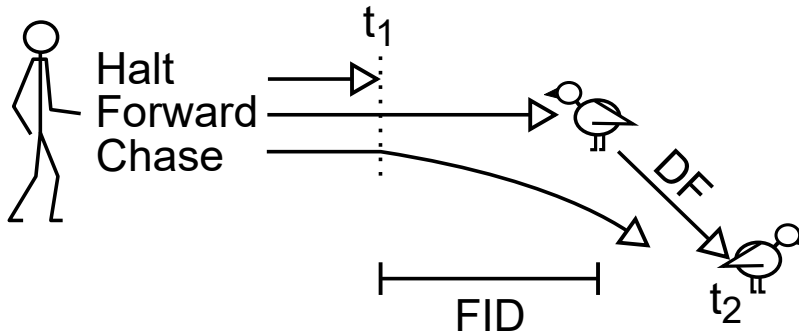
the observer approached it to measure parameters related to escape behaviour. A standard protocol for measuring FID was followed (e.g. Blumstein, 2003; Møller, 2008), where the focal bird is approached at a constant speed (0.5 or 1.3 m/s depending on the study) until it escapes. First, the initial distance between the observer and the focal bird was recorded as the starting distance. Second, the distance between the two at the moment when the bird became visibly alert of the approaching human (as described earlier) was recorded as the alert distance. Third, the distance between the observer and the individual when it began to flee was the FID (Fig. 5). These distances were measured by counting steps and were later converted to metres by multiplying by the average step length of the observer. Whenever there was reasonable doubt about whether the bird escaped in relation to the observer or some other disturbance (e.g. alarm call, another pedestrian, car), the observation was not recorded, as suggested in Blumstein et al. (2015). In study V, Laser Rangefinder PROSTAFF 3i (Nikon Vision Co., Ltd., Tokyo, Japan; measurement range 7.3–590 m, accuracy 0.1 m) was used to measure starting distance. Studies I and V made effort to limit the range of starting distance by not targeting individuals spotted at close range (as a result, all starting distances were over 23 m). In studies II and III, the distance between the starting distance and the alert distance was used as a measure of pre-detection distance. In addition, assessment interval (called buffer distance in studies I and III) was calculated by subtracting FID from the alert distance (Fernández-Juricic, Jimenez, & Lucas, 2002) (studies I, II, and III). Whenever the bird was not on the ground, the Euclidian distance was calculated between the observer and the bird (Blumstein et al., 2004). However, studies I and V were carried out only on individuals on the ground to account for the potential effect of perching height.



**Figure 5.** Schematic illustration of how escape-related distances were measured. X marks the endpoint of escape. See Chapters 4.2.3, 4.2.4, and 4.3 for details. Figure adapted from Fig. 1 in study I with permission from Elsevier.

### 4.2.3. Approach types

In study V, I tested whether birds change their escape duration according to experimentally manipulated level of predation risk. For that, birds were approached in three ways: “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. 6; see study V for details). It was predicted that the perceived risk of predation, and consequently escape effort, will be the lowest in the case of approach type “halt”, intermediate with type “forward”, and the highest with type “chase”. For approach type “forward”, the initial location of the bird was selected as the termination point because sometimes it is not possible to continue walking indefinitely beyond the initial spot due to physical obstacles. The order, in which approach types were executed, followed a continuous loop, i.e. “halt”–“forward”–“chase”–“halt”–“forward”–“chase” etc.



**Figure 6.** Schematic illustration of the three approach types compared in study V.  $T_1$  = time when bird initiated escape,  $t_2$  = time when bird stopped escaping,  $t_2 - t_1$  = escape duration, FID = flight initiation distance, DF = distance fled. Arrows indicate movement. Termination of approach is determined by  $t_1$  for type “halt”, and by  $t_2$  for “forward” and “chase”. Figure reproduced from Fig. 2 in study V with the permission of Elsevier.

### 4.2.4. Distance fled, escape duration, and escape angle

In studies I and V, the shortest distance between the spot where the bird escaped and the spot where it ended its escape was termed distance fled (Fig. 5). A total of 70% of distance fled measurements were recorded with the aforementioned laser range finder, but all distances below the range finder’s minimum measuring range (7.3 m) were measured by counting steps. Pythagorean theorem was used to standardize distance fled measurements, so all would reflect distance from ground level (instead of eye level) to the spot where the bird decided to stop

fleeing. In study **I**, all observations, where it was not possible to measure distance fled, were excluded from the analysis after it was found that these did not differ significantly ( $P > 0.05$ ) from other observations by any measured variable.

In study **V**, escape duration was measured with a stopwatch from the moment escape was initiated until the bird stopped (i.e. during distance fled) with centi-second (cs) precision. Escape duration was used instead of distance fled in study **V** because it takes into account the fact that not all escapes are linear. Still, there was a strong positive correlation between escape duration and distance fled,  $r = 0.79$ ,  $N = 301$ ,  $p < 0.001$ . Counting was immediately stopped whenever a bird escaped out of sight. In study **V**, escape trajectories (path taken by the fleeing birds) were drawn onto a circle by visual estimation to measure initial and final escape angle in relation to the observer. The difference between initial and final escape angles was defined as change in escape angle.

All studies noted whether birds walked, flew or swam during fleeing, but only studies **I** and **V** used escape method (terrestrial versus aerial) in statistical analyses as it is an important predictor of distance fled (Rodríguez-Prieto, Fernández-Juricic, & Martín, 2008). Study **V** also recognised a third escape method that consisted of both terrestrial and aerial movements, but due to the small number of such observations, it was put together with terrestrial escape method in most statistical models.

### 4.3. Other parameters

Flock size was recorded as the number of individuals within a fixed radius around the focal bird before approaching it (~10 m in studies **II**, **III** and **IV**; ~15 m in studies **I** and **V**). The number of relatively close companions is sometimes suggested to better reflect the effect of group size than considering all visible individuals as part of the group (Blumstein, Daniel, & Evans, 2001; Treves, 1998). Studies **II**, **III**, and **IV** recorded only conspecifics as members of the flock, while studies **I** and **V** included other species near the focal bird as part of the flock as well. After eliciting escape response in an individual from a flock, that flock was not approached again, except in the rare instances brought out in study **V**.

In study **II**, initial perching height was classified as low or high, depending on whether the birds were perched lower than 2 m or higher, respectively. It was expected that perching height over 2 m positions birds above the human observers gives a significant rise in the sense of safety.

In study **I**, vegetation cover was visually estimated in 30 m radius around the point of escape following the suggested scale and cover charts by Prodon & Lebreton (1981) to account for possible habitat effects. Foliage of the canopy was projected onto a horizontal plane to calculate this relative degree of cover. While separate estimates were initially made for bush and tree cover, these were later summed to calculate a single predictor of vegetation cover. Study **V** used

an alternative approach by measuring density of trees ( $\geq 2$  m of height) in a 15 m radius of the focal bird.

Studies **I** and **V** measured the horizontal distance to the closest potential refuge because distance to refuge can be an important predictor of distance fled (Martín & López, 2000). While both studies regarded trees, bushes, posts, and fences as potential refuges, only study **I** included buildings as refuges. Similar to other measurements, a laser range finder and – if needed – counting steps were used to measure these distances. The types of the closest and the chosen refuges were also noted.

Data on mean body mass of the species were obtained from Cramp & Perrins (1994) and Pearman et al. (2014), and information on mean brain mass from Møller and Erritzøe (2014). Information about latitude and human population size of the cities (study **III**) were extracted from Wikipedia (<https://www.wikipedia.org>). In study **IV**, all species were classified into five main categories as granivorous, granivorous–insectivorous, insectivorous, carnivorous, and omnivorous, based on the main type of food consumed (data from Pearman et al., 2014). All studies recorded whether there were any predators (including domesticated animals) or pedestrians present in a 50 m radius from the focal bird, but these variables were left out during the initial data exploration phase as there were no significant correlations that would indicate potential confounding effects.

## 4.4. Statistical analyses

### 4.4.1. Phi index

Studies **II**, **III**, and **V** used the phi index (Samia & Blumstein, 2015) when analysing the relationships between some of the escape variables to overcome the issue of mathematical constraints tied to the components of these measurements (i.e. starting distance  $\geq$  alert distance  $\geq$  FID) (Dumont et al., 2012). The phi index ( $\Phi$ ) is a standardized goodness-of-fit metric (range 0–1) that, in studies **II** and **III**, was used to estimate how close alert distance is to starting distance (pre-detection- $\Phi$ ), FID to alert distance (assessment- $\Phi$ ), and, in study **V**, FID to starting distance (FID- $\Phi$ ). The phi index is generally calculated as follows:

$$\Phi = 1 - \sum_{i=0}^n \frac{(e_i - o_i)}{e_i}.$$

For pre-detection- $\Phi$ ,  $e_i$  is the starting distance and  $o_i$  is the alert distance of an individual bird, and, therefore, values closer to 0 indicate that the birds were relatively slow at detecting approaching humans, while a value of 1 would imply that the bird was immediately aware of the human as the approach began.



When calculating assessment- $\Phi$ ,  $e_i$  represents the alert distance and  $o_i$  is the FID. Hence, assessment- $\Phi$  values closer to 0 indicate a longer risk assessment, while a value of 1 would imply immediate escape after becoming alert (i.e. risk assessment took less time than it took for the observer to make one step). To calculate rural-urban differences in  $\Phi$  values, the  $\Phi$  of an urban population of a species was subtracted from the  $\Phi$  of the nearby rural population of the same species (study **III**).

In study **V**, the equation for calculating FID- $\Phi$  was simpler:  $1 - (\text{distance approached} / \text{starting distance})$ , so that the values could be interpreted similarly to ordinary FID, with larger values indicating an earlier escape. In this study, using FID- $\Phi$  instead of regular FID was necessary because approach type “chase” did not allow us to directly measure the remaining distance to the bird because the observer had to start following it during its escape. The results of FID- $\Phi$  are not directly comparable with regular FID, but FID- $\Phi$  should similarly indicate how tolerant the bird was of the approaching human.

#### **4.4.2. Other transformations**

Continuous variables were  $\log_{10}$ -transformed to make the data conform more closely to normal distributions that facilitate to ensure normality of residuals. If a variable contained zeros, a constant of one was added to the values before transformation. In study **I**, vegetation cover (%) was square root transformed. To reduce multicollinearity from the included interaction terms in statistical models, the sample means from the values of continuous predictors were subtracted. In study **I**, each independent numeric input variable was standardized by dividing by two times its standard deviation (Gelman, 2008). In study **V**, only escape angle was scaled that way to put it on a similar scale of units with other predictors.

#### **4.4.3. Statistical modelling**

The main hypotheses were tested using general linear mixed models in R (R Core Team, 2019). Dependent variables are brought out in Table 1 and the list of independent variables, along with specific hypotheses, can be found in each of the individual papers. Species identity and/or site were used as random factors to account for species-specific and site-specific variation and unequal sample sizes. In studies **III** and **IV**, models were weighted by sample size to account for differences in sampling effort among populations (Garamszegi & Møller, 2010). All studies, except **V** where species identity was treated as an independent variable, incorporated a phylogenetic distance matrix in the models to remove the confounding effect of common ancestry that could violate the assumptions on statistical independence (Garamszegi & Møller, 2010). The introduced phylogeny subset was obtained from the latest bird phylogeny

available (Jetz et al., 2012) following the guidelines by Rubolini et al. (2015). The R library *ape* (Paradis, Claude, & Strimmer, 2004) was used to find the consensus trees and calculate branch lengths. More details about the calculations of consensus trees and phylogenetic signals can be found in the Methods section of papers **I**, **II**, and **IV**. In study **IV**, a log–log–linear regression between FID and body mass was first made and then the residuals of that regression were used in order to reduce the confounding effect of body mass on FID (Blumstein, 2006). Studies **I**, **II**, and **III**, however, simply used multiple regression to control for undesirable confounding effects (Freckleton, 2002).

In study **III**, stepwise backward model selection was used to rank models based on corrected Akaike Information Criteria (AICc), using a threshold AICc value of 2. Both full and minimum adequate models were presented. Studies **I**, **II**, **V** used the function *dredge* from the library *MuMIn* (Bartoň, 2017) to generate all combinations of predictors from the full model, that were then ranked by AIC values. A set of top models ( $\Delta\text{AIC} < 4$  or 95% confidence model set) was then chosen for model averaging using the function *model.avg* with the natural average method (Bartoň, 2017). In study **V**, uninformative parameters were removed from the top model set according to the criteria suggested by Leroux (2019). Estimates of predictors were considered to have support for an effect on the dependent variable whenever their 95% confidence intervals did not overlap zero. Studies **III** and **IV** practiced null hypothesis significance testing based on *P* values. In study **V**, R library *emmeans* (Lenth, 2017) was used for pairwise comparisons with Tukey's method, and for creating corresponding plots of estimated marginal means.

Oriana 4 software (Kovach 2011) was used for circular statistics (study **V**). 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. Escape angle of 180° indicates an escape straight away from the human observer, while an angle of 0° indicates escape towards the observer.

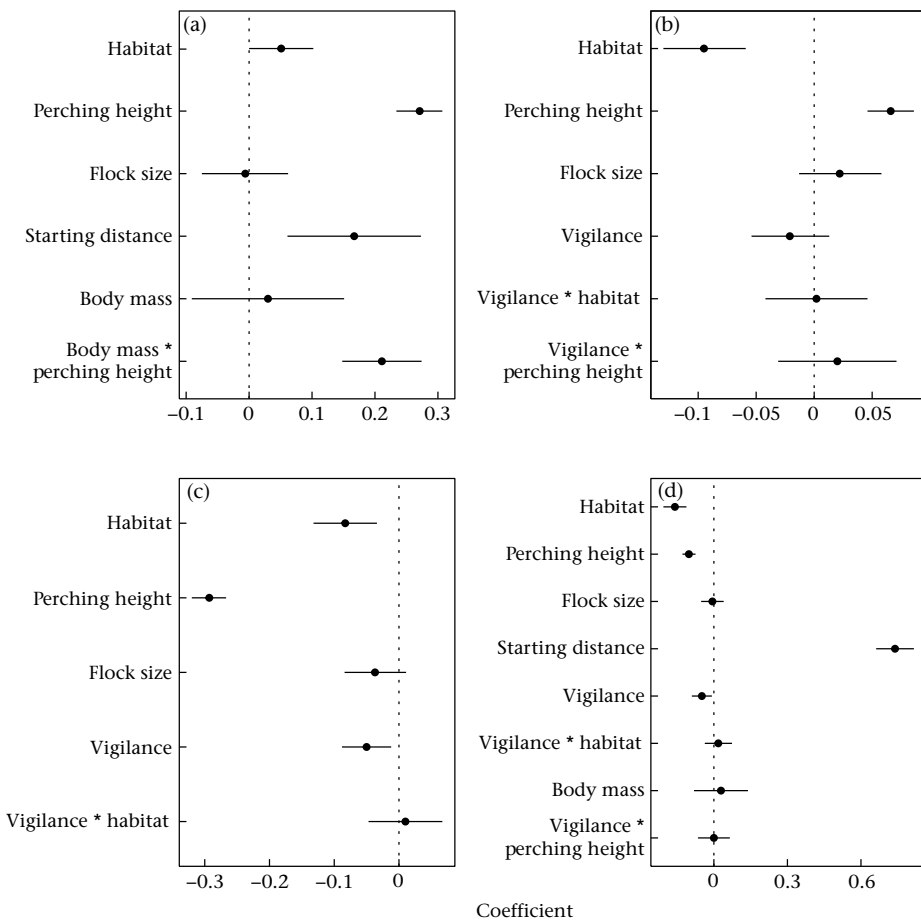
## 4.5. Ethical note

The chosen method for eliciting an escape response causes only a brief disturbance of birds that should not cause any pain or lasting harm, and is similar to the frequent disturbances involuntarily caused by other pedestrians, and amateur and professional ornithologists and photographers. Targeted birds were not endangered, juvenile, or in visual proximity to their nests or fledglings.

## 5. RESULTS

### 5.1. Vigilance

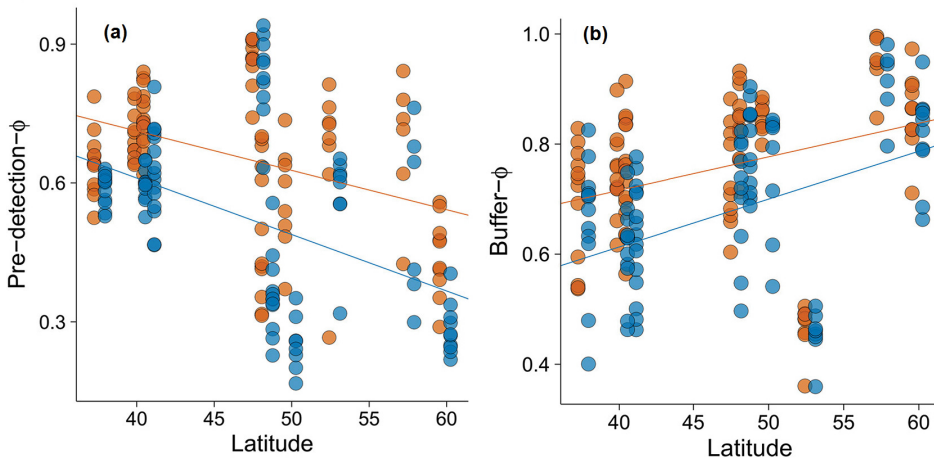
In study **II**, it was found that birds were generally more vigilant in urban than in rural habitats. When using pre-detection- $\Phi$  as a proxy for detection distance, more vigilant individuals were not faster at detecting approaching observers. Assessment interval increased with vigilance, while FID showed an opposite pattern. Vigilance increased with mean body mass for birds on higher but not on lower perches. Vigilance was also in a positive relationship with starting distance. There was no significant relationship between flock size and vigilance. Interactions between vigilance and habitat type, and vigilance and perching height showed that the (non-)effect of vigilance on pre-detection- $\Phi$ , buffer- $\Phi$ , and FID did not depend on the type of habitat or perching height. See Fig. 7 for a summary of the results from study **II**.



**Figure 7.** Model-averaged parameter estimates (dots) with 95% confidence intervals (horizontal lines) for predicting changes in (a) vigilance, (b) pre-detection- $\Phi$ , (c) assessment- $\Phi$  and (d) flight initiation distance. An estimate can be considered to have support for a relationship if its confidence intervals do not overlap zero. See Chapter 4.4.1. for details on the  $\Phi$  index. Figure reproduced from study **II** with the permission of Elsevier.

## 5.2. Pre-detection distance

In studies **II** and **III**, pre-detection- $\Phi$  was smaller in urban habitats, indicating delayed detection, even though starting distances were shorter in urban habitats. The rural-urban difference in pre-detection distance increased with latitude (Fig. 8a). Perching heights over 2 m, compared with lower perching heights, increased pre-detection- $\Phi$  (note: in study **II** it was erroneously stated that this corresponds to longer pre-detection distance, but the opposite is true; a corrigendum on this error is in press). There was no support for flock size as a predictor of pre-detection- $\Phi$  (study **II**), nor did the rural-urban difference in flock size relate to rural-urban difference in pre-detection distance (study **III**). In addition, the rural-urban difference in mean starting distance was not related to the rural-urban difference in pre-detection- $\Phi$  (study **III**).



**Figure 8.** The relationships between (a) latitude and pre-detection- $\Phi$ , and (b) latitude and assessment- $\Phi$  by habitat. Orange points and orange regression line represent rural populations, while blue points and blue regression line represent urban populations. Urban birds were displaced  $0.7^\circ$  to the right to improve readability. See Chapter 4.4.1. for details on the  $\Phi$  index. Figure reproduced from Figs. 4 and 6 in study **III**, licenced under the CC BY 4.0 licence.

## 5.3. Assessment interval

Assessment- $\Phi$  (termed buffer- $\Phi$  in study **III**) was lower in urban areas implying that the assessment interval was longer (studies **II** and **III**). In study **III**, the rural-urban differences in assessment interval increased with the difference in their mean alert distance. Rural birds did not have a significant relationship between mean alert distance and assessment- $\Phi$ , while urban birds had a negative relationship between these variables, meaning that assessment intervals were

longer when birds became alert at longer distances. However, the latter relationship was not significant when an outlier was kept in the analysis. It was also found that rural-urban differences in assessment interval decreased as latitude increased – urban birds delayed escape more at low latitudes when compared with rural birds (Fig. 8b). A negative relationship between pre-detection- $\Phi$  and assessment- $\Phi$  was found in urban populations, implying that a relatively long detection distance will be followed by a short assessment interval in urban sites. No such relationship was found in rural habitats. In study **II**, assessment interval was longer individuals on higher perches.

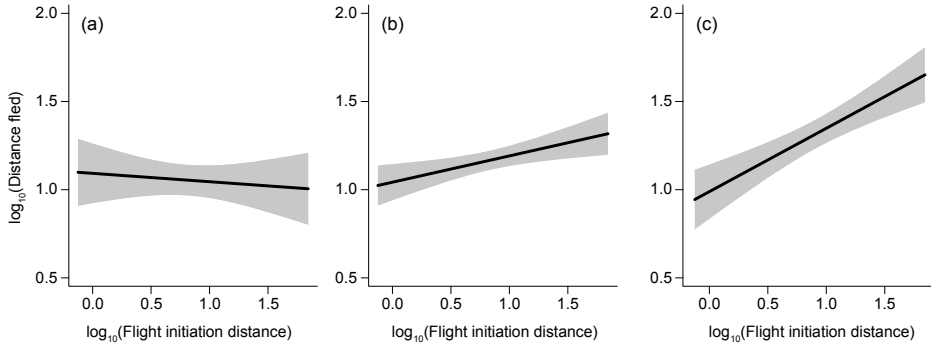
#### 5.4. FID

FID was significantly shorter in urban habitats, compared to rural habitats (studies **I**, **II**, **III**, and **IV**). Birds on higher perches had shorter FID, implying a delayed escape reaction (study **II**). Starting distance was positively related to FID (studies **II** and **IV**). However, study **I** showed that the relationship with starting distance was positive in rural but not in urban sites. FID increased with flock size in both urban and rural habitats (studies **I** and **IV**), but no significant relationship was found in study **III**. FID was in a positive relationship with the mean body mass of the species in study **IV** but not in studies **I** and **II**. However, a subset of individuals with assessment intervals longer than zero meters showed a positive relationship between body mass and FID in study **I**. Among the four compared diet niches in the 23 gregarious species, insectivorous and granivorous-insectivorous species had the shortest mean FID, while granivores and omnivores had the highest mean FID (study **IV**). Assessment interval was not a reliable predictor of FID nor DF in study **I**, but assessment- $\Phi$  initially showed a strong positive relationship with FID ( $\beta = 0.738$ ,  $SE = 0.0172$ ) in study **II**, indicating that FID decreased as assessment interval increased. However, assessment- $\Phi$  was later removed from the model of FID in study **II** because the reviewers of the paper wished for more focused models, and rightly so.

#### 5.5. Distance fled and escape duration

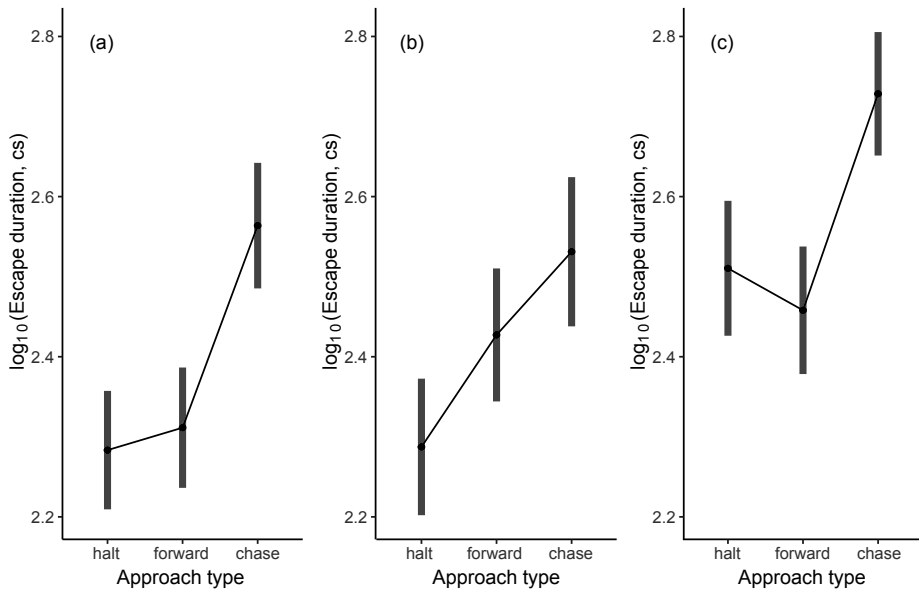
DF was shorter in urban habitats but longer for heavier species (study **I**). An interaction between FID and the mean body mass of the species indicated that the strength of the correlation between FID and DF increased with the size of the species (Fig. 9). Study **V** supplemented these results by showing that while the relationship between FID- $\Phi$  and escape duration is positive for approach type “halt”, i.e. the same standard method used in study **I**, there is no clear relationship between FID- $\Phi$  and escape duration for approach types “forward” and “chase”. Terrestrial escape method, compared to aerial escape method, resulted in shorter DF and escape duration (studies **I** and **V**, respectively). In contrast, escape duration was longer for terrestrial escape when using approach

type “chase” (study V). During escape, more individuals changed their escape method from terrestrial to aerial for approach type “chase” than for approach types “halt” and “forward”. There was no significant difference in the frequency of chosen escape methods between approach type “halt” and “forward”. Neither DF nor escape duration was related to flock size (studies I and V). In study V, there was a positive relationship between starting distance and escape duration for the rook, but not for the Eurasian jackdaw or the hooded crow. There was no general relationship between starting distance and DF in study I.



**Figure 9.** Relationships between flight initiation distance (m) and distance fled (m) across (a) 10th (20.75 g), (b) 50th (92.10 g) and (c) 90th quantile (453.50 g) of  $\log_{10}$ (body mass) of 699 birds from 17 species. Predicted model estimates (black line) are shown with 95% confidence intervals (grey area). Figure adapted from Fig. 6 in study I with permission from Elsevier.

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 methods, but there was no statistically significant difference between approach types “halt” and “forward” (study V). When comparing escape duration among the three approach types by species, only the hooded crow showed an increase in escape duration during approach type “forward” in comparison with approach type “halt”, while all species increased escape duration during approach type “chase” in comparison with approach type “halt” (Fig. 10).



**Figure 10.** Relationships between approach type and escape duration for (a) Eurasian jackdaw, (b) hooded crow, and (c) rook in study V. Black circles represent estimated marginal means and grey rectangles represent confidence intervals based on predictions from a linear mixed model. Figure adapted from Fig. 3 in study V with permission from Elsevier.

## 5.6. Refuge use

DF and escape duration increased with the distance to refuge (studies I and V). Ground was the most frequent destination of escape (about 60% of observations), followed by trees, posts and fences, buildings, and bushes, respectively (studies I and V). Preference for refuge types was equally distributed among approach types (study V) and habitats (study I). In study I, 36.7% of escapes that ended in a refuge (i.e. not on the ground), the closest available refuge was chosen. Distributions of closest available refuges and closest chosen refuges appeared to be similar.

## 5.7. Other parameters

The relationship between escape angle and escape duration was positive only for the rook (study V). All three species in study V had an average initial escape angle of about 120° with no distinctive peaks. The change in escape angle during escape depended on approach type, with the change in escape angle being larger for approach type “chase” than for approach type “halt”, but a significant difference was found only for terrestrial escape method and not for aerial.

Vegetation cover was not related to FID or DF (study **I**). Similarly, the number of nearby trees was unrelated to escape duration, escape angle, and change in angle during escape (study **V**). FID did not covary with latitude in study **IV**. There was a significant phylogenetic signal for mean FID of a species, but no such signal was found for mean vigilance of a species (studies **II** and **IV**). Rural-urban differences in pre-detection- $\Phi$  and assessment- $\Phi$  did not increase with the city's human population size.



## 6. DISCUSSION

Quantifying how animals perceive risk of predation in different scenarios is a useful practice for understanding the impact human-related disturbances could have on animal populations (Frid & Dill, 2002). Furthermore, as antipredator behaviour is often traded against other fitness-enhancing activities, the strength of antipredator responses can indicate energetic and opportunity costs induced by higher levels of perceived risk (Beauchamp, 2015; Ciuti et al., 2012; Cooper & Blumstein, 2015; Ydenberg & Dill, 1986). One of the most common measures of the perceived risk of predation are flight initiation distance and vigilance (Frid & Dill, 2002). Raising awareness of the nearby predators is presumed to be one of the main functions of vigilance, but the validity of this presumption is usually not tested (Beauchamp, 2015). Indeed, FID and vigilance are usually studied independently and there have been few empirical investigations into their relationship in natural conditions. What is more, much uncertainty exists about the relationship between FID and post-escape responses, such as distance fled (Cooper & Blumstein, 2015). In order to understand the mechanisms responsible for variation in antipredator behaviour, it is often wise to study multiple behavioural parameters together and analyse their relationships (e.g. Fernández-Juricic, Jimenez, & Lucas, 2002; Samia, Møller, & Blumstein, 2015). In addition, a more complete view of the predatory sequence helps to rule out the possibility that a change in one behavioural response is not compensated by other related responses. Therefore, a better understanding of the full predatory sequence should make it more clear which behavioural parameters to measure and what these measures could imply. Accordingly, present thesis sought to explain the interconnectedness of escape-related behaviours, while also exploring which environmental, behavioural, and morphological factors potentially come into play during escape behaviour. The behaviour of birds was compared between urban and rural habitat to assess how birds cope with factors related to urbanization.

### 6.1. A step-by-step look at the findings from different stages of the predatory sequence

#### 6.1.1. Vigilant birds exhibit relaxed escape behaviour

Contrary to the prevalent theory that suggests that detection of threats is one of the main functions of vigilance (e.g. Beauchamp, 2015; Quenette, 1990), more vigilant birds did not have shorter pre-detection-distances, i.e. the distance at which the focal animal becomes visibly alert to the approaching predator (Fig. 7; study II). Furthermore, birds with higher vigilance levels spent more time on risk assessment after becoming alert, and had shorter FIDs, indicating a more relaxed escape response. Similarly, it was evident that birds were more vigilant

in urban habitat although all four studies of this thesis, that explored the urban-rural differences in FID, found that birds generally delay escape in urban habitats. Lastly, higher perching height increased vigilance of larger birds, while decreasing FID. Therefore, the results from study II on vigilance indicate that vigilance, as measured by the proportion of time spent in a head-up posture, does not characterise the perceived risk of predation in birds in a similar fashion as FID. The relationships with FID fit better with the current knowledge on the factors that shape the landscape of fear: urban habitats can be relatively safe in terms of predation (Díaz et al., 2013; Eötvös, Magura, & Lövei, 2018; Møller, 2012), and higher perching heights should increase, not decrease, the sense of safety (Fernández-Juricic, Vaca, & Schroeder, 2004; Samia et al., 2016).

The unexpected relationships with vigilance, however, do not necessarily imply that vigilance does not belong to the predatory sequence. It could be that vigilance still benefits the detection of predators but that the investment in vigilance, which is needed for optimal detection distance, depends on individual qualities. For example, individuals may differ in their visual and auditory perception of the surroundings due to differences in genetic, neurochemical and anatomical factors (Kondo et al., 2017). Vigilance has also been shown to decrease with age in the domestic fowl (*Gallus gallus domesticus*), suggesting that experience with predation threats allows vigilance rates to be reduced (Beauchamp, 2018). Therefore, some individuals may need to allocate more time to vigilance to achieve the same wariness as others. The finding that the more vigilant individuals had longer assessment intervals could be similarly explained by suggesting that the same individuals, that need to increase time spent on vigilance, also need more time to assess risk and to decide on an optimal escape strategy. Alternatively, existence of personality types could explain such behavioural variation. For example, birds with higher vigilance levels and longer assessment intervals could be slower but more accurate in their decisions (Sih & Del Giudice, 2012). With that point of view, the opportunity costs involved with maintaining higher vigilance levels could be compensated by making fewer or shorter escape flights.

Another explanation, which does not necessarily rule out the previous suggestions on why vigilant birds showed relaxed escape behaviour, is that measuring the head-up ratio is not specific to antipredator vigilance (Allan & Hill, 2018; Beauchamp, 2015). Therefore, other factors may be more influential on the time spent vigilant. For example, Favreau, Goldizen & Pays (2010) found that vigilance of peripheral eastern grey kangaroos (*Macropus giganteus*) did not change as group size increased because the decrease in antipredator vigilance was compensated by an increase in social vigilance, i.e. more surrounding conspecifics increase the need for social monitoring. It is difficult to determine the targets of vigilance in birds due to their visual system (Fernández-Juricic, 2012), but the finding that birds were more vigilant in urban habitat gives a hint that non-predatory distractions could indeed have a significant effect on vigilance. While several studies show that vigilance levels either do not change with urbanization (Lehrer, Schooley, & Whittington, 2012; McGiffin et

al., 2013), or even decrease (Ramirez & Keller, 2010; Valcarcel & Fernández-Juricic, 2009), human-caused disturbances generally evoke higher vigilance levels in animals (Beauchamp, 2015). A positive relationship between urbanization and vigilance could be explained by a higher amount of distractions, e.g. cars, noises, conspecifics, and pedestrians, found in the cities (Forman, 2014; Sarno, Parsons, & Ferris, 2015). Distractions can require animals to reallocate part of their finite attention which in turn can interfere with their response to an approaching threat (Chan et al., 2010). Accordingly, more vigilant birds had longer assessment intervals in study II.

### **6.1.2. Delayed alert reaction in areas with low perceived risk of predation**

Even when vigilance was not related to pre-detection distance, there were significant urban-rural differences in pre-detection distances. By using pre-detection- $\Phi$ , a relative metric to describe how close starting distance is to alert distance, studies II and III showed that urban birds took relatively longer to become alert to an approaching human, which is an indication of delayed detection (Cooper & Blumstein, 2014). In contrast, proximity to human infrastructure elicited earlier detection in roe deer (*Capreolus capreolus*), possibly because they perceived such habitat features as more threatening (Bonnot et al., 2017). However, a recent meta-analysis has shown that direct predation rates on birds are significantly lower in urban compared to rural habitats (Eötvös, Magura, & Lövei, 2018), which should justify the lower standards for becoming alert to potential threats. Reducing awareness would allow birds to reallocate more time to other fitness-enhancing activities, such as foraging and social activities.

As expected, pre-detection distance also increased with latitude, implying a delayed reaction. A previous geographical study on escape behaviour has suggested that the more relaxed antipredator behaviour in higher latitudes is caused by the negative relationship between latitude and predator abundance, as indicated by similar gradient in raptor abundance (Díaz et al., 2013). Indeed, the strength of biotic interactions is generally more profound at low latitudes (Schemske et al., 2009). Interestingly, the difference in pre-detection distance between urban and rural populations increased with latitude (Fig. 8a). One possible explanation is that the rural habitats in Northern Europe are typically sparsely populated (Eurostat, 2016), and, hence, there is less potential for rural birds to become habituated to humans. In other words, when FID is measured as a response to a human observer, it is likely that prior experience with pedestrians has an effect on the strength of the response (Engelhardt & Weladji, 2011; Mikula, 2014). On the same note, urban-rural differences in escape behaviour could also partly be explained by habituation (Cavalli et al., 2018), although not fully (Holtmann et al., 2017; Møller, 2008). However, some species do not habituate to frequent human encounters (Carrete & Tella, 2009), some sensitize,

rather than habituate (Blumstein, 2014), and a complementary effect of risk allocation cannot be ruled out (Rodriguez-Prieto et al., 2008).

### 6.1.3. Safety in trees but not in numbers?

The formation of groups can benefit individuals in various aspects. Group living can benefit individuals when information about the location of food is shared, or when a group is more successful at capturing food, e.g. by causing more panic in the prey (Davies, Krebs & West, 2012). The antipredator benefits of group formation are risk dilution, predator confusion, communal defence, and improved vigilance for predators (Caro, 2005; Hamilton, 1971; Davies, Krebs & West, 2012; Pulliam, 1973; Roberts, 1996). As collective vigilance increases with the size of the group, individuals have better odds of detecting a predator when in a group (Pulliam, 1973). In addition, individual vigilance can be significantly reduced in a group, leaving more time to foraging (Beauchamp, 2015; Ciuti et al., 2012; Fortin et al., 2014). However, the reduction of individual vigilance in a group could also be related to risk dilution (Roberts, 1996)

Contrary to expectations, vigilance did not vary with flock size in study II, nor was flock size related to pre-detection distance, assessment interval or FID. Similarly, flock size was not a significant predictor of post-FID responses in study V. These findings are not exceptional – meta-analysis on the effect of group size on vigilance revealed that in almost one-third of published studies on birds the relationship between group size and vigilance was not significant (Beauchamp, 2008). Still, studies I and IV found that FID increased with the size of the group in both urban and rural habitats. One explanation would be that the detection of predators is improved in bird flocks (Pulliam, 1973; Stankowich & Blumstein, 2005). Alternatively, large flocks may have escaped earlier because the odds of having a more sensitive individual in a group can be expected to increase with group size. Therefore, when a sensitive individual escapes early, it could send a signal to other group members that it is time to escape. For example, crested pigeons (*Ocyphaps lophotes*) have modified flight feathers which produce a distinct alarm signal, when taking off in the face of danger (Hingee & Magrath, 2009). A playback experiment showed that crested pigeons escaped immediately over 70 per cent of the time after hearing that alarm signal but never took off after hearing a regular escape. Of course, the use of alarm signals varies among species (Zuberbühler, 2009). As such, we hypothesized that individuals of gregarious species are more adapted at extracting information from group members than individuals from non-gregarious species. However, it was not reasonable to directly compare individuals from gregarious and non-gregarious species because the latter rarely formed groups as large as the gregarious species. Still, some of the mixed results among studies could perhaps be related to the selection of species. Also, differences in ecological factors, such as food abundance and risk of predation, could decrease the need for monitoring companions (Beauchamp, 2008).

The origin of modern avian flight is often associated with the need to escape from predators to a higher ground (Elzanowski, 2000; Videler, 2006). Indeed, birds are often characterized by higher sense of safety when in or near trees (Fernández-Juricic, Jimenez, & Lucas, 2002; Fernández-Juricic, Vaca, & Schroeder, 2004; Samia et al., 2016). Accordingly, study II found that birds had shorter FIDs when perched  $\geq 2$  m off the ground, compared to birds on lower heights. Furthermore, the results indicated that birds on higher perches were relatively quicker to detect an approaching human, but as assessment interval was relatively longer and FID was shorter in such cases, it cannot be regarded as a sign of increased perception of risk. Rather, it could be suggested that the better view of surroundings is responsible for shorter pre-detection distance. In contrast, Blumstein et al. (2004) found that there was no general relationship between perching height and FID among the 34 tested bird species; seven species increased FID when perched  $\geq 3$  m off the ground, while three species showed an opposite relationship. Study II also found that there is a positive relationship between body mass and vigilance on higher perches, but not on lower. It is rather contradictory to the general understanding that vigilance should decrease with body mass (Brivio et al., 2014; Lank & Ydenberg, 2003; Underwood, 1982), and that higher perching heights reduce perceived risk of predation (e.g. Fernández-Juricic, Vaca, & Schroeder, 2004). Thus, it is likely that the increase in the proportion of head-up posture of larger birds is not related to risk of predation, but rather indicates that larger birds are less likely to be seen in a head-down position in a tree because large birds are less likely to forage in the canopy (Cramp & Perrins, 1994; Pearman et al., 2014). However, another explanation would be that larger birds have more non-foraging time available due to a lower mass-specific basal rate of metabolism (Collop et al., 2016; McNab, 1988), as suggested by Beauchamp (2010b) as an explanation for his results showing a similar positive relationship between vigilance and body mass in birds belonging to herbivorous clades. Either way, it would be difficult to associate these higher levels of vigilance of large birds in trees with anti-predator behaviour.

#### **6.1.4. No significant relationship between starting distance and FID in urban birds – another sign of reduced awareness?**

Starting distance – the initial distance between an observer and prey – is shown to positively correlate with alert distance and FID (Blumstein, 2003; Stankowich & Coss, 2006). It is suggested that these relationships are caused by the attention costs derived from monitoring approaching predators (Blumstein, 2003 & 2010), and also by heteroscedasticity due to mathematical constraints where starting distance  $\geq$  alert distance  $\geq$  FID (Dumont et al., 2012). While starting distances were generally shorter in urban habitats, the urban-rural difference in starting distances did not predict the urban-rural difference in pre-detection- $\Phi$  (study III). Furthermore, study I found a positive relationship between starting

distance and FID in rural but not in urban habitats. Knowing that urban birds took relatively longer to become alert to humans, despite shorter starting distances, it can be suggested that the lower perceived risk of predation in urban habitats allows birds to lower their zone of awareness (the maximum distance at which animals monitor threats) in order to avoid getting distracted by surrounding frequent human-caused disturbance stimuli. That would also explain why longer starting distances did not evoke earlier escape response. Somewhat similar dependence on predation risk was found in Balearic lizard for which the positive relationship between starting distance and FID existed only when approached rapidly, i.e. during high perceived risk of predation (Cooper, Hawlena, & Pérez-Mellado, 2009). An alternative point of view would be that the reduction in awareness is not something that birds aim for, but rather an inevitable consequence of living in urban environments, where a constant flow of distractions greatly increases the amount of information that animals need to process, hence decreasing their reaction speeds to individual stimuli. For example, individuals in conditions with higher anthropogenic background noise levels have delayed escape responses (Chan et al., 2010; Petrelli et al., 2017).

Study V found that the relationship between starting distance and escape variables can be species-specific: the rook showed a positive relationship between starting distance and escape duration, while no such relationship was apparent for the Eurasian jackdaw and the hooded crow. A possible explanation for that interspecific difference is that the rook is less adapted to human disturbances, which makes them more wary. Hence, they could be more likely to become alert at longer distances. Indeed, a database on bird FIDs shows that the rook generally has longer FIDs than the Eurasian jackdaw and the carrion crow (*Corvus corone*), a species closely related to the hooded crow (Livezey, Fernández-Juricic, & Blumstein, 2016). In addition, the rook had longer escape durations than the other two corvids, and the rook was the only species of the three that showed a positive relationship with escape angle (study V). The latter implies that when the rook chooses an escape angle that helps with maximizing the distance from the predator, it also chooses to increase escape duration.

#### **6.1.5. Should we expect longer or shorter assessment interval in urban habitat?**

Notably, earlier detection, as indicated by shorter pre-detection distance, increased assessment interval in urban but not in rural habitats, and assessment interval decreased with latitude (study III). A similar positive relationship between alert distance and assessment interval was found by Stankowich & Coss (2005). The most straight-forward explanation for these findings is that the later the first reaction to the predator takes place, the less time is left for risk assessment. While our analyses were done using relative distances, it is hypothesized that at very short predator-prey distances, prey flee immediately without further risk assessment, possibly because they are close to or have exceeded

their optimal escape distance (Fig. 2; Blumstein 2003; Cooper & Blumstein, 2015). Therefore, by reducing awareness towards potential predators, birds at higher latitudes and in urban habitats will have their first alert reaction closer to their optimal FID, which is likely the reason why pre-detection- $\Phi$  and assessment- $\Phi$  showed opposite trends with latitude and with differences between habitats (Fig. 8). Indeed, the urban-rural difference in mean alert distance had the largest effect in a model explaining the urban-rural difference in the relative assessment interval (study **III**).

Birds in urban habitats took longer to assess risk before escaping than did rural birds, as indicated by lower assessment- $\Phi$  values in studies **II** and **III**. The explanation in the previous paragraph about the negative trade-off between pre-detection distance and assessment interval does not explain why urban populations had relatively longer assessment intervals if they also had relatively longer pre-detection distances, compared to rural populations. This finding, however, is in line with the earlier predictions made about vigilance being higher and pre-detection distance being longer in urban habitats due to a higher degree of environmental distractions. That is, the pressure put on cognitive and sensory systems could inhibit decision making during assessment interval (Chan et al., 2010). Alternatively, longer assessment intervals in more disturbed areas could be an indicator of learnt tolerance towards humans (Fernández-Juricic, Jimenez, & Lucas, 2002). While Blumstein (2003, 2010) predicted that animals tend to flee early rather than late to decrease monitoring costs, it is possible that birds in urban habitats have become aware that it is more economic not to escape until the intent of the approaching human is clear. For example, it is found that animals increase FID when the direction of the approach and gaze of the human observer is direct compared to tangential (Bateman & Fleming, 2011; Møller & Tryjanowski, 2014; Sreekar & Quader, 2013). However, the results from Møller & Tryjanowski (2014) do not support the previous urban-rural hypothesis as they showed that there was a significant difference in FID between direct and tangential approaches in rural but not in urban habitats. Based on these results, it is unlikely that birds in urban habitats delay escape in order to gather more information on the approaching threat.

#### **6.1.6. FID and its relationship with the mean body mass of a species**

Results from studies **I** and **II** offered mixed results about the relationship between assessment interval and FID. Study **II** indicated that a longer assessment interval decreased FID, which is a logical mathematically constrained predicament when assuming that alert distance remains the same. However, study **I** did not find such a relationship. A relationship between assessment interval and FID does not have to exist when alert distance varies with assessment interval, as was the case in study **III** and in Stankowich & Coss (2005). An alternative, more technical, explanation for the lack of a relationship in study **I** is that the data contained a lot of immediate escapes (a phenomenon more common in

Northern Europe, where study **I** was carried out, as indicated by study **III**) and did not use the relative metric  $\Phi$  to analyse that relationship.

Body mass is one of the most significant variables to explain interspecific variation in FID, with heavier species initiating flight earlier (Blumstein, 2006; Møller, 2015; Samia et al., 2015; Weston et al., 2012). Variable suggestions have been made about the reasons why larger species escape earlier: inferior agility, longer take-off time, better vision, differences in energetics, and a greater vulnerability because larger objects are easier to spot (Blumstein, 2006; Møller, 2015; Samia et al., 2015; Piratelli, Favoretto, & Maximiano, 2015; Weston et al., 2012). Surprisingly, body mass was only significantly positively related to FID in study **IV** but not in studies **I** and **II**. However, an initial analysis showed that without controlling for phylogenetic dependence, body mass would have had a positive effect on FID in study **II**. Therefore, a positive relationship could still be expected with a larger dataset or one containing more unrelated species. In addition, a positive relationship between body mass and FID was present in study **I** when analysing a subset of individuals whose length of risk assessment exceeded zero. It has also been found that larger bird species have decreased their FID the most under high levels of human disturbance (Samia et al., 2015). However, body mass had no support for predicting the urban-rural difference in pre-detection- $\Phi$  and assessment- $\Phi$  (study **III**). In other words, larger species did not have a larger difference in relative pre-detection distances and relative assessment intervals between urban and rural populations, as one would have expected based on the results from Samia et al. (2015). Thus, it is possible that some of the interspecific variation in FIDs of different sized birds is related to a confounding positive relationship between body mass and starting distance. Standardization of starting distance is usually not achievable in natural conditions (e.g. van Dongen et al., 2015). If observers are more likely to spot a large animal from afar than a small one, as expected, then larger animals will consequently be approached from a longer starting distance. However, accounting for such species dependent natural variation in starting distances is important when trying to obtain meaningful values of FID (Blumstein, 2003). Better detectability – that results in greater vulnerability – can be considered an inevitable characteristic of larger prey (Blumstein, 2006). Some interspecific variance in FID could perhaps be explained by differences in diet because species adapted to spotting moving prey could be more attentive to movement (Blumstein, 2006; but see Møller, & Erritzøe, 2014). Blumstein (2006) and study **IV** found that the effect of diet was independent of body mass. In study **IV**, it was shown that omnivorous and granivorous bird species had longer FID than granivorous-insectivorous and insectivorous species. However, these results must be interpreted with caution because that study was limited to 23 gregarious species.



### 6.1.7. How is FID related to distance fled?

In study **I**, comparison of urban and rural habitats revealed that DF was shorter in urban habitats, similar to FID. DF also increased with the mean body mass of a species, i.e. larger species flew further. That finding is consistent with that of Fernández-Juricic et al. (2006). There are at least three likely reasons for why larger species escape to longer distances. First, cost of transport per unit weight and distance covered decreases with increasing body mass (Videler, 2006). Second, as also suggested by Fernández-Juricic et al. (2006), smaller species take advantage of finer-grained features of the habitat than larger species (Haskell, Ritchie, & Olff, 2002). For example, smaller animals could have a higher probability of finding a suitable refuge nearby (Arsenault & Himmelman, 1998). Similarly, the next suitable food patch is more likely to be closer for smaller animals. Third, better manoeuvrability of smaller animals could make it easier for smaller birds to reach a nearby refuge (Domenici, 2001).

While many escape-related measurements have mathematically bound relationships, e.g. FID is always shorter than alert distance, the relationship between FID and DF is more open to variation. That is also probably one of the reasons for why previous studies have found more variable results regarding the FID-DF relationship (Chapter 2.3.). In study **I**, the relationship between FID and DF varied according to mean body mass of species: lighter birds did not show a clear relationship between FID and DF, but a positive relationship became more evident as body mass increased (Fig. 9). That is, heavier birds were more prone to move longer distances after early escape, while there was no such trend for lightweight birds. Theoretically, the three aforementioned reasons for why larger birds generally have longer distance fled, can be seen as a cause of discrepancy between small and large birds. That is, a better access to refuges, coupled with higher costs of flight and more abundant resources, should force smaller species to have shorter distance fled even when the perceived risk of predation is high, or when the benefits of remaining are small. Meanwhile, when a larger species is in an area with few resources, it has little motivation to delay escape when approached by a predator, but it must fly a longer distance than a small bird under the same conditions if it intends to find a suitable refuge, or land at a spot of superior quality. In conclusion, body size plays an important role in post-FID behaviour, and the body size related differences in post-FID behaviour could also partly explain why larger animals need to escape earlier (Blumstein, 2006; Fernández-Juricic et al., 2006).

Study **V** examined the relationship between FID- $\Phi$  (a relative measure of how far the observer was able to approach in relation to starting distance before the animal initiated flight) and escape duration of three species of corvids. That relationship was positive when the bird was approached in a similar manner as in study **I**, when the observer immediately stopped approaching when the bird began escaping (approach type “halt”). That finding is in agreement with that obtained in Study **I** as corvids are relatively large birds. However, the relationship disappeared when the approach was continued in a straight line (approach

type “forward”), or when the observer started to follow the bird (approach type “chase”), after the bird initiated flight (Fig. 10). When the observer stops approach, then the perceived risk of predation should significantly decline as the observer is not showing willingness to continue with the predatory sequence. Thus, when a bird is already not motivated to escape, as indicated by short FID, it can invest relatively little into post-FID responses. However, when the observer continues to behave in a threatening manner (as was the case during approach types “forward” and “chase”), the minimal effort required to escape increases, especially during a chase where the bird chose a terrestrial escape method.

### **6.1.8. What if the perceived risk of predation changes while fleeing?**

In order for birds to differentiate between different approach types during escape, they have to continue monitoring the predator after initiating escape. While existing research recognizes that monitoring approaching predators before initiating flight is important for making the optimal escape decisions (Cooper & Blumstein, 2015; Samia & Blumstein, 2015; Stankowich & Blumstein, 2005; Ydenberg & Dill, 1986), the extent to which they monitor while fleeing is less clear. The main aim of study V was to provide evidence that birds pay attention to the actions of the predator while escaping. I expected that monitoring predators during escape would first require an escape angle that would not prohibit monitoring. Birds have previously been characterized by having two peaks in escape angle: 180° to maximize distance from the predator, and 90° for rapid evasion from the line of attack (reviewed by Domenici, Blagburn, & Bacon, 2011). While there was no clear peak in study V, the mean angle of escape was around 120° in all three species, and obtuse angles (closer to 180°) were less preferred than more acute angles. Therefore, rather than maximizing the distance from the predator by escaping at 180°, the results suggested that corvids choose an escape angle that could potentially allow monitoring the predator during escape. Second, I also expected that the birds would increase escape duration according to the perceived risk of predation. Indeed, all species had longer escape durations for approach type “chase” than “halt”, and the hooded crow also increased escape duration for approach type “forward”, compared to “halt”. The increase in escape duration was independent of escape method. In addition, more individuals changed their escape method from terrestrial to aerial during escape for approach type “chase” compared with approach types “halt” and “forward”. Last, birds using terrestrial escape had a larger difference between the initial and final escape angles during approach type “chase” than during types “halt” and “forward”, implying that birds try outmanoeuvring when needed, i.e. during terrestrial escape which is the slower method. All in all, this indirect evidence of monitoring suggests that DF is not a simple function of the perceived risk of predation before escape, but can be modified according to changes to predation risk that happen during escape.

### 6.1.9. Proximity to refuge decreased DF but not FID

A closer distance to a potential refuge is predicted to decrease the perceived risk of predation, and, accordingly, numerous studies have found a positive relationship between distance to refuge and FID (Cooper & Wilson, 2007; Engelhardt & Weladji, 2011; Guay et al., 2013; Samia et al., 2016; Stankowich & Blumstein, 2005). Few studies have also shown a positive relationship between distance to refuge and distance fled (e.g. Cooper, 1997). While study **I** did not find a relationship between distance to the nearest refuge and FID, there was a positive relationship with both distance fled (study **I**) and escape duration (study **V**). In other words, birds close to a refuge were not more relaxed in terms of FID, but the proximity of a refuge benefitted the birds by reduced investment in escape. In contrast to the findings that showed increased escape effort during more threatening approach types (Chapter 6.1.8.), the preference for refuge types remained the same among approach types. Studies **I** and **V** also showed that birds generally did not choose the closest available refuge, and when they did, the distribution of chosen refuges did not visibly differ from the distribution of available refuges. One could therefore assume that measures of habitat density could have a larger effect on escape behaviour than distance to the nearest refuge. For example, Bonnot et al. (2017) found that roe deer had significantly shorter pre-detection distances in relatively open landscapes, and Cappa et al. (2017) showed that guanacos (*Lama guanicoe*) increase FID when in areas with reduced vegetation cover. However, neither vegetation cover (study **I**), nor density of nearby trees (study **V**) had any impact on FID or DF, similar to a study on the blackbird (*Turdus merula*) (Rodriguez-Prieto et al., 2008). Habitat openness was also not a significant predictor of FID in Blumstein (2006). A likely reason is that vegetation cover can also obstruct the detection of predators, and, therefore, increase the possibility of a surprise attack (Beauchamp, 2010a). Thus, the benefits and costs of nearby cover may cancel each other out in terms of safety, but that relationship could be highly species-specific as species differ in their preferences for nearby vegetation characteristics (Lima, 1993).

### 6.1.10. A recap with implications

FID and vigilance are the most widely used measures of perceived risk of predation with books worth of information published over the years using these indices (Beauchamp, 2015; Cooper & Blumstein, 2015; Frid & Dill, 2002). However, in this thesis I argue that we should be looking more into how these measures relate to other parts of the predatory sequence because that would give us a better understanding of the reasons for variation in these behaviours, and would help to rule out the possibility that a decrease in the strength of one behavioural response is not compensated by an increase in other behaviour. For example, Rodriguez-Prieto et al. (2008) found that blackbirds with shorter FIDs (i.e. more relaxed escape response) are more likely to use energetically costly aerial escape method for escape.

The most obvious finding to emerge from this thesis is that the escape response in birds is delayed in urban habitats (studies **I–IV**). It is generally suggested that urban birds have a more relaxed escape behaviour because the perceived risk of predation is weaker due to lower predation pressure in urban environments (Díaz et al., 2013; Eötvös, Magura, & Lövei, 2018; Fischer et al., 2012; Møller, 2012). The results from studies **I** and **III** indicated that urbanized birds have lowered their zone of awareness, i.e. it takes relatively more time for urban birds to react to the approaching threat. Therefore, we expected that birds in urban habitats spend less time being vigilant. However, the investigation of the relationships between vigilance and escape behavioural parameters lead to unanticipated findings that urban birds were more vigilant, and that the more vigilant individuals were not quicker at reacting to threats, but were characterised by more relaxed escape behaviour (study **II**). Since head-up posture – a typical indicator of vigilance – is not specific to antipredator vigilance (Allan & Hill, 2018; Beauchamp, 2015), it could be possible that the variation seen in vigilance was influenced by variable external disturbances. Anthropogenic disturbances, e.g. traffic, noise, pedestrians, generally increase vigilance (Beauchamp, 2015; Ciuti et al., 2012; Clinchy et al., 2016). Thus, it could be suggested that birds in urban habitats are not more vigilant because they perceive a higher risk of predation, but because their vigilance reaction is more often evoked by external factors that do not require an escape response, but are still too distracting to go unnoticed. Since distractions can interfere with the response to an approaching threat (Chan et al., 2010), it is possible that such disturbances cause even further delay in risk assessment and escape when encountering a potential predator. Accordingly, vigilant birds and urban birds took relatively longer to monitor approaching predators after becoming alert (studies **II** and **III**). An alternative hypothesis is that the optimal level of vigilance differs among individuals due to innate deficiencies, personality traits, or lack of experience (see Chapter 6.1.1.). Anyhow, the observed discrepancy between the results for vigilance and escape parameters call for caution when using the proportion of time spent in a head-up posture as an indicator of perceived risk of predation in birds. However, it is possible that other indicators of vigilance, such as the head-up rate or rate of head turning, could produce results that highlight the antipredator component of vigilance (Cresswell et al., 2003; Fernández-Juricic, 2012; Jones, Krebs, & Whittingham, 2007).

A detailed examination into post-FID behaviour showed that, similar to FID, distance fled is also decreased in urban habitat (study **I**). The study also confirmed previous findings that larger species tend to escape longer distances (Collop et al., 2016; Fernández-Juricic et al., 2006). However, a more interesting result of study **I** was that the relationship between FID and DF of an individual bird depended on the mean body mass of the species: while no relationship was present in lightweight birds, the slope of the relationship increased with mean body mass (Fig. 9). In other words, an early escape response in large bird species is more likely to be followed with long distance fled, but that is not the case in smaller species. The possible reasons for such dependence on body mass

indicate that interspecific differences in escape strategies could be highly nuanced due to differences in energetics, manoeuvrability, and in the interactions with the environment (see Chapter 6.1.7.). However, study **V** found that it is not simply the perceived risk of predation experienced before escape that shapes the strength of individual post-FID responses. The duration of the escape also depends on how the perceived risk changes during flight. It was evident that when the risk of predation was experimentally increased during escape, then escape durations and angular changes in escape trajectory were also increased. Furthermore, a larger proportion of individuals changed from terrestrial to aerial escape method during escape when the predation risk was increased. Accordingly, the relationship between FID- $\Phi$  and escape duration depended on the post-FID behaviour of the predator (study **V**). To make things even more complicated, the interspecific comparisons of relatively closely related species of corvids indicated that the cues used for estimating the intent of the predator, and the choice of subsequent escape strategies, differ among species. Based on the finding that birds likely monitor predators during escape, it can be suggested that researchers studying post-FID responses should choose an experimental approach type that fits with their research question, i.e. typical pedestrians do not stop when a bird initiates flight, while a natural predator might stop or, instead, start chasing the prey. However, the generalizability of these results is currently limited as study **V** investigated post-FID dynamics in three closely related species of a family that is known for their high cognitive abilities (Emery & Clayton, 2004).

The decision making of wildlife managers could be improved by making more broad-scale generalizations of escape behaviour (Blumstein, Samia, & Cooper, 2016). This thesis found that FID is decreased in urban habitats across Europe among most studied species (studies **II**, **III**, **IV**). These results are consistent with a previous broad-scale study in European birds which also showed that FID decreases with latitude (Díaz et al., 2013). Study **IV** did not find a latitudinal decrease in FID, but that study was restricted to 23 gregarious bird species, while Díaz et al. (2013) analysed that relationship in a sample of 159 species. Still, study **III** complemented Díaz et al. (2013) by showing that pre-detection distance increases with latitude in Europe, while assessment interval decreases (Fig. 8). As mentioned earlier, urban birds had relatively longer pre-detection distances and relatively longer assessment intervals than rural birds. Taken together, these results indicate that birds prioritize the reduction of monitoring costs when the perceived risk of predation is low, i.e. in urban areas and in higher latitudes. However, we should be cautious about how to interpret the findings that escape behaviour is more relaxed in disturbed habitats because, when making urban-rural comparison, we rely on the information gathered from species that have adapted to urban conditions, but these species are in a minority and are not a random selection of species (McKinney, 2002; Lowry, Lill & Wong, 2013; Sol et al., 2014). For example, Bötsch et al. (2018a) found that birds in disturbed forests have reduced FIDs, compared to less disturbed forests, but Bötsch et al. (2018b) also demonstrated that density of birds and

species richness in forests decline with closeness to recreational trails. The implications of such “filtering processes”, as mentioned in Blumstein, Samia, & Cooper (2016), should be further studied in the context of responses to anthropogenic stressors. Another potential limitation of the studies is that the variety in habitat types was low, and that some bird taxa, e.g. many waterfowl and nocturnal birds, were excluded due to the choice of methods.

Being able to predict FID based on the mean body mass of a species could help with calculating the appropriate set-back distance, when FID has not been previously measured for a species in question (Guay et al., 2016). Previous research has established that there is a positive relationship between body mass and FID (Blumstein, 2006; Møller, 2015; Samia et al., 2015; Weston et al., 2012). However, in the current thesis, the relationship between the mean body mass of a species and FID provided mixed results, but it could have been a matter of sample size (see Chapter 6.1.6.). Blumstein (2006) has suggested that larger species are more threatened by anthropogenic disturbances because they are more easily disturbed. In contrast, Samia et al. (2015) have argued that larger species are better off because they have been able to reduce FID more in relation to urbanization. However, due to the previously mentioned “filtering process”, we should be careful about such interpretations. I propose that the larger reduction in FID of larger birds in response to urbanization should be treated as evidence of a larger behavioural barrier needing to be overcome to habituate with anthropogenic disturbances. Especially considering that not all species show patterns of habituation to frequent human disturbances (Blumstein, 2014; Carrete & Tella, 2009). Study I showed that large birds also invest more into post-FID responses than smaller birds. Collop et al. (2016) found that same pattern, but they were not convinced that this would be an indication of higher costs of escape after their calculations showed that the energetic cost per flight response as a percentage of daily energy requirement was not higher for larger species. Still, when considering that the longer FIDs in larger birds (Blumstein, 2006) imply that they escape more frequently in relation to human-caused disturbances, and that species with longer distance fled tend to land higher in the substrate and take longer to resume the behaviour prior to disturbance (Fernández-Juricic et al., 2006), it is unclear whether these differences in energetics are sufficient to balance all these costs. If these differences are sufficient, wildlife management should perhaps still focus on larger species as they are generally more likely to be at risk of extinction (Gaston & Blackburn, 1995). However, in terms of coping with the risks related to urban life, it is possible that the biologically relevant difference in escape behaviour could be more dramatic when FID is reduced from a short distance to marginally shorter distance in small birds than from a large distance to a short distance in large birds, because smaller birds could be in relatively more danger due to the relatively higher number of mesopredators than apex predators in urbanized areas, compared to more natural areas (Cove et al., 2012; Fisher et al., 2012; McKinney, 2002).

This thesis also highlights that for fine-scale predictions on escape behaviour, covariates such as perching height and flock size should be taken into account. While birds on higher substrates were relatively quicker at becoming alert to the approaching predator, they were characterised by more relaxed escape behaviour, and also by higher levels of vigilance in large birds (study **II**). One easy way to have more standardized measurements of FID and vigilance would be to focus only on birds foraging on ground, as done in studies **I** and **V**. Of course, that would not work on species that rarely descend to lower substrates. Flock size, on the other hand, increased FID in studies **I** and **IV**, indicating that detection of threats is improved in larger flocks. Based on these results, it can be hypothesized that birds adapted to group living could be more disturbed by human-caused disturbances. Similarly, Blumstein (2006) found that cooperative breeders were more likely to be flighty than non-cooperative breeders, and suggested that this difference results from social species needing to be more vigilant because they also need to monitor conspecifics.

This thesis has provided a deeper insight into the decision making processes involved in the antipredator behaviour of birds. By recording behavioural patterns at different stages of the predatory sequence and analysing their relationships with each other, we showed that some components of escape are indeed interconnected (e.g. pre-detection distance with assessment interval, FID with distance fled), but also found that these relationships can differ among variable levels of perceived risk of predation (**aim 1** of the thesis). For example, there was a positive relationship between starting distance and FID in rural but not in urban habitat, and the relationship between FID and escape duration depended on the post-FID behaviour of the predator. On the other hand, some previously suggested relationships, most notably the notion that higher vigilance results in earlier escape, found no support. The findings reported in this thesis also shed new light on post-FID risk assessment – it was indicated that corvids continue to assess risk during escape (**aim 2**). Escape behaviour depended on situational differences (relationships with distance to refuge, flock size, perching height, and intent of the predator), habitat level differences (distinct differences between urban and rural habitat), geographical differences (latitudinal gradients in pre-detection distance and assessment interval), and biological differences (relationships with mean body mass, diet, species identity, and possibly vigilance), implying that the perceived risk of predation is a combination of ecological conditions from variable ecological scales (**aim 3**). These general findings and theories contribute to the assessment of the perceived risk of predation in birds, which in turn can help to investigate the impact of human-caused disturbances on wildlife (**aim 4**). Further research should be undertaken to make sense of how urban birds have become less wary of pedestrians, while maintaining higher vigilance. In addition, an important issue for future research is to develop an evidence based understanding of how the size of the species is related to the choice of escape strategies, and how to compare the overall costs of escape across different sized species when considering interspecific differences in energetics.

## 7. SUMMARY

Predator-prey interactions have had an immense impact on the diversification of life. In addition to variable morphological and physiological adaptations, animals have come up with behavioural adaptations to resolve these interactions. The first line of defence for prey is generally avoidance of areas with high perceived risk of predation and keeping a lookout for potential threats. On an encounter with a predator, prey are ultimately faced with a trade-off between continuing to benefit from current activity and escaping to reduce risk of predation. The optimal decision on when to escape can be complicated because the prey needs to assess, for example, the intent of the predator, the fitness benefits from current activity, and the time it takes for it to reach the safety of a refuge. Importantly, the time spent on antipredator vigilance, and the decision on when to escape, are highly influenced by the perceived risk of predation. Consequently, measures called vigilance (indicated by the head-up posture of an animal) and flight initiation distance (FID, the distance between prey and an approaching threat when the prey begins to flee) are often used as indicators of the perceived risk of predation in animals.

Animals exhibit a similar trade-off between reducing perceived risk and continuing with fitness-enhancing activities when encountering a non-lethal disturbance. Accordingly, vigilance and FID have been used to describe how animals react to hunting and to reintroduction of predators, as well as to humans, vehicles, and urbanization in general. Human-caused rise in the perceived risk of predation can be viewed as a novel ecological threat because it could cause animals to make sub-optimal behavioural decisions that can lead to population declines. Therefore, measuring changes in the perceived risk of predation in response to different human-caused disturbances can provide valuable information for wildlife management. In addition, the values of FID are used for calculating set-back distances, i.e. the space where human activity should be restricted to reduce disturbance to wildlife.

Despite vast knowledge on the factors affecting vigilance and FID, there has been relatively little quantitative analysis of how these behavioural indicators are related to other behavioural actions in the predatory sequence. For example, a relationship between high levels of vigilance and early escape is usually suggested, but rarely tested in natural conditions. Also, literature offers contradictory findings about how FID is related to post-FID behaviour, such as distance fled during escape. A short FID would usually indicate a low perceived risk of predation, but how would we interpret a short FID followed by a long distance fled? Finer knowledge of such sequential behaviours would help to understand the mechanisms underlying antipredator responses, and ascertain that the use of a single behavioural indicator of perceived risk of predation, such as vigilance or FID, is justified. The thesis also aimed to find out whether birds continue to monitor predators during escape, and to identify covariates of escape related behaviours. Multi-species studies in different countries were carried out to make



broad-scale generalizations of escape behaviour that could benefit the decision making of wildlife managers.

This thesis studied escape behaviour in birds by experimentally approaching birds in a standardized way to elicit an escape response while carrying out appropriate behavioural measurements. The studies ranged from local inter-specific comparisons focusing on situational differences to European-wide research efforts to find latitudinal gradients in escape decisions. In addition, four of the five studies examined differences in escape behaviour among urban and rural bird populations. It was expected that birds perceive a higher risk of predation in rural habitat because there are fewer natural predators in the urbanized areas. The studies of the thesis also incorporated multiple covariates, such as flock size, distance to refuge, vegetation cover, perching height, and mean body mass of species, into statistical models to account for factors that are suggested to have a large impact on the perceived risk of predation.

A cross-European study on escape behaviour showed that birds took relatively longer to become alert to an approaching human as latitude increased. That result supported an earlier study that found FID in birds to decrease with latitude, and linked it to a negative relationship between latitude and predator density. The findings that the length of risk assessment decreased with latitude, and that urban birds showed a positive relationship between alert distance and risk assessment, imply a potential trade-off between reduced awareness and length of risk assessment. An analysis of the potential trade-off between assessment interval and FID provided mixed results among the studies. The urban-rural comparisons showed that urban birds were characterised by more relaxed escape behaviour: delayed alertness, longer risk assessment, no relationship between starting distance and FID, shorter FID, and shorter distance fled. These results suggested that urban birds have reduced antipredator wariness, but a study on vigilance showed that urban birds were more vigilant than rural birds. Furthermore, assessment interval increased, while FID decreased with vigilance, implying that more vigilant birds had more relaxed escape behaviour regardless of habitat type. These results on vigilance raise doubt whether vigilance, as measured by the proportion of time a bird spends in a head-up posture, should be used as an indicator of the perceived risk of predation in birds. Based on these results, it can be postulated that the high amount of distractions in urban habitats could perhaps simultaneously elicit higher vigilance, while further delaying escape, but the thesis also discusses other possible explanations.

Analyses of post-FID behaviour highlighted two important aspects. First, distance fled generally increased with the mean body mass of the species, and the relationship between FID and distance fled of an individual bird also depended on the mean body mass of the species. In essence, FID of an individual did not predict subsequent distance fled in smaller bird species, but FID was positively related to distance fled in larger species, i.e. earlier escape results in longer distance fled. We hypothesize that these interspecific differences in escape strategies could be related to body size related differences in

energetics, manoeuvrability, and interactions with the environment. Second, the results indicated that birds dynamically change their escape strategies according to the changes in the perceived risk of predation during escape. When the risk of predation was experimentally increased during escape, it was found that escape duration and angular change in escape trajectory were also increased. Furthermore, a larger proportion of individuals changed from terrestrial to aerial escape method during escape when the predation risk was increased. As such, the post-FID behaviour of the predator is also important when assessing how FID is related to distance fled.

This thesis also identified that perching height and flock size should be taken into account for fine-scale predictions on escape behaviour. While birds on higher substrates were relatively quicker at becoming alert to the approaching predator, they were otherwise characterised by more relaxed escape behaviour. Larger bird flocks escaped earlier – although not in all the studies – indicating that as the size of the group increases, it is more likely that a member of the group will detect a threat and that the following reaction will cause others to escape as well. Last, the thesis showed that even similar sized related species can differ in the finer nuances of escape behaviour.

In the present thesis, I showed that by analysing how behavioural reactions at different stages of the predatory sequence are interconnected, it is possible to extract novel information about escape decisions in birds. Notably, the results on escape behaviour indicated that birds in urban habitats have reduced anti-predator awareness and delay escape, but head-up vigilance is not a reliable indicator of these behavioural patterns. The current thesis also argues that it is beneficial to include measurements of post-FID behaviour in studies of escape behaviour because it provides a more complete view of the costs of escape, and could help to clarify the reasons for behavioural variation in preceding escape decisions. Another major finding was that the post-FID escape decisions depend on how the perceived risk of predation changes while fleeing. That indicates that birds continue to monitor predators after initiating escape to find an optimal balance between the probability of getting caught and spending too much time and energy on escaping. In addition, the evidence from the thesis complements previous research that has found body mass, latitude, distance to refuge, group size, starting distance, and perching height to influence escape decisions in animals. This new insight should help to improve predictions about the impact of human-caused disturbances on the perceived risk of predation in birds, which in turn benefits decision making in wildlife management.

## SUMMARY IN ESTONIAN

### Lindude põgenemiskäitumine erineva kisklusriskiga olukordades: terviklikum käsitlus

Kiskja-saaklooma interaktsioonidel on olnud tohutu mõju elurikkuse kujunemisele Maal. Lisaks mitmesugustele morfoloogilistele ja füsioloogilistele adaptatsioonidele on loomadel nende interaktsioonide lahendamiseks välja kujunenud ka käitumuslikud kohastumused. Enamasti on saakloomade esimeseks kaitseliiniks kõrge kisklusriskiga alade vältimine ja ohtude suhtes valve pidamine. Kiskja ilmudes on saakloomal vaja teha lõivsuhteline otsus, kas jätkata käimasolevast tegevusest kasulõikamisega või põgeneda, et kisklusriski kahandada. Optimaalse põgenemishetke üle otsustamine võib olla keeruline, sest saakloom peab arvesse võtma näiteks kiskja kavatsusi, käimasolevast tegevusest saadavat kasu ja peidupaika jõudmiseks kuluvat aega. Kisklusriskile valvsusele kulutatava aja ja põgenemisotsuse langetamise juures mängib väga tähtsat rolli saaklooma poolt tajutav kisklusrisk (ingl *perceived risk of predation*). Seetõttu kasutatakse loomade tajutava kisklusriski mõõdikutena sageli just valvsust (ingl *vigilance*) ja põgenemiskaugust (ingl *flight initiation distance; FID*). Põgenemiskaugus on defineeritud kui saaklooma ja kiskja vaheline kaugus hetkel, mil saakloom alustab põgenemist ning valvsusele kulutatud aega hinnatakse enamasti looma püstise peahoiaku alusel.

Sarnane lõivsuhteline otsus kisklusohtu vähendamise ja kohasust suurendavate tegevuste vahel tuleb loomadel teha ka siis, kui nad on silmitsi mõne mitteeluohtriku häiringuga. Seetõttu on loomade valvsust ja põgenemiskaugust kasutatud selleks, et kirjeldada, kuidas loomad reageerivad nii küttimisele ja reintrodutseeritud kiskjatele kui ka inimestele, liiklusvahenditele ja üldisemalt linnastumisele. Tajutava kisklusriski inimtekkelist kasvu võib pidada uudseks ökoloogiliseks ohuks, sest see võib põhjustada mitteoptimaalseid käitumisotsuseid ja populatsiooni arvukuse langust. Mõõtes, kuidas tajutav kisklusrisk erinevate inimtekkeliste häiringute tõttu muutub, on võimalik teha targemaid looduskaitselisi otsuseid. Keskmisi põgenemiskaugusi kasutatakse ka selleks, et luua sobivaima suurusega puhveraladid ehk alasid, kus inimtegevust tuleks piirata vältimaks eluslooduse häirimist.

Vaatamata laialdastele teadmistele teguritest, mis mõjutavad loomade valvsust ja põgenemiskaugust, on läbi viidud alles suhteliselt vähe kvantitatiivseid analüüse selgitamiseks, kuidas need käitumis põhised indikaatorid on seotud teiste kiskja-saaklooma vahelise interaktsiooni etappidega. Näiteks eeldatakse, et kõrgem valvsustase on seotud varasema põgenemisega, aga looduslikes tingimustes saadud teaduslikke tõendeid selle kohta napib. Lisaks pakub erialakirjandus vastuolulisi tulemusi selles kohta, kuidas põgenemiskaugus on seotud käitumusstrategiaga, mis leiavad aset pärast põgenemise alustamist, näiteks põgenemisteedkonnaga. Lühike põgenemiskaugus osutab harilikult madalale tajutavale kisklusriskile, aga kuidas peaks tõlgendama lühikest põgenemis-

kaugust, millele järgneb pikk põgenemisteed (ingl *distance fled*)? Täpsem arusaam selliste järjestike käitumismustrite omavahelistest seostest aitaks paremini mõista kisklusvastaste reaktsioonide mehhanisme ja kindlaks teha, kas üheainsa käitumispõhise indikaatori – eeskätt valvsuse või põgenemiskauguse – mõõtmisest piisab, et loomade tajutavat kisklusriski veenvalt kirjeldada. Doktoritöö eesmärkideks oli veel välja selgitada, kas linnud jätkavad kiskja jälgimist põgenemise ajal ja milliseid põgenemiskäitumisega seotud kovariaate tuleks uurimustöodes kasutada. Läbi viidud uurimustööd hõlmasid korraga kümneid linnuliike eri riikidest, et pakkuda looduskaitsetele suurema üldistusvõimega tulemusi põgenemiskäitumise osas.

Kirjeldamiseks lindude põgenemiskäitumist, kasutati antud doktoritöös metoodikat, mis seisnes standardiseeritud viisil lindudele lähenemises ja samaaegses käitumismustrite mõõtmises. Doktoritöö raames viidi läbi nii lokaalseid liikidevahelisi võrdlusi, mis keskendusid situatsioonipõhiste erinevustele, kui ka üle-Euroopalisi uurimustöid, mis püüdsid välja selgitada laiuskraadilisi erinevusi põgenemisotsustes. Viiest tööst neljal oli uurimisfookuseks ka maa- ja linnalindude põgenemiskäitumise võrdlemine. Viimati mainitud tööd lähtusid eeldusest, et maal elavad linnupopulatsioonid tajuvad kõrgemat kisklusriski, sest linnastunud aladel esineb vähem looduslikke kiskjaid. Doktoritöö raames läbi viidud uurimustööd kaasasid statistilistesse mudelitesse mitmeid erinevaid tajutava kisklusriskiga seotud kovariaate, näiteks parve suurus, kaugus peidupaigani, taimkatte tihedus, kõrgus maapinnast ja linnuliigi keskmine kehamass.

Euroopa eri laiuskraadidel läbi viidud uurimustöö näitas, et kõrgematel laiuskraadidel häirisid linnud inimese lähenedes suhteliselt hiljem. See tulemus oli kooskõlas varasema uurimustööga, mis leidis, et lindude põgenemiskaugus väheneb laiuskraadi kasvades, seletades seda laiuskraadi ja kiskjate esinemistiheduse vahelise negatiivse seosega. Tulemustest selgus veel, et ohuhindamise suhteline kestus väheneb laiuskraadi kasvades. Samuti selgus, et mida varem linnalinnud häiritust välja näitasid, seda kauem nad ohtu hindasid. Eelmainitud tulemus viitab, et madalam valvsustase vähendab ohuhindamise kestust. Ohuhindamise kestuse ja põgenemiskauguse vahel eri tööde lõikes selget seost ei ilmnenud. Maa- ja linnalindude põgenemiskäitumise võrdlus viitas sellele, et linnapopulatsioonid on kiskjate suhtes vähem ettevaatlikud, aga valvsust mõõtnud töö näitas samas, et linnalinnud on valvsamad kui maalinnud. Peale selle tuli välja, et valvsuse suurenedes ohuhindamise kestus pikenes ja põgenemiskaugus vähenes sõltumata elupaigast, viidates sellele, et valvsamad linnud on kiskjate suhtes vähem kartlikud. Mainitud tulemused äratavad kahtlust, kas valvsust, mida mõõdetakse pea püsti hoitud aja põhjal, üldse kõlbab kasutada tajutava kisklusriski indikaatorina lindude puhul. Antud tulemuste põhjal näib tõenäolisem seletus, et linnakeskkonnaga kaasnev kõrge häiringutase võib tõsta valvsust, kuid samas reaalselt põgenemist edasi lükata, kuid doktoritöös käsitletakse ka teisi võimalikke seletusi.

Põgenemise alustamisele vahetult järgneva käitumise analüüs tõstis esile kaks olulist asjaolu. Esiteks, põgenemisteedonna pikkus korreleerus positiivselt linnuliigi keskmise kehamassiga ja põgenemisteedonna pikkus oli seotud ka

põgenemiskaugusega, kuid viimase seos sõltus jällegi liigi kehamassist. Lühidalt, põgenemiskaugus ei ennustanud põgenemisteedonna pikkust väiksema keha-kaaluga linnuliigi isenditel, aga raskema kehakaaluga liikidel oli vastav seos positiivne – varem põgenenud isendid põgenesid kaugemale. Mainitud liikidevahelised erinevused põgenemisstrateegiates võivad olla seletatavad keha suurusest tingitud erinevustega energeetikas, manööverdusvõimes ja keskkonnaga suhestumises. Teiseks, tulemused viitasid sellele, et põgenemise ajal muudavad linnud oma põgenemisstrateegiaid vastavalt muutustele kisklusriski tajumises. Kui tajutavat kisklusriski põgenemise ajal eksperimentaalselt suurendati, suurenes lindudel ka põgenemisele kuluv aeg ja nad muutsid põgenemisteedondade trajektoore rohkem. Tõstetud kisklusriski korral lülitus suhteliselt suurem hulk maad mööda põgenemist alustanud linde ümber lendamisele. Sellest võib järeldada, et ka kiskja käitumine põgenemise ajal on oluliseks teguriks põgenemiskauguse ja põgenemisteedonna pikkuse vahelise seose kujunemisel.

Antud doktoritöö tuvastas ka seda, et põgenemiskäitumise täpsemaks ennustamiseks tuleks arvesse võtta ka linnu kõrgust maapinnast ja linnuseltsingu suurust. Kuigi kõrgemal asetsevad linnud häirusid läheneva ohu suhtes suhteliselt kiiremini, olid nad muude põgenemiskäitumise näitajate poolest ohu suhtes tolerantsemad. Kahes uurimustöös leiti, et suuremad linnusalgad põgenevad varem, viidates sellele, et suuremas salgas suureneb tõenäosus, et mõni lind märkab lähenevat ohtu ja tema järgnev reaktsioon kutsub esile terve salga põgenemise. Lisaks tuli doktoritöö käigus ilmsiks, et põgenemiskäitumise peennüanssides võivad erineda isegi sarnase suurusega ja fülogeneetiliselt lähedased linnuliigid.

Kokkuvõttes näitas doktoritöö, et käitumuslike reaktsioonide omavaheliste seoste uurimine kiskja-saaklooma vahelise interaktsiooni eri etappides pakub täiendavaid võimalusi saada kvalitatiivselt uusi teadmisi lindude põgenemiskäitumise kohta. Väga tähelepanuväärne on tulemus, et kuigi põgenemiskäitumise analüüs viitas linnalindude väiksemale ettevaatlikkusele ja põgenemisega viivitamisele, ei osutunud lindude peasendi põhjal hinnatud valvsus nende käitumusmuutrite usaldusväärseks indikaatoriks. Doktoritöös leiti veel, et lisaks põgenemiskaugusele on kasulik mõõta põgenemishetkele vahetult järgnevaid käitumusmuutmeid, sest nii saab terviklikuma ülevaate põgenemisega seotud kulutustest, mis omakorda võib aidata kaasa eelnevate põgenemisotsuste mõistmisele. Üks olulisemaid leide oli tulemus, et põgenemishetkele järgnev põgenemiskäitumine sõltub tajutava kisklusriski muutumisest põgenemise ajal. Leitud seaduspära osutab, et linnud jätkavad kiskja jälgimist ka pärast põgenemise alustamist, et saavutada optimaalne tasakaal kinnipüütud saamise riski ja põgenemisele kuluva aja ja energia vahel. Doktoritöö tulemused toetasid ka varasemaid töid, mis on leidnud, et liigiomane kehamass, laiuskraad, peidupaiga lähedus, seltsingu suurus, isendi kõrgus maapinnast ja kiskja poolt lähenemise alustamise kaugus on olulise mõjuga loomade põgenemisotsuste langetamisel. Doktoritööst saadud teadmised võivad aidata paremini ennustada, kuidas lindude tajutav kisklusrisk võib inimtekkeliste häiringutega seoses muutuda, mis omakorda aitab kaasa looduskaitsemeetmete planeerimisele.

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- Zuberbühler, K. (2009). Survivor signals: the biology and psychology of animal alarm calling. *Advances in the Study of Behavior*, 40, 277–322.



## **PUBLICATIONS**

## CURRICULUM VITAE

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### Education:

2015–2020 University of Tartu, doctoral studies in Zoology and Hydrobiology  
2012–2014 University of Tartu, master's studies in Ecology and Biodiversity Conservation, supervisor Jaanus Elts, “Spatial characteristics in habitat selection of the ortolan bunting (*Emberiza hortulana*)”  
2009–2012 University of Tartu, bachelor's studies in Ecology and Biodiversity Conservation, supervisor Jaanus Elts, “Habitat selection in the ortolan bunting (*Emberiza hortulana*)”  
1997–2009 Gustav Adolf Grammar School

### Publications:

- Tätte, K.**, Møller, A.P., Mänd, R. (2020). Corvids exhibit dynamic risk assessment during escape. *Behavioural Processes*, 170, 104017.  
<https://doi.org/10.1016/j.beproc.2019.104017>
- Tätte, K.**, Ibáñez-Álamo, J. D., Markó, G., Mänd, R., & Møller, A. P. (2019). Antipredator function of vigilance re-examined: vigilant birds delay escape. *Animal Behaviour*, 156, 97–110.  
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<https://doi.org/10.1515/eje-2015-0003>

**Conference presentations:**

- Tätte, K.** Møller, A.P., & Mänd, R. Escaping from a predator: run for your life or take another look? ASAB Summer 2019: New Frontiers in the Study of Animal Behaviour. 26.08–28.08.2019, Konstanz, Germany. Poster presentation.
- Tätte, K.** Møller, A.P., & Mänd, R. Escape decisions in birds: relationship between flight initiation distance and distance fled. Behaviour 2017. 30.07–04.08.2018, Estoril, Portugal. Poster presentation.
- Tätte, K.** Who's afraid of Kunter Tätte? ZO-BO conference. 12.01.2018, Mooste, Estonia. Oral presentation.
- Tätte, K.** Kiskja eest põgenemine kui kaalutletud otsus? (Is escaping from predators a calculated decision?). Conference in celebration of the 95. anniversary of the Estonian Ornithological Society. 11.11.2017, Tartu, Estonia. Oral presentation.

**Other:**

I have reviewed manuscripts for Behaviour, Current Zoology, Ethology, Frontiers in Ecology and Evolution, Journal of Asia-Pacific Entomology. I have been a reviewer for the 2019 competition of Estonian students' environmental studies. I have contributed to popularization of science by creating educational videos, writing articles for popular science journals, and by helping to organize Researchers' Night Festival 2016. I have achieved award-winning places at several nature photography contests.

## ELULOOKIRJELDUS

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### Hariduskäik:

2015–2020 Tartu Ülikool, doktoriõpe, Zooloogia ja hüdrobioloogia eriala  
2012–2014 Tartu Ülikool, magistriõpe, Ökoloogia ning elustiku kaitse eriala, juhendaja Jaanus Elts, “Põldtsiitsitaja elupaigavaliku ruumilised eripärad”  
2009–2012 Tartu Ülikool, bakalaureuseõpe, Ökoloogia ning elustiku kaitse eriala, juhendaja Jaanus Elts, “Põldtsiitsitaja elupaigavalik”  
1997–2009 Gustav Adolffi Gümnaasium

### Publikatsioonid:

- Tätte, K.**, Møller, A.P., Mänd, R. (2020). Corvids exhibit dynamic risk assessment during escape. *Behavioural Processes*, 170, 104017. <https://doi.org/10.1016/j.beproc.2019.104017>
- Tätte, K.**, Ibáñez-Álamo, J. D., Markó, G., Mänd, R., & Møller, A. P. (2019). Antipredator function of vigilance re-examined: vigilant birds delay escape. *Animal Behaviour*, 156, 97–110. <https://doi.org/10.1016/j.anbehav.2019.08.010>
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**Konverentsi ettekanded:**

**Tätte, K.** Møller, A.P., & Mänd, R. Escaping from a predator: run for your life or take another look? ASAB Summer 2019: New Frontiers in the Study of Animal Behaviour. 26.08-28.08.2019, Konstanz, Saksamaa. Stendiettekanne.

**Tätte, K.** Møller, A.P., & Mänd, R. Escape decisions in birds: relationship between flight initiation distance and distance fled. Behaviour 2017. 30.07–04.08.2018, Estoril, Portugal. Stendiettekanne.

**Tätte, K.** Who's afraid of Kunter Tätte? ZO-BO konverents. 12.01.2018, Mooste, Eesti. Suuline ettekanne.

**Tätte, K.** Kiskja eest põgenemine kui kaalutletud otsus? Konverents Eesti Ornitoloogiaühingu 95. tegevusaasta tähistamiseks. 11.11.2017, Tartu, Eesti. Suuline ettekanne.

**Muud:**

Olen retsenseerinud artikleid ajakirjadele Behaviour, Current Zoology, Ethology, Frontiers in Ecology and Evolution, Journal of Asia-Pacific Entomology. Olen olnud retsensent Õpilaste keskkonnaalaste uurimistööde 2019. aasta konkursil. Olen aidanud kaasa teaduse populariseerimisele tehes hariduslikke videoid, kirjutades artikleid Eesti Loodusele ja aidates korraldada Teadlaste Öö Festivali 2016. Olen saanud auhinnalisi kohti mitmetel loodusfoto konkurssidel.

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