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Anti-predator Behavior of Birds and Conservation

Yiting Jiang

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Anti-predator Behavior of Birds and Conservation

Thèse de doctorat de l'Université Paris-Saclay
préparée à l'Université Paris-Sud

École doctorale n°567 : Sciences du végétal : du gène à l'écosystème (SDV)
Spécialité de doctorat : Biologie

Thèse présentée et soutenue à Orsay, le 4 Mai, par

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“争渡，
争渡，
惊起一滩鸥鹭。”

宋 1099 · 李清照, 《如梦令》

“ OÙ est mon chemin de retour,
Où est mon chemin de retour,
Je fais fuir les aigrettes along.”

LI Qingzhao (dynastie Song, 1099, Chine),
"Une chanson de rêve"

“Where is my way home,
Where is my way home,
I scare away a flock of egrets.”

LI Qingzhao (Song dynasty, 1099, China),
“A dream song”

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This thesis is composed of five manuscripts written in English, which make up my research. The first was published in *Journal of Evolutionary Biology*, and was presented as a poster in August 2015 at ICCB-ECCB (27th International Congress for Conservation Biology and the 4th the European Congress for Conservation Biology: Mission Biodiversity: Choosing new paths for conservation, Montpellier, France). The second manuscript was published in *Behavior Ecology*, and was presented as an oral presentation June 2016 at ISBE (16th congress of the International Society for Behavioral Ecology, Exeter, UK). The other manuscripts are currently submitted.

A general introduction in English provides general scientific background, summary and conclusions, and it brings the manuscripts together in a common context. I then shortly discuss the implications of this research, and I present the perspectives that I consider to be interesting to develop.

Contents

Introduction	1
I Anti-predator strategy and escape behavior	1
i Plumage coloration	1
ii Flocking	1
iii Alarm calls	2
iv Escape behavior	2
II Flight initiation distance	4
III The heritability of escape behavior	9
IV Predation risk and FID	10
i Predation risk and FID	10
ii Three potential variables predicting interspecific variation in FID	11
V Consequences of FID	14
i Population consequences	15
ii Urbanizaion	16
iii Non-lethal effects	17
VI Conservation and management implications	18
Research questions	19
I Does escape behavior interfere with genetic variance?	19
II Could FID perform as an indicator of threat status of species?	19
III Could FID contribute to long-term trait evolutionary distinctiveness?	20
IV Is there any “side-effect” of early escape?	20
V Does social behavior affect escape behavior?	21
Summary	21
I Escape from predators and genetic variance in birds	21
II Anti-predator escape distances of common and threatened birds	22
III Evolutionary distinctiveness covaries with anti-predator behavior in bird communities	23
IV Flight initiation distance is correlated with oxidative stress in birds	23
V Contagious fear: Flight initiation distance increases with flock size in gregarious birds	24

Perspectives	24
Reference	27
Manuscripts	41
I Escape from predators and genetic variance in birds	41
II Antipredator escape distances of common and threatened birds	51
III Evolutionary distinctiveness covaries with anti-predator behavior in bird communities	58
IV Flight initiation distance is correlated with oxidative stress in birds	80
V Contagious fear: Flight initiation distance increases with flock size in gregarious birds	101
Résumé en français	125

Introduction

I Anti-predator strategy and escape behavior

Animals assess the surrounding environment including the threat status posed by this environment and make decisions about responses to such information by behavioral means. The interactions between predator and prey represent one of the most substantial events in nature and pose important questions for most creatures dealing with one or more likely predators. To cope with the pressure of predation and survive, prey have evolved many sequential protective measures and complex anti-predator strategies. Numerous anti-predator behavior metrics have evolved to partly reduce the risk of predation, such as mimicry, clustering in groups, alarm calls, warning signals and escape behavior (Caro, 2005), and the origin and the maintenance of this diversity begs an explanation.

i Plumage coloration

Prey can avoid predation by concealing themselves in the environment so that predators would fail to find them. Many studies have addressed anti-predator benefits of cryptic plumage in adults (Götmark, 1992; Götmark & Hohlfalt, 1995; Slagsvold *et al.*, 1995), and predation is a selective force partially because of the potential benefits of plumage coloration (e.g. Caldwell, 1986). In some species, individuals change color across seasons (e.g. Slagsvold & Lifjeld, 1985; Steen *et al.*, 1992) and/or breeding (Slagsvold *et al.*, 1995), which provides additional though not conclusive evidence that pelage or plumage color reduces predation risk. Color resemblance is more beneficial in certain species than others (Cott, 1940). For instance, nocturnal species such as owls need to be cryptic as they tend to remain still and sleep during daylight as suggested by Cott (1940). However, even after long lasting research, there is still little systematic evidence revealing that plumage coloration has clear impact on predator avoidance. Scientists gradually turned their attention to the correlation between plumage coloration and mate preference (e.g. Bennett *et al.*, 1997; Ballentine & Hill, 2003; Leitão *et al.*, 2014) and offspring sex allocation (e.g. Sheldon *et al.*, 1999; Griffith *et al.*, 2003; Romano *et al.*, 2015).

ii Flocking

Many species evolved social aggregations. A flock has a higher likelihood of detecting danger than a solitary individual (Darwin, 1871) because of collective detection (Pulliam, 1973). Individual response distance of detecting a predator also increases with flock size, which results in an increased probability of escape (Kenward, 1978). If a predator only takes one prey individual or a number less than the size of a group, the probability of getting captured would be smaller than for a solitary individual of a prey (Hamilton, 1971). This dilution of risk, the reduced probability of being captured in larger groups, has been observed numerous times (e.g. Munro & Bedard, 1977; Cresswell, 1994; Beauchamp & Ruxton, 2008). The detection and dilution benefits intertwine at some point (Bednekoff & Lima, 1998): vigilance provides relatively less and dilution more benefits in larger groups, but both benefits could reach limits, and the probability slightly decreases as group size continues to increase. Besides reducing predation risk, gathering in a group also reduces time spent vigilant, and it enhances foraging opportunities for individual prey (Morse, 1977; Fernández *et al.*, 2003; Beauchamp, 2014, 2015).

iii Alarm calls

When a prey individual has already discovered a predator, prey may emit alarm calls or perceive warning signals from other individuals. Alarm calls convey information about the threat, including the type of predator (Seyfarth *et al.*, 1980), the size of a predator (Templeton *et al.*, 2005), the behavior of a predator (Griesser, 2008), the urgency to respond (Leavesley & Magrath, 2005) and many other clues for the threat. Thus, alarm calls protect individuals in the group that parasitize the anti-predator behavior of the individual that emits the alarm call, while benefiting the alarmed individual itself. There are false alarm calls performed as a means of resource usurpation, thereby increasing the callers' own probability of accessing food (e.g. Munn, 1986; Møller, 1988). Recognition of intra- and inter-species warning signals constitutes an important part of the anti-predator strategy of individuals that reduce the costs of responding to false alarms (Treisman, 1975; Koops, 2004; Magrath *et al.*, 2007).

iv Escape behavior

If all of these previous actions fail, prey will have to face the predator directly. Prey can do nothing but escape when this encounter is inevitable. Unlike other anti-predator behavior

with potential follow-up strategies in the case of failure, escape behavior is the last line of defense (Cooper & Blumstein, 2015). Thus, escape behavior is of particular importance for survival and constitutes a specific part of the anti-predator strategy. Simultaneously, predator-prey interaction has been a major driving force causing evolutionary change to reduce the risk of predation and increase fitness.

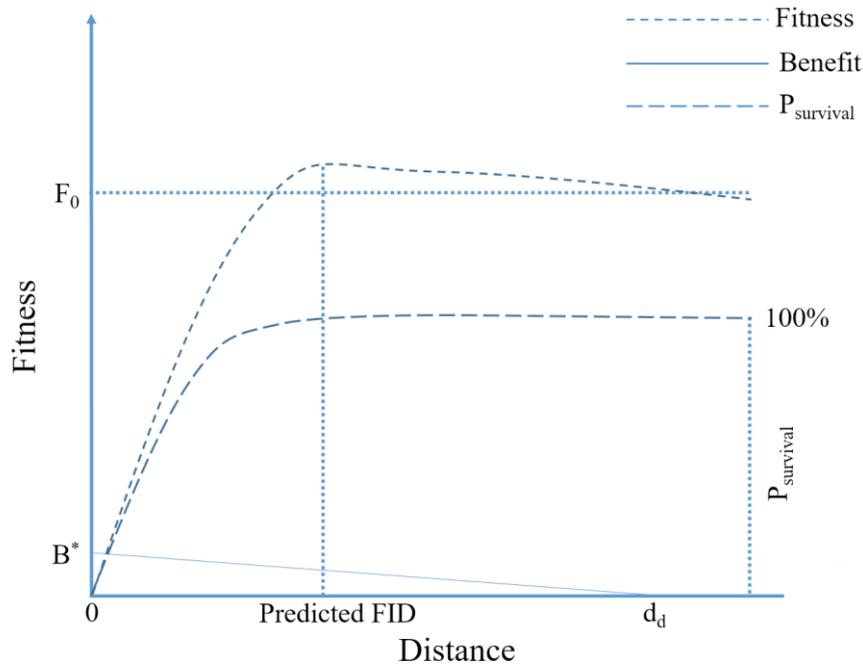


Fig. 1. Optimal escape model. F_0 is fitness at the outset of the encounter; B is benefit during the encounter shown as a linear function rising from zero when the prey detects the predator at distance d_d to B^* (the maximum benefit obtainable by not fleeing); the cost of escape is omitted from the graph (including energy expended while not engaging in fitness-enhancing activities and during escape) and $P_{\text{survival}}(d) = 1 - e^{-kd}$, $0 \leq d \leq d_d$, is the probability of survival. The expected fitness (residual reproductive value) exceeds initial fitness where the benefits accrue more rapidly than risk increases. The optimal approach distance, predicted FID, occurs where fitness is maximized. Modified from Cooper & Frederick (2007).

The shorter the distance between the prey and the predator, the higher the probability that the prey will be killed as escape takes time before starting while the predator gets closer. An individual who failed to escape when facing a predator ends up dead. An inefficient escape could cause injury to the prey although this may still imply survival (Dickey & McCarthy, 2002; Heithaus *et al.*, 2002) and even its subsequent breeding opportunities if they have damaged tails or wings (Fitzpatrick & Price, 1997; Jennions & Petrie, 1997). Escape appears to be a simple action: As long as the prey runs at the moment a predator is detected, the prey

will achieve the maximum probability of survival from this encounter. An individual's response to a potential predator may be subject to trade-offs (Ydenberg & Dill, 1986; Blumstein & Bouskila, 1996; Cooper & Frederick, 2007) because prey in addition to avoiding being pursued, also has to forage and reproduce. Direct flight implies termination/change of behavior in progress, which means giving up potential benefits. Even if individuals are resting when encountering a predator, leaving immediately causes them to consume extra energy (Tatner & Bryant, 1986), give up potential foraging habitat (Brown, 1999), and subsequently reduce individual fitness. Thus, animals have to optimize the distance at which they start escape, so the benefits of staying put are balanced against the costs of flight (Fig. 1; Ydenberg & Dill, 1986). This distance reflects the life history compromise between risk of predation and the benefits of foraging.

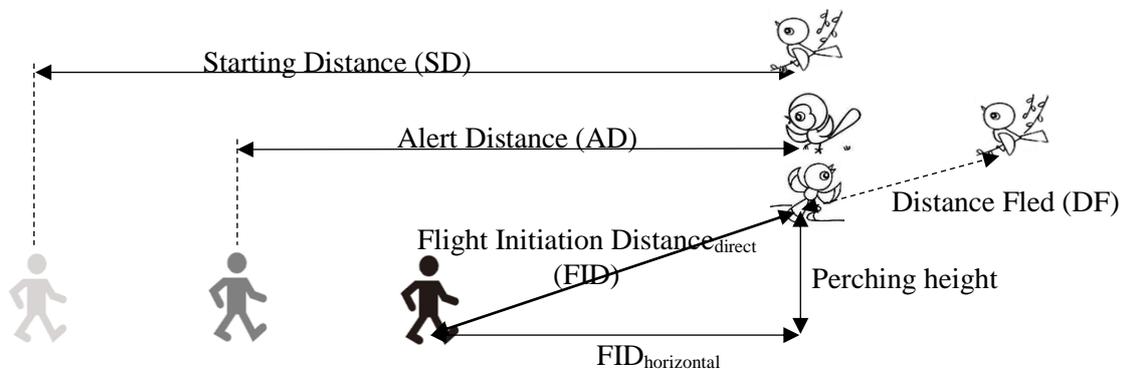


Fig. 2. Schematic illustration of several escape-behavior related distances and flight initiation distance calculation.

II Flight initiation distance

All animals flee from potential predators and humans, and wildlife react to humans in similar ways as they do to predators (Frid & Dill, 2002). Predation events characteristically follow a sequence: encounter, detection, identification, approach, subjugation and consumption from the perspective of predators (Endler, 1991). For this study of escape distance, humans are the presumed predators in the encounter. When an individual bird is initially seen, it is identified to species. The starting distance (SD) is the distance at which a human starts to approach the target individual, and alert distance (AD) is the distance at which the target individual shows clear alert behavior (Fig. 2). Flight initiation distance (FID) is the distance at which an individual animal takes flight when approached by a human. The encounter is interrupted at this time and distance fled (DF) records what happens afterwards. SD is

positively correlated with FID (e.g. Blumstein *et al.*, 2004; Cooper, 2005, 2008). This relationship is first mathematical controlled (FID can only equal or be smaller than SD), but it has a biological component as well (Dumont *et al.*, 2012). Animals accrue an attentional cost for continued monitoring of an approaching predator (Blumstein, 2003; Samia & Blumstein, 2015).



Fig. 3. Photo showing a similar situation as how FID was collected. The approaching person would stop when the target individual flew or walked away and then record the distance in meters.

In this thesis, I target an individual with a binocular and approach the target from 100m away for large-sized species (heavier than 150g) or 30m away for smaller species (Fig. 3; Møller & Erritzøe, 2014) to eliminate this potential problem. I used the Pythagorean theorem to calculate the direct FID:

$$FID_{\text{direct}} = \sqrt{FID_{\text{horizon}}^2 + \text{Perching height}^2}$$

shown in Fig. 2. Flight is defined as when a focal individual is moving away either by foot or flight in response to approach. Finally, I record the height at which the individual was perching off the ground (if it was off the ground, otherwise this value was 0m). Distances were either measured in paces and converted to meters or by using a hand-held laser

rangefinder. Height was estimated by visually rotating the location of the individual comparing the position with the approaching person's height (Møller, 2008a).

There is an extensive literature on methodology of studies of FID, and they found a strong positive relationship between FID recorded by different observers, temporal consistency of FID in estimates from different years and consistent FID among different sites (e.g. Blumstein, 2003; Blumstein *et al.*, 2003; Møller *et al.*, 2008; Møller & Erritzøe, 2014). In those studies that have followed marked individuals, FID has been verified to have high repeatability (Carrete & Tella, 2010, 2013), which is a measure of intra-individual consistency. Thus, FID is a reliable metric of actual predation risk. The literature on FID, focusing on birds (Møller, 2015), mammals (Stankowich & Reimers, 2015) and lizards (Cooper, 2015), have identified a variety of factors that are correlated with FID (Cooper & Blumstein, 2015) as presented in Table 1. FID, as an indicator of anti-predator behavior, is also known to be heritable and subject to directional selection (Dall *et al.*, 2004; Blumstein *et al.*, 2010; Møller & Nielsen, 2010; Bize *et al.*, 2012).

Table 1 Studies that examine different variables related to FID in birds

Category	Variable	Reference examples
Body	Body mass	(Holmes <i>et al.</i> , 1993; Blumstein, 2006; Møller & Garamszegi, 2012; Samia <i>et al.</i> , 2015b)
	Wing shape	(Fernández-Juricic <i>et al.</i> , 2006)
	Wing area	(Møller <i>et al.</i> , 2013b)
Brain	Brain size	(Carrete & Tella, 2011; Guay <i>et al.</i> , 2013; Samia <i>et al.</i> , 2015a)
	Cerebellum size	(Møller & Erritzøe, 2014; Symonds <i>et al.</i> , 2014)
Sex	Sexual dichromatism	(Møller <i>et al.</i> , 2016)
Physiology	Basal metabolic rate	(Møller, 2009)
	Haematocrit	(Møller <i>et al.</i> , 2013b)
Visual ability	Eye size	(Møller & Erritzøe, 2010)
Life history	Age at first reproduction	(Blumstein, 2006)
	Clutch size	(Møller & Liang, 2013)
	Incubation duration	(Seltmann <i>et al.</i> , 2012)
	Age	(Eason <i>et al.</i> , 2009)
	Senescence	(Møller & Garamszegi, 2012)
Sociality	Flock size	(Geist <i>et al.</i> , 2005; Laursen <i>et al.</i> , 2005; Thiel <i>et al.</i> , 2007)
	Mixed flock	(Bregnballe <i>et al.</i> , 2009)
Parasitism	Blood parasite infection	(Møller, 2008b)
	T-cell response	(Martín <i>et al.</i> , 2006)
Predation	Predator playback	(Zanette <i>et al.</i> , 2011)
	Abundance of predators	(St. Clair <i>et al.</i> , 2010; Díaz <i>et al.</i> , 2013)
	Susceptibility to predation	(Møller, 2008b, 2014)
	Direct and indirect approach	(Burger & Gochfeld, 1981; Eason <i>et al.</i> , 2009; Møller & Tryjanowski, 2014)
Range	Latitude	(Díaz <i>et al.</i> , 2013; Møller & Liang, 2013; Samia <i>et al.</i> , 2017)
	Range size	(Møller & Garamszegi, 2012; Díaz <i>et al.</i> , 2013)
Dispersal	Dispersal	(Lin <i>et al.</i> , 2012)
	Dispersal distance	(Møller & Garamszegi, 2012; Garamszegi & Møller, 2017)
Habitat	Habitat openness	(Blumstein, 2006; Møller <i>et al.</i> , 2006)

	Locations on and away from paths	(Eason <i>et al.</i> , 2009)
	Distance to refuge	(Fernández-Juricic <i>et al.</i> , 2006; Rodriguez-Prieto <i>et al.</i> , 2009; Braimoh <i>et al.</i> , 2018)
Urbanization	Urban and rural habitat	(Carrete & Tella, 2013; McGiffin <i>et al.</i> , 2013; Møller <i>et al.</i> , 2013a; Samia <i>et al.</i> , 2017)
	Urban invasiveness	(Carrete & Tella, 2011, 2015)
	Urban gradient	(Clucas & Marzluff, 2012; McGiffin <i>et al.</i> , 2013)
Disturbance	Hunting	(Laursen <i>et al.</i> , 2005; Thiel <i>et al.</i> , 2007; Braimoh <i>et al.</i> , 2018)
	Human disturbance	(Bregnballe <i>et al.</i> , 2009; Ge <i>et al.</i> , 2011)
	Noise level	(Petrelli <i>et al.</i> , 2017)
	Distance to human settlements	(Bjørvik <i>et al.</i> , 2015)

III The heritability of escape behavior

Escape behavior is the last step in anti-predation behavior before capture. The individual is likely to face death once its escape fails. Therefore, effective escape behavior should have a strong hereditary component as its strong and direct link to survival affording limited opportunities for “practice”. Most characters have a quantitative genetic basis with offspring resembling their parents in phenotype. Repeatability is an upper limit to heritability, and the product of heritability and the intensity of selection equals response to selection (Falconer & Mackay, 1996). Thus, unbiased heritability estimates and selection estimates can be used to predict micro-evolutionary response. So, if for example the intensity of selection increases, we should be able to predict the increase in phenotype due to the response to selection. Generally, escape behavior is a response to the surrounding environment and is subject to natural selection. Fewer studies have investigated the heritability of behavior. Behavior itself is a result of comprehensive performance in response to various factors (Sih *et al.*, 2004; Bonduriansky & Day, 2009), including the physiological regulation (Ricklefs & Wikelski, 2002), cognitive ability (Griffin *et al.*, 2000; Cole *et al.*, 2012) and morphological constraints (Foster *et al.*, 2015). For many species, parents and their offspring live in geographically adjacent (if not the same) territories, and they are likely to behave similarly (Wilson, 1998). Maternal effects may also play an important role in affecting offspring behavioral responses to the environment including the maternal environment (Eising *et al.*, 2006). In addition, learning and imitation may be other explanations for similarities in behavior between generations, which may originate from parental care as well as among peers (Koolhaas *et al.*, 1999; Hamm, 2000).

There are only few studies that provide evidence that escape behavior is heritable as it is difficult to study the heritability of escape behavior under field conditions. Juvenile scallops *Argopecten purpuratus* showed significant heritability and significant genetic correlation among several escape response traits using the full-sib/half-sib design (Brokordt *et al.*, 2012). Garter snakes *Thamnophis ordinoides* showed significant heritabilities and genetic correlations among escape traits using pedigree-based quantitative genetic analysis (Brodie, 1989), and its flight initiation distance showed a significant family effect (King, 2002). Antipredator behavior of adult Alpine swifts *Apus melba* was significantly repeatable and heritable based on long-term behavioral observations of parents and cross-fostered offspring (Bize *et al.*, 2012). Long-term data on FID in a population of barn swallows *Hirundo rustica* reported significant heritability of FID with a maternal clutch size effect and similar heritabilities based on father-offspring and mother-offspring resemblance (Møller, 2014). The latter may suggest that maternal effects are not major determinants of FID in this species.

IV Predation risk and FID

i Predation risk and FID

Predation risk is likely to have a concave upward relationship with distance to potential predators, and it increases sharply at short distances (Fig. 1; Cooper & Frederick, 2007). This inherent assumption about risk-taking and FID has been confirmed by empirical evidence based on intra- and inter-species differences. A study on 30 Namibian rock agama *Agama planiceps* males found that bold males with relatively short FID suffered higher levels of tail loss, possibly due to predation (Carter *et al.*, 2010). Møller (2014) analysed long-term data on FID in a population of barn swallows *Hirundo rustica* during 1984–2013 with 2196 records for 1789 individuals. Among these birds, a total of 13 adults killed by cats *Felis catus domesticus* and 5 adults preyed on by sparrowhawks were identified from remains including rings. These 18 individuals that died from predation had significantly shorter FID than survivors. More indirect evidence from paired tropical bird species and closely related temperate bird species showed that tropical species had relatively shorter FID, as predicted by the large difference in abundance or diversity of the predator community related to latitude (Møller & Liang, 2013).

The difference among species in mean FID also reflects the difference in risk of predation among species. For instance, in a comparative analysis of 40 bird species, species particularly susceptible to predation by sparrowhawks took flight at shorter distances (Fig. 4; Møller *et al.*, 2008). The risk of predation by domestic cats (Møller *et al.*, 2010) and the risk of getting hit by vehicles (Møller *et al.*, 2011) were likewise negatively related to FID among species, and these relationships remained robust even after controlling for additional factors associated with risk of predation such as body mass and sexual dichromatism. Thus longer FIDs are associated with lower actual risk of predation and smaller levels of risk-taking when experiencing a real predator.

Some studies have shown an effect of perceived risk of predation on FID of birds. Artificially modified visibility did not affect flight decision of crimson rosellas *Platycercus elegans* when their overall perception of risk remained the same (Boyer *et al.*, 2006). Double-banded plovers *Charadrius bicinctus* reacted to the presence of cats and other mammalian predators by increasing FID in response to approaching humans (St. Clair *et al.*, 2010). A intraspecific study found that FID in nesting female song sparrows *Melospiza*

melodia was significantly longer following experimental playback of predator calls than non-predator vocalizations (Zanette *et al.*, 2011).

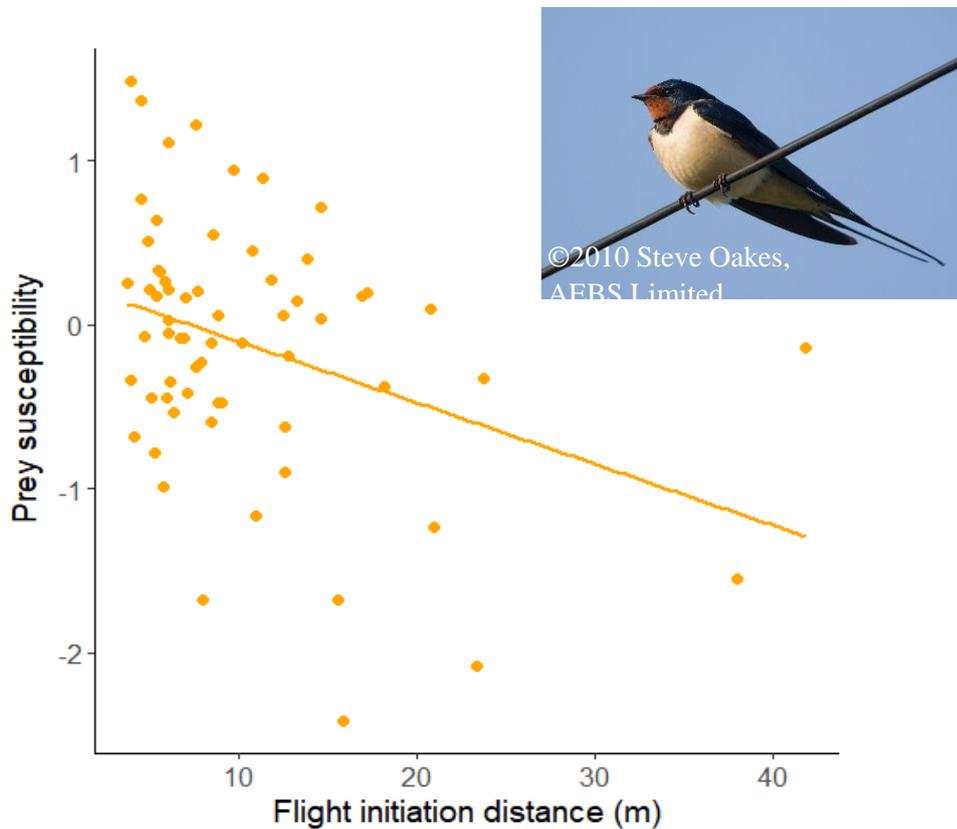


Fig. 4. Vulnerability to predation by the sparrowhawk in relation to flight initiation distance (m) by different species of birds. Prey susceptibility is calculated as the observed \log_{10} -transformed number of prey minus the \log_{10} -transformed expected number of prey. The line is the linear regression line. Modified from Møller *et al.* (2008).

ii Three potential variables predicting interspecific variation in FID

a Body mass

Take-off performance is reported to decline with increasing body mass (Metcalf & Ure, 1995; Warrick & Dial, 1998). A relatively large flying organism takes longer before take-off as with increasing body size the power requirements of flight increase faster than the ability of muscle to provide power (Tobalske & Dial, 2000). Besides the direct relation between body mass and flight performance, body mass is also the best predictor of life-history, behavior, physiology and risk of extinction (Bennett & Owens, 2002). There are reasons to believe that FID and body mass are significantly associated. Scientists noticed

that smaller birds were more approachable than larger species long age (Hemmingsen, 1951; Cooke, 1980). One of the best predictors of response of birds to human disturbance is body mass (Samia *et al.*, 2015b). Many studies reported consistent positive correlations between FID and body mass. Blumstein (2006) reported an effect size in terms of Pearson's product-moment correlation coefficient of 0.044 for 150 bird species. Fernández-Juricic *et al.* (2006) specifically analyzed body mass and FID of 83 species from 29 families and found an effect size of 0.585, while Weston *et al.* (2012) reported FIDs and body mass information for 250 Australian birds and found an effect size of 0.48. Møller (2008a) studied urban populations of 40 bird species and reported an effect size of 0.78. A meta-analysis dealing with FID in birds reported the second largest (following urbanization) mean effect size (0.39) of body mass among different categories of phenotypic traits (Møller, 2015). Thus large species have relatively long FID (Fig. 5).

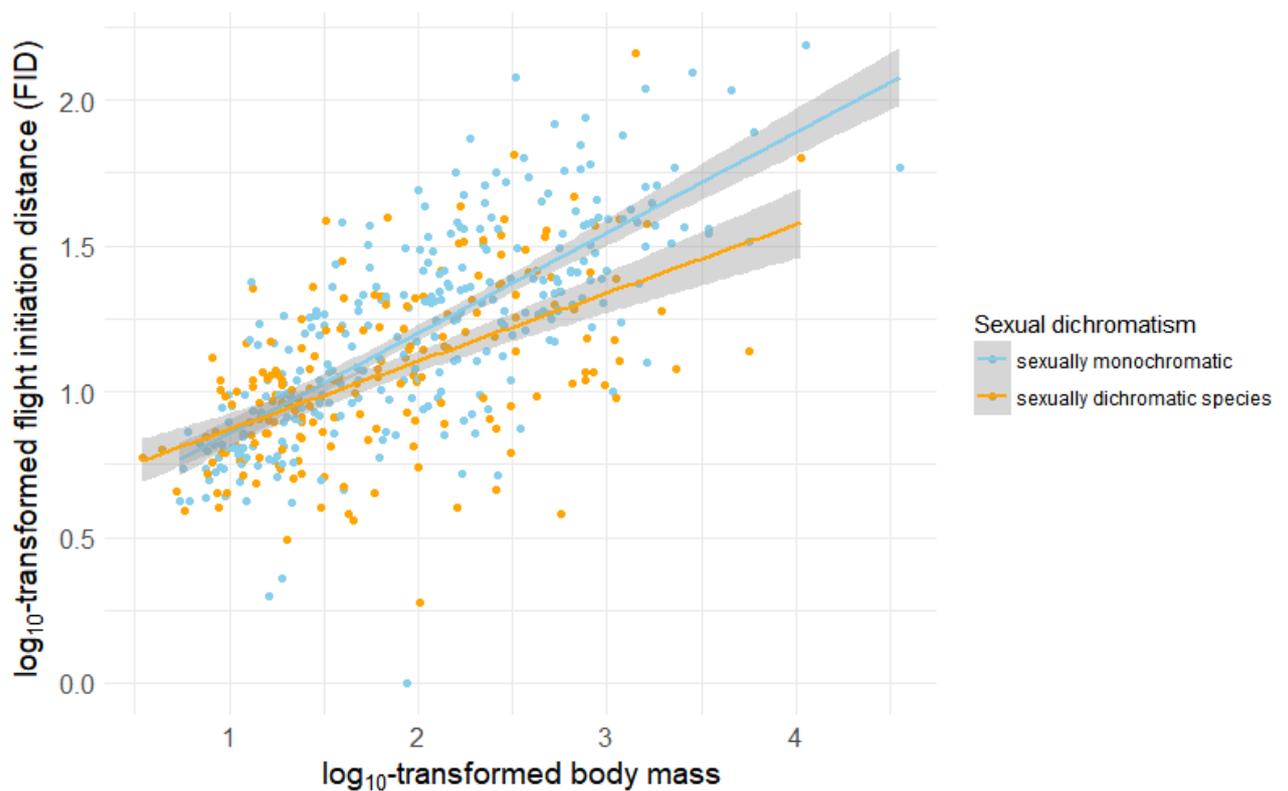


Fig. 5. Flight initiation distance in relation to body mass and sexual dichromatism. The two lines are the linear regression lines for sexually monochromatic (blue points and blue line) and sexually dichromatic species (orange points and orange line). The grey areas are the 95% confidence intervals for each linear regressions. Modified from Møller *et al.* (2016).

While studies have commonly shown mean flight distances for species increasing significantly with body mass, the slope of this relationship is always smaller than one. For

instance, in a study of 250 Australian bird species, $R^2 = 0.480$, slope = 0.293 (0.046; Weston *et al.*, 2012). Møller (2008c) found that this relationship was much weaker in a phylogenetic regression based on observations of 100 European bird species with a slope (SE) = 0.20 (0.10), much smaller than one. Thus, FID increases slower than body mass and large species have relatively shorter FID for their body mass.

b Morphology

Morphological and behavioral characteristics influence interspecific variation in escape behavior. Bauwens *et al.* (1995) found that the evolution of escape behavior (high maximum sprinting abilities) was mechanistically related to the evolution of morphology (longer hindlimbs relative to body length) across 13 species of lizards. Morphology of birds was closely related to flight performance and energy cost as predicted by flight dynamic theory (Rayner, 1988). Migratory birds showed a decreased escape speed with increasing wing loading (mass/wing area) (Burns & Ydenberg, 2002). The morphology of wingtip shape and hind limb morphology also influence interspecific variation in predation rates in passerines (Swaddle & Lockwood, 1998). Thus, FID in birds could vary with wing and hind limb morphology. For instance, a comparative study on 83 bird species showed that birds with more pointed wings fled at longer distances and landed farther away than species with rounded wings (Fernández-Juricic *et al.*, 2006). Similarly, species with long FID for their body size also had large wing areas and aspect ratios (Fig. 6; Møller *et al.*, 2013b). The relationship between morphology of species and FID could also be explained from a physiological perspective as FID is negatively related to haematocrit, a measure of packed red blood cell volume and as such indicates the oxygen transport ability and hence the flight muscle contraction reaction of individuals (Møller *et al.*, 2013b). Basal metabolic rate (BMR), representing the minimum level of metabolism that allows normal functioning by an individual in its environment, was also positively related to FID (Møller, 2009). Thus, escape behavior has cooperated with a number of different adaptations and constrains in prey in terms of morphology.

c Cognitive ability and brain size

Information on potential predation risk is collected by the sense organs and subsequently processed by the brain. Cognitive ability biases animal behavior and influences how animals interact with natural habitats (Dukas & Ratcliffe, 2009). A number of studies has shown that animals use cognitive abilities for assessing the behavior of predators manifested as changed

flight distance. For instance, birds have shorter FID if they are approached tangentially rather than directly (Fernández-Juricic *et al.*, 2005; Geist *et al.*, 2005; Møller & Tryjanowski, 2014), or if they are approached with human eyes looking elsewhere rather than looking directly at them (Bateman & Fleming, 2011). In a comparative study of 107 species, Møller & Erritzøe (2014) found that birds with relatively large brains for their body size avoided the rush when a predator approached. The negative correlation could be caused by species with relatively large brains experiencing more opportunity costs monitoring the intention of the predator (e.g. through a better assessment of a predator's distance and speed) (Cooper & Blumstein, 2014). They make the least expensive escape decision after assessment and monitoring of the threat of predation thereby reducing the energy costs of flight (Samia *et al.*, 2015b). Relative brain size also indirectly influenced invasion of urban habitats through its positive effect on inter-individual variability in FID (Carrete & Tella, 2011).

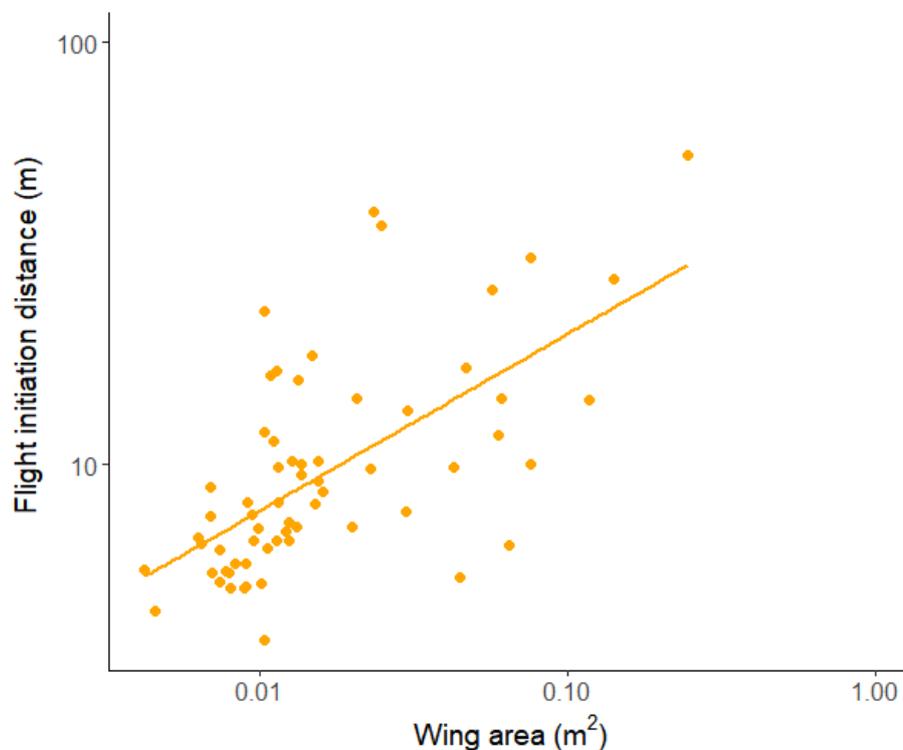


Fig.6 Flight initiation distance (m) in relation to wing area (m²) in 63 different species of birds. The x- and y-axis are logarithmic scaled. The fit is the linear regression line. Modified from Møller *et al.* (2013b).

V Consequences of FID

Manuscript No. 1 p. 55-64 (Escape from predators and genetic variance in birds)

Manuscript No. 3 p. 72-99 (Evolutionary distinctiveness covaries with anti-predator behavior in bird communities)

Manuscript No. 4 p. 100-126 (Flight initiation distance is correlated with oxidative stress in birds)

i Population consequences

Flight initiation distances provide information about the risk that individuals are willing to take given their state and the environment, and species with relatively long FIDs should more often suffer from disruption of their activities by potential predators than species with short FIDs. Based on an extensive data set of more than 4000 FIDs for 133 species across Europe, the size of breeding populations in the Western Palearctic was smaller in species with long mean FIDs and small variances in FID (Møller & Garamszegi, 2012). In a comparative study of 56 species across Europe, species with long FID also showed a higher frequency of declining populations than species with short FID (Møller, 2008c). These findings suggest that mean FID for different species provides reliable information about the population consequences of risk-taking behavior by individuals and the susceptibility of different species to disturbance.

Nevertheless the association between FID and population trend is more complex than it seems. In an intercontinental study considering 193 species of birds from three continents, North America, Australia and Europe, continent and FID showed a significant interaction among all variables explaining population changes of birds. While bird populations were declining with increasing FID in Australia and Europe, the opposite pattern was found in North America (Møller *et al.*, 2014). Another study on 46 bird species in England also failed to find a significant relationship between species population change and FID (Thaxter *et al.*, 2010). These cases triggered studies on the geographic pattern of escape behavior, and a follow up study showed interactive effects of species escape behavior and geographical location on European bird population trends (Díaz *et al.*, 2015). The susceptibility to predation by sparrowhawks (Møller, 2014) and adult survival rate (Møller & Garamszegi, 2012) was significantly positively related to mean FID. Still, population size and population trend tend to be the net result of complex interactions between habitat alteration at the breeding grounds, climate change and migratory strategies (Cuervo & Møller, 2013; Reif, 2013) combined with escape behavior (Díaz *et al.*, 2015).

Scientists have noticed that urban species generally have relatively short FID compared to their rural counterparts (**Fig. 7**; Cooke, 1980; Sol *et al.*, 2013; Møller, 2015; Samia *et al.*, 2017). The magnitude of the difference is directly related to time since urbanization (Møller, 2008a). The variation in relative FID (controlled by body mass) of urban populations is positively related to urban population density of different species (Lin *et al.*, 2012). The magnitude of variance could also be predicted by the number of generations since urbanization (Møller, 2008a), as expected by a gradual selection for urban life. Six different components of escape behavior were related to urbanization, suggesting that antipredator behavior has diverged between ancestral rural populations and recently established urban populations (Møller & Ibáñez-Álamo, 2012). Thus, the difference in FID between rural and urban habitats is likely related to recent changes in the predator community following urbanization. Indeed, this difference in FID paralleled trends in raptor abundance, as it decreased with increasing latitude (Díaz *et al.*, 2013). Besides differences in the community of predators, other potential impacts of urbanization that increase individuals' body condition (Geue & Partecke, 2008; Delgado-V. & French, 2012), the availability and reliability of food (Jokimäki *et al.*, 1996; Galbraith *et al.*, 2015) also reduce the relative cost of flight. For instance, the presence of feeders in urban habitats also independently accounted for a reduction in FID as shown by a study of winter populations in Poland and differences in predators between urban and rural environments (Møller *et al.*, 2015).

However, not all species are equally adapted to urbanization (McKinney, 2002, 2006; Morelli *et al.*, 2016). For instance, the ubiquitous presence of humans and constant disturbance by vehicles could preclude most species from successfully invading cities. A study in Europe found that species successfully colonizing urban areas had larger variances in FID in their rural populations than unsuccessful colonizers (Møller, 2010). This supports the hypothesis that urbanization resulted from differential colonization of urban areas by species with heterogeneous levels of fear in the ancestral rural populations. A study on 42 bird species in a recently established South American city also found that inter-individual variability in fear of humans was positively related to contemporary urban invasion in birds, positively enhanced by species relative brain size (Carrete & Tella, 2011). Thus, FID may play a crucial role in urbanization of birds and species with relatively large variance in escape behavior rather than tame animals are expected to adapt better to the urban environment. In addition, urban environments are likely to create a safe refuge for prey because predators show greater levels of fear toward the proximity of humans than do their

prey (Møller, 2012). Species-specific mean and variance of FID leads to distinct population trends for different species and contributes to biotic homogenization in urban environment.

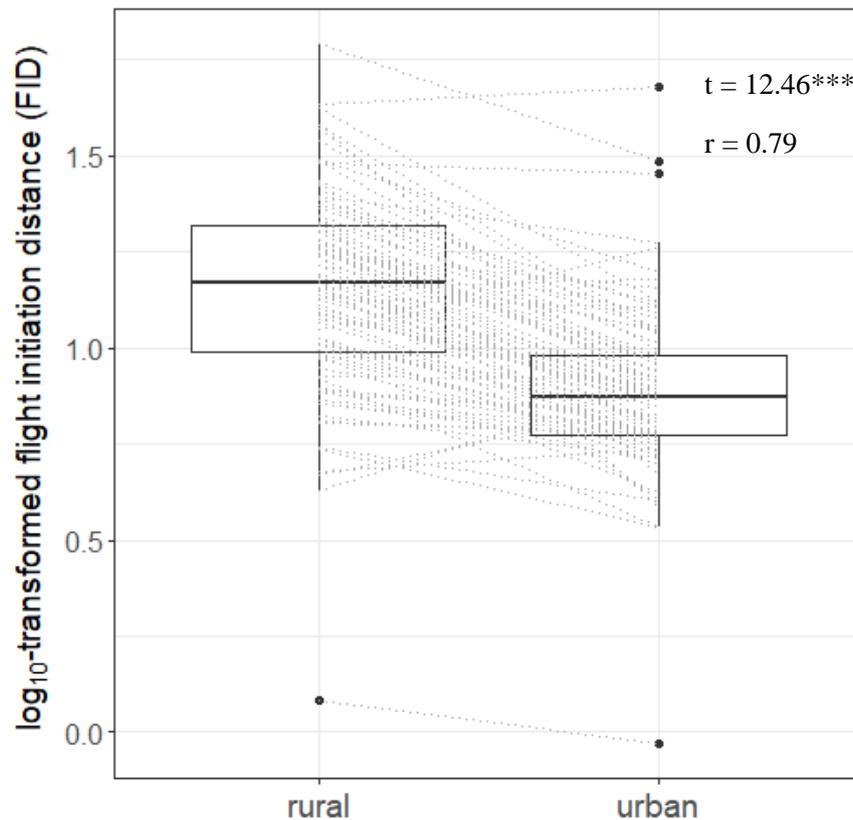


Fig. 7. Rural-urban differences in FID for 92 bird populations studied in Europe. Box-plots show median, quartiles, 5- and 95-percentiles and extreme values. Each population's trajectory is illustrated with a gray dashed line. t-values and effect sizes calculated as partial correlation coefficients are shown. The t-values was highly significant (***P < 0.001). Modified from Samia *et al.* (2017).

iii Non-lethal effects

As FID is determined by the conflicting benefits of energy gain and the risk of mortality from predation or other causes, relatively longer FID implies earlier abandonment of local resources and more energy consumption under the same level of disturbance than short FID. The immediate cost of lowered resource availability can then be translated into a reduction in reproductive output or in long-term survival (Lima, 1998). Besides the energy cost of flight, the attentional cost of monitoring predators to assess predation risk also requires energy consumption, which explains why FID increases as alert distance (AD), or its

surrogate, starting distance (SD) increases (Cooper & Blumstein, 2014). The nonlethal effects of FID, together with direct predator consumption and other nonlethal effects that reduce or limit energy intake, can all reduce population density of prey (Abrams, 1984).

As a quantitative measure of tolerance of birds to disturbance, variance of FID is expected to predict the diversity of behavioral responses to the environment. Species with a greater diversity of escape behavior exploit more different habitats by successfully coping with different unpredictable environmental conditions. Given the strong individual consistency in FID, the distribution of individuals among habitats is largely depending on their susceptibility to human disturbance as shown by burrowing owls *Athene cunicularia* (Carrete & Tella, 2010). Evidence from 133 bird species in Europe supports that species with a greater variance in FID exploits a greater diversity of habitats than those with relatively smaller variance (Møller & Garamszegi, 2012). Both within and between population variance in FID were significant indicators of habitat diversity of species (Garamszegi & Møller, 2017). Microhabitat choice and song post exposure of male collared flycatcher *Ficedula albicollis* during sexual signalling is closely related to FID, as mediated by intrinsic individual temperament (Garamszegi *et al.*, 2008). The effect of variance in FID on habitat selection can also be reflected in differences of invasions of urban habitat, as mentioned in the previous section.

VI Conservation and management implications

Manuscript No. 2 p. 65-71 (Anti-predator escape distances of common and threatened birds)

Humans extensively influence other creatures living on the planet and perhaps, therefore, we experience a loss of biological diversity (McNeely, 1992; Andr n, 1994; Vitousek *et al.*, 1997; Parmesan & Yohe, 2003). Surprisingly, the disturbance from human activity was found to be the most important factor for richness, supplanting even habitat loss and fragmentation in many cases in a model selection study on land bird communities in an urbanizing environment (Schlesinger *et al.*, 2008). This is plausible because human-caused stimuli could be regarded as a form of predation risk considering its similarity to predation risk. It indirectly affects fitness components and population dynamics via energetics and lost opportunity costs of risk avoidance (Frid & Dill, 2002). Although disturbed populations are more tolerant to human disturbance than less disturbed populations (Samia *et al.*, 2015b), a problematic situation emerges when humans are regarded as potential predators, and a growing tolerance in prey might increase their vulnerability to predators (Geffroy *et al.*,

2015). With the continuous expansion of human impact, the protection of wild species is getting increasingly important. Escape behavior provides important means for resolving conservation problems in the pursuit of more efficient means of conservation.

Nowadays, the most common application of FID on conservation is to define “buffer distance” or “buffer zones” (e.g. Rodgers & Smith, 1995; Rodgers & Schwikert, 2002). Similarly, FID is also used as a reference for landscape design in nature reserves or parks (Fernández-Juricic *et al.*, 2001a, b; Blackwell *et al.*, 2009) to reduce human impacts on wildlife. Some of these studies focused on threatened species (e.g. González *et al.*, 2006; Zuberogitia *et al.*, 2014), while others tried to include as many species as possible to establish a uniform standard for local species conservation as Weston *et al.* (2012) suggested for managing disturbance to Australian birds.

Research questions

I Does escape behavior interfere with genetic variance?

While scientists have found significant though complex relationship between population size, population trend and FID, there is little knowledge about the relationship between effective population size and FID. Inbred populations are threatened because they have little scope for micro-evolutionary responses to environmental change, and the fecundity and the viability of inbred individuals is often reduced compared to outbred individuals. Escape behavior provides the underlying behavioral mechanism accounting for the response of individuals to adverse environmental conditions. I predict that species with relatively long FID are also those with large genetic variability. Short FID indicating higher predation risk either promotes a smaller population size with genetic variability or could be a result of low genetic variability in such species. By establishing a correlation between antipredator escape distances and genetic variability, we may be better able to understand the mechanisms accounting for reductions in population size, but also adopt better choice of individuals for recovery projects considering the large numbers of predators in the wild.

II Could FID perform as an indicator of threat status of species?

Threat status of species is assessed based on the extent of their habitat, population size, population development in recent years, and many other factors. Meanwhile, flight initiation

distance reflects the life history compromise between risk of predation and the benefits of foraging both at short and long term time frames. Species with relatively short FID are better able to cope with the proximity of humans and may have relatively more time and opportunities to get food and a superior reproductive and survival prospect in the environment with high human interference. Thus, FID may be a practical predictor of threat status of different species. I expect that relatively threatened species should have longer FID compared to closely related species, given the increasing rate of human disturbance and the standards for threat status. I verified the relationship between mean FID of species and threat status in closely related species.

III Could FID contribute to long-term trait evolutionary distinctiveness?

Predator-prey coevolution may result in rapid divergence in both predators and prey, and escape behavior as the last line of predator evasion should play a crucial role in the survival of individuals. Evolutionary distinctiveness (ED) reflects the phylogenetic isolation of taxa with high values characterizing species with unique phenotypes that deviate the most from other taxa. While most conservation concern is put on the world's most evolutionarily distinct species, the over-all phylogenetic distinctiveness in urban areas is decreasing across the world. Appropriate escape decisions should balance the costs from lost foraging or mating opportunities, and the benefits of escape from reduced predation risk. Such anti-predator behavior should affect the ability to avoid predation and should therefore contribute to high ED values of certain species. I expect that ED is positively related to FID because species that take the smallest risks when encountering predators are less susceptible to predation. Testing for this correlation between ED and behavioral traits under strong selection may help us understand the evolution of ED and hence allowing for better protection of such species.

IV Is there any “side-effect” of early escape?

Although individuals that take early flight from approaching predators take small risks in encounters, they also have to take off more frequently at the same frequency of interference. Short and brief aerial flapping flight is metabolically expensive that may result in 23 times basal metabolic rate (Tatner & Bryant, 1986). Frequent escape flights when encountering potential predators are energetically expensive and stressful, potentially contributing to the

production of free radicals and hence oxidative stress, an outcome of metabolism. Oxidative stress plays a core role in the evolution of optimal investment patterns between reproduction and survival and other fitness components. Physical activity is an important potential cause of oxidative stress but surprisingly, no study has examined how oxidative stress is related to escape behavior which reflects the life history compromise between risk of predation and the benefits of foraging. I predict that species with relatively short FID for their body mass would experience more oxidative stress as frequent flight take-offs result in high energy consumption and stress. I tested this possible causal relationship in comparative analyses with three different indicators for oxidative stress and considered body mass and brain size as confounding factors.

V Does social behavior affect escape behavior?

Sociality (directly related to group size) is found to have an intermediate mean effect size of 0.26 on FID in a meta-analysis of cooperating factors in birds (Møller, 2015). Group size has also been suggested to be an important prey trait that influences escape decisions (Samia *et al.*, 2017). Both collective detection (i.e. increased likelihood of detecting a predator in larger groups; Pulliam, 1973) and the dilution of risk (i.e. reduced probability of being captured in larger groups; Hamilton, 1971) could potentially affect individual's escape behavior as group size changes. Previous studies had demonstrated that FID was positively related with flock size (Laursen *et al.*, 2005; Tätté *et al.*, 2018). However, gregariousness (the tendency to live in flocks) could potentially affect individual's capacity to communicate with others and subsequently affect individual's escape behavior. As a consequence, the aim of this study was to test if FID in birds increased with flock size, focusing on differences between gregarious and non-gregarious species.

Summary

I Escape from predators and genetic variance in birds

This study used phylogenetic generalized least square analyses weighted with sample size in 128 species of birds. The results revealed that three proxies for genetic variability, (1) minisatellite band sharing (Fig. 8), (2) heterozygosity and (3) inbreeding coefficient, were all related to the robust proxy of real predation risk (FID). Thus, higher levels of genetic

variability were consistently associated with longer FID. These findings were robust to potentially confounding effects of variables such as breeding range, population size and body mass.

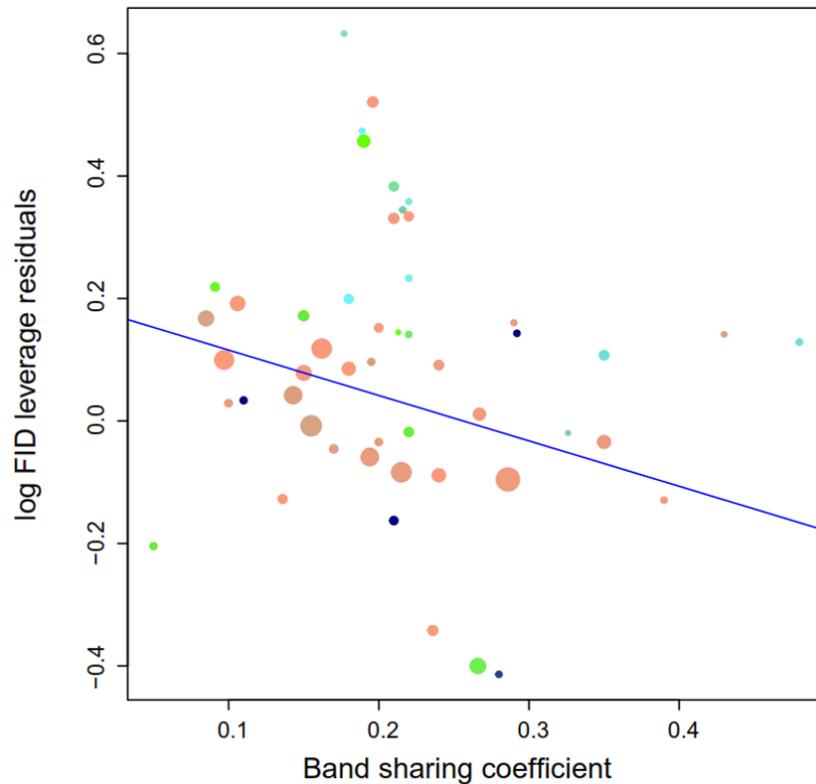


Fig. 8 Log₁₀-transformed flight initiation distance (FID (m)) decreased with increasing band sharing coefficient across 52 species of birds. Symbol sizes are proportional to square-root transformed sample sizes. The colors represent different species with more closely related species having more similar colors. The line is the linear regression line.

II Anti-predator escape distances of common and threatened birds

This study associated extinction risk to escape distance in European birds. By analyzing the FID of 48 pairs of closely related bird species differing in their threat status, I concluded that threatened birds generally have a higher FID than non-threatened close related species. This difference in FID between common and threatened species was almost two-fold and was consistent in both parametric and non-parametric tests.

III Evolutionary distinctiveness covaries with anti-predator behavior in bird communities

This chapter focused on the possible role of escape behavior (FID) in an evolutionary context in waterbirds. A total of 48 migratory and 30 resident water birds were investigated. The phylogenetic generalized linear model results showed a significant positively correlation between ED score and the relative FID (controlled by body mass) (Fig. 9). This result was robust to differences in sampling effort and the potentially confounding effects of body mass, migratory status, the extent breeding ranges and similarity among taxa due to common phylogenetic descent.

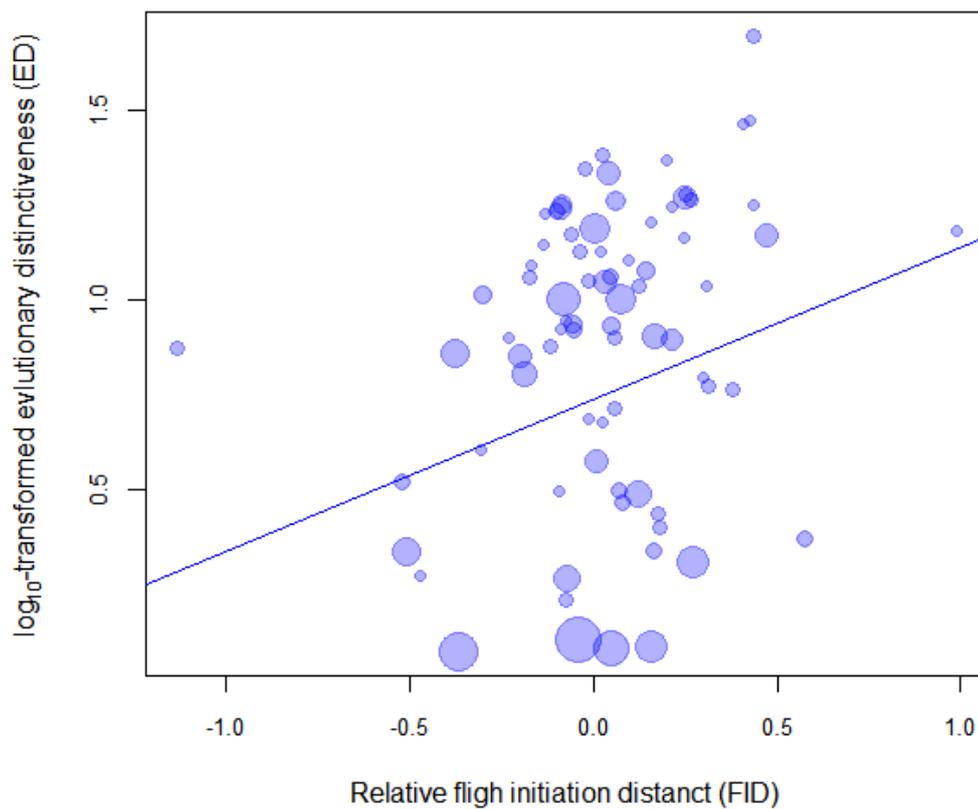


Fig. 9 Evolutionary distinctiveness (ED) increased with increasing relative flight initiation distance (FID (m)) across 78 species of European waterbirds. Each point represents one species. Symbol sizes are proportional to square-root transformed sample sizes. The line is the linear regression line.

IV Flight initiation distance is correlated with oxidative stress in birds

This study tested the relationship between FID and three oxidative stress markers (malondialdehyde, MDA, total antioxidant status, TAS and uric acid, UA) over 72 bird species. To model the relationship, I used phylogenetic generalized least square (PGLS) regression models, followed by phylogenetic path analysis to examine the potential causal relationships between several traits. The main finding of this study was that mean FID of different species of birds was positively correlated with species-specific MDA and UA levels and mediated through their relationship with body mass. This result was robust to differences in sample size and similarity due to common phylogenetic descent.

V Contagious fear: Flight initiation distance increases with flock size in gregarious birds

A total of 7,768 observations of 35 bird species from eight different European countries was collected. Different species were classified based on three ecological variables: trophic guild, body mass and gregariousness. Two series of models were run: First controlling for the phylogenetic signal among species and then non-phylogenetic models using flock size as a fixed factor and other variables as random factors. The main finding of this study was that social birds reacted to a potential predator quickly (as represented by relatively long FID) when aggregated in large flocks (Fig. 10), while that was not the case in non-gregarious species. These effects were independent of body mass and geographic area where data were collected, as well as phylogenetic signal among species.

Perspectives

At least three mechanisms have been proposed to account for differences in FID between populations of animals living in urban and rural habitats (Møller *et al.*, 2015; Samia *et al.*, 2015b; Miranda, 2017). First, the increased tolerance could result from habituation. Habituation-like processes occur when individuals are particularly sensitive to unexpected behavior from humans and potential predators but not expected behavior. Changes in population mean FID could be due to the fact that human activities are harmless and regular most of the time. Second, differential selection among behavioral syndromes could explain variation in recruitment to urban habitats leading to phenotypic sorting under different interference pressures between urban and rural habitat. Third, local adaptation to urban habitats implies that specific genotypes have increased in frequency or become favored

among urban individuals and should generally result in genetic differentiation (Atwell *et al.*, 2012; Carrete & Tella, 2013; Miranda *et al.*, 2013). In order to understand the underlying mechanism of these differences, we need well-designed experiments.

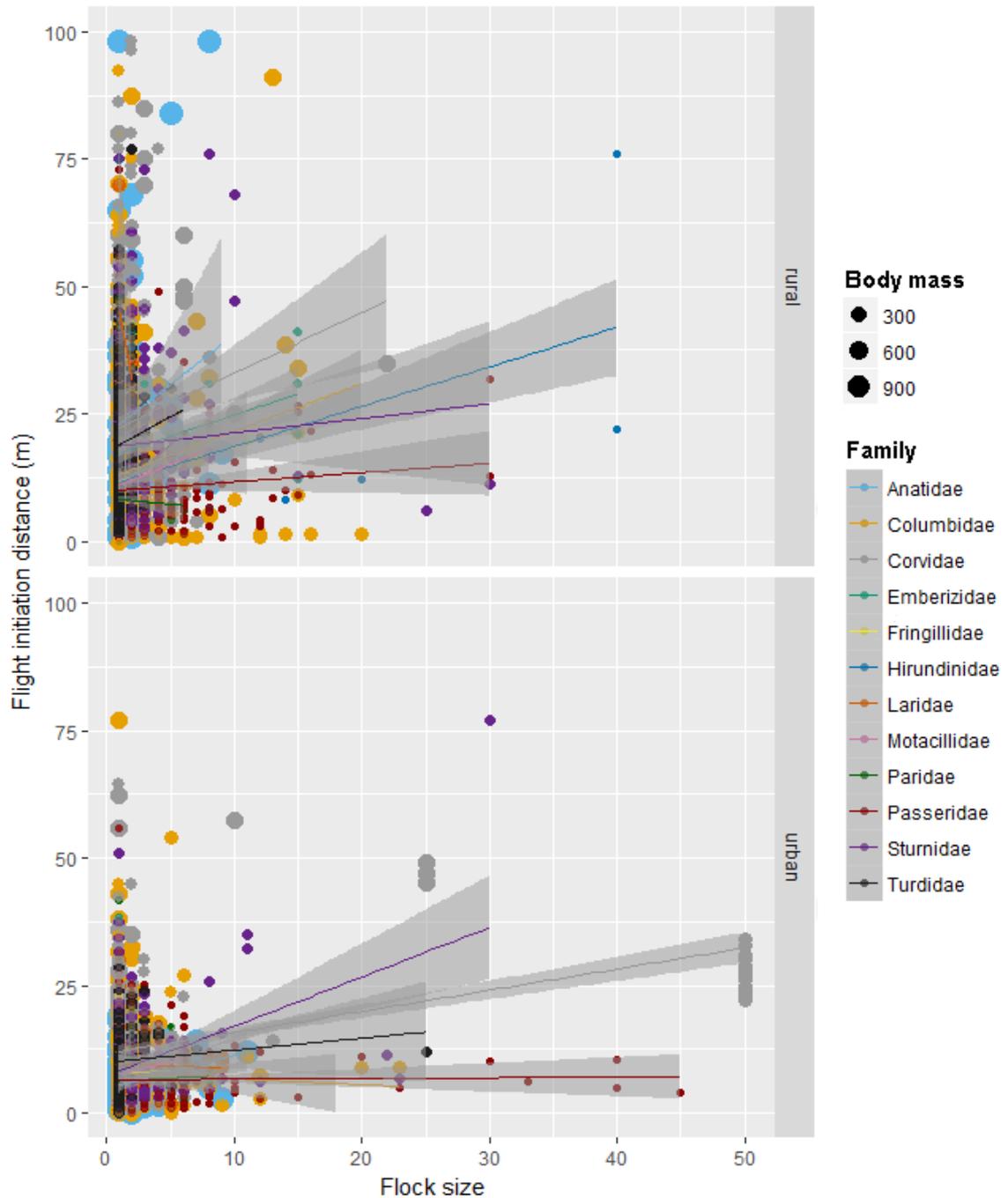


Fig 10. Linear regression lines between flight initiation distance (FID, m) and flock size in gregarious bird species from rural and urban environments in eight European countries. Colors indicate bird family, and circle size is proportional to body mass of birds (g). Envelopes around lines are 95% confidence intervals.

Escape behavior is often highly integrated with other aspects of an organism's biology e.g. mating and reproduction strategies (Møller, 2014), genetic systems (Storfer & Sih, 1998) and morphology (Losos *et al.*, 2002). These correlations suggest that escape behavior has potential use as a relatively easily accessed indicator of an organism's overall status in its environment. Relative mean FID and variance in FID of species should be regarded more as a predictor of identifying species that are potentially more vulnerable to increasing human disturbance rather than just measurements of "buffering distance". By involving antipredator escape distances in conservation plans and recovery projects, it may be possible to assess why some species become threatened while others do not. It might also be possible to identify species that are prone to population declines beforehand by relying on FID as a predictive tool. Such behavioral differences may provide means of recovery of such threatened species from threats caused by the presence of predators including humans.

Nevertheless, well-designed experiments may allow analysis of the direction of causation and give a better understanding of FID, behavioral syndromes and their ecological significance.

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Manuscripts

I Escape from predators and genetic variance in birds

Escape from predators and genetic variance in birds

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microsatellites.

Abstract

Predation is a common cause of death in numerous organisms, and a host of antipredator defences have evolved. Such defences often have a genetic background as shown by significant heritability and microevolutionary responses towards weaker defences in the absence of predators. Flight initiation distance (FID) is the distance at which an individual animal takes flight when approached by a human, and hence, it reflects the life-history compromise between risk of predation and the benefits of foraging. Here, we analysed FID in 128 species of birds in relation to three measures of genetic variation, band sharing coefficient for minisatellites, observed heterozygosity and inbreeding coefficient for microsatellites in order to test whether FID was positively correlated with genetic variation. We found consistently shorter FID for a given body size in the presence of high band sharing coefficients, low heterozygosity and high inbreeding coefficients in phylogenetic analyses after controlling statistically for potentially confounding variables. These findings imply that antipredator behaviour is related to genetic variance. We predict that many threatened species with low genetic variability will show reduced antipredator behaviour and that subsequent predator-induced reductions in abundance may contribute to unfavourable population trends for such species.

Introduction

Predation is a common cause of death in numerous organisms, and prey rely on appropriate escape decisions when confronted with predators to gain benefits of staying and avoiding a decrease in fitness due to flight and increased risk of predation (Ydenberg & Dill, 1986). Flight initiation distance (FID, the distance at which a bird takes flight when approached by a human) represents a compromise between minimizing the threat of predators and maximizing foraging, and hence signifies the antipredator strategy of the species (Cooper & Blumstein, 2015).

Several studies have demonstrated a genetic basis for antipredator behaviour (Arnold, 1982, 1992), and there is evidence of significant heritability of FID (Blumstein *et al.*, 2010; Møller, 2014). Domesticated species living in close proximity with humans (Clutton-Brock, 1992),

urban birds occupying cities for generations (Symonds *et al.*, 2016) and many species on islands in the absence of predation (Cooper *et al.*, 2014) have consistently lost antipredator responses. Thus, there is good reason to believe that there is considerable standing genetic variation in antipredator response among domesticated, but also wild animals and that changes in genetic variation may be associated with changes in behaviour. However, there is little published information on genetic variability and risk of predation.

Inbreeding depression is substantial enough to affect both individual and population performance (Keller & Waller, 2002). Such reductions in genetic variability are predicted to decrease population mean fitness and population size (Frankham, 1996; Szulkin *et al.*, 2010). Inbred populations are threatened because they have little scope for microevolutionary responses to environmental change (Grueber *et al.*, 2008; Keller *et al.*, 2008), and the fecundity and the viability of inbred individuals are often reduced compared to outbred individuals (DeRose & Roff, 1999). Lower levels of genetic variability are associated with reduced hatching success across species, even where the choice of partners is less constrained and breeding may not occur among close

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relatives (Spottiswoode & Møller, 2004). Both natterjack toads *Bufo calamita* and willow ptarmigan *Lagopus lagopus* with reduced genetic variability suffered from increased risk of predation (Rørvik *et al.*, 1999a, b; Rowe & Beebee, 2005). Bird species with less genetic variation as reflected by higher band sharing coefficients for minisatellites suffered disproportionately from predation by two species of hawks, the sparrowhawk *Accipiter nisus* and the goshawk *A. gentilis* (Møller & Nielsen, 2015). Hence, there is intraspecific evidence showing that risk of predation increases with increasing level of genetic similarity. Genetic variation has also been suggested to be closely related to the evolution of antipredator behaviour. The proportion of individuals emitting fear screams in different species of birds increased with the degree of genetic similarity among adults in local populations (Møller & Nielsen, 2010).

Extant populations show considerable genetic variation ranging from highly outbred to highly inbred (Nevo *et al.*, 1984). Some of this variation is caused by genetic bottlenecks or by changes in population size caused by recent persecution by humans. FID relates directly to life history, longer FIDs being associated with shorter levels of risk-taking and smaller risk or mortality due to predation (Møller *et al.*, 2008b). A long-term study based on 2196 records of FID for 1789 adult barn swallows *Hirundo rustica* showed that individuals that died from predation had shorter FID than survivors (Møller, 2014). The objective of this study was to investigate the association between antipredator behaviour and genetic variability in birds. If genetic variance is explained by life-history traits and positively related to fitness, we should expect a positive correlation between genetic variance and FID. More specifically, we predicted that (i) FID should be positively related to observed microsatellite heterozygosity and negatively related to inbreeding coefficients for microsatellites and (ii) FID should be negatively related to band sharing coefficients for minisatellites in different species of birds. We used extensive data on genetic variance and FID from Europe to test these predictions.

Materials and methods

Collection of field data

Flight initiation distance data were collected in Orsay, France (48°42'N, 2°11'E), from 2005 to 2011 combined with additional data collected in Finland, Norway and Spain using a standard protocol (Blumstein, 2006). In brief, the observer moved at a normal walking speed towards a foraging or resting individual bird and recording the distance at which the individual took flight or walked away as horizontal distance. The height above ground was also recorded if the individual was positioned in the vegetation. FID was estimated as the Euclidian distance and the other two sides were

horizontal distance and the perching height, respectively. Observers avoided pseudoreplication by flushing birds in different locations and collecting data during the breeding season when most individuals are sedentary (Møller, 2008). Here, we provided information derived from a restricted data set of 128 species with information on band sharing minisatellite markers and FID (3821 estimates of 52 species) and microsatellite markers and FID (5186 estimates of 111 species for observed heterozygosity and 5069 estimates of 105 species for the inbreeding coefficient F).

Band sharing coefficient for minisatellite markers

The band sharing coefficient is an estimate of the number of shared minisatellite bands in relation to the total number of bands among adults, originally proposed by Wetton *et al.* (1987) as a measure of genetic similarity. A high band sharing coefficient implies that many bands are shared among individuals and hence that genetic similarity in the population is relatively high. This estimate of band sharing has commonly been used as an index of genetic similarity among individuals within a species (Reeve *et al.*, 1990; Hoelzel, 1992; Blomqvist *et al.*, 2002). Information on band sharing coefficients in the present study was derived from an extensive survey of the literature using the Web of Science, with all information being reported in Appendix S1. We used species-specific mean band sharing values calculated as the mean band sharing coefficient for all probes of a given study, with the mean subsequently being calculated for the means of the different studies. This approach is supported firstly by the significant repeatability (Becker, 1992) of band sharing coefficients among studies of the same species using the same probe, based on 25 studies of nine species ($R = 0.55$ (SE = 0.20), $F_{8,16} = 3.90$, $P = 0.0099$). This result demonstrates that band sharing coefficient estimates are consistent between populations of the same species, even when molecular analyses are made in different laboratories with inherent differences in procedures and hence gel quality. Secondly, Papangelou *et al.* (1998) showed in a review of 129 published studies of 70 bird species that mean band sharing between dyads of unrelated individuals from populations or species defined as outbred on the basis of independent evidence was nearly 50% smaller than that for populations defined as small or inbred (these were, for example, rare species threatened by immediate extinction). In addition, mean band sharing between dyads of unrelated individuals in many small or inbred populations was similar to that for dyads of first-order relatives in outbred populations (Papangelou *et al.*, 1998). This implies that mean band sharing coefficients of populations reliably reflect the degree of genetic similarity within a species. The number of fingerprinting probes ranged from one to three per study (mainly 33.15,

33.36, per, M13 and others). Repeatability of band sharing coefficients among probes in the same study, based on 47 studies of 20 species of birds, was large and highly significant ($R = 0.86$ (SE = 0.06), $F_{19,27} = 17.16$, $P < 0.0001$), demonstrating that the use of multiple probes should not cause any significant bias. Finally, restriction enzymes did not cause bias because band sharing was highly repeatable across restriction enzymes (Møller, 2001). Band sharing coefficients for 62 species of birds in the Western Palearctic were strongly negatively correlated with distribution range and population size (Møller *et al.*, 2008a), as expected for estimators of genetic variation, implying that analyses should control statistically for the potentially confounding effects of these variables.

Microsatellite markers

Microsatellites have been found in every organism investigated so far and have played a major role in modern population genetics studies for the past decades. Average heterozygosity of an individual measured from microsatellite data should more closely reflect inbreeding than using allozymes (Goldstein & Schlötterer, 1999). We obtained information on observed heterozygosity (H_o) for microsatellites in birds by a search of Web of Science using the terms micro-sat*, micro-sat* and bird*. In total, we obtained 11 681 entries for 500 species of birds with information on number of individuals and H_o , with all references being reported in Appendix S5. We used H_o value at every given locus and calculated the mean H_o for all alleles in a given study, with the mean subsequently being calculated for the means of the different studies weighted by sample size for estimating average H_o . We tested for consistency in H_o between populations of the same species from different laboratories and found the repeatability for H_o to be 0.30 with a standard error of 0.02 (Becker, 1992; $F = 1.75$, d.f. = 315, 5398, $P < 0.01$). We also calculated the inbreeding coefficient F ($F = 1 - H_o/H_c$) (Wright, 1922) for 454 species with 10 437 entries. Inbreeding in an actual pedigree can be compared with any system of mating using F (Wright, 1922). Repeatability of F among studies of the same species was 0.04 with a standard error of 0.02 (Becker 1992; $F_{315,5398} = 1.75$, $P < 0.01$). The correlation between H_o and F was intermediate with Pearson's $r = -0.29$, $t = -3.04$, $P < 0.01$.

Additional variables

Information on body mass was extracted from Dunning (1992). We recorded current minimum and maximum breeding population sizes for all countries in Europe using Burfield *et al.* (2004) as a source. We used the mean of these two estimates for the analyses. Information on breeding range size was extracted from Møller

et al. (2008a). The entire data set is reported in Appendix S1.

Comparative analyses

We log₁₀-transformed population density, body mass and population size to obtain variables that were normally distributed allowing for the use of parametric statistics. Closely related species are more likely to have similar phenotypes than species that are more distantly related due to shared evolutionary history. Previous studies of band sharing coefficients (Spottiswoode & Møller, 2004) and susceptibility to predation (Møller & Nielsen, 2006, 2007) have shown evidence of a phylogenetic component to such variation. Therefore, a phylogenetic analysis was required to control for statistical dependence of data. We extracted the phylogenetic relationship for band sharing coefficient species and H_o species from the phylogeny available online (Jetz *et al.*, 2012, 2014) and obtained both consensus phylogenies from 100 trees with Mesquite 3.04 (Maddison & Maddison, 2017). To control for the phylogenetic relationship among species, we used phylogenetic generalized least-squares regression models as implemented in the R (R Core Team, 2017) statistical environment, using the libraries ape (Paradis *et al.*, 2004) and nlme (Pinheiro *et al.*, 2016) and the function gls with correlation equals consensus tree.

Models were weighted by sample size (the number of prey individuals) to account for the fact that sample sizes differed among taxa. Most statistical analyses assume that single observations provide equally precise information about the deterministic part of total process variation; that is, the standard deviation of the error term is constant over all values of the predictor variable (Sokal & Rohlf, 1995). Garamszegi & Møller (2010, 2011, 2012) have shown that bias due to variation in sample size among observations is a major problem in comparative analyses and equally significant as the biases caused by treating species-specific estimates as statistically independent. If this assumption of similarity in sampling effort is violated, weighting each observation by sampling effort allows the use of all data, giving each datum a weight that reflects its degree of precision due to sampling effort (Draper & Smith, 1981; Sokal & Rohlf, 1995). This procedure also allows both rare and common species to be included and hence avoids any bias in sampling due to rarity (Garamszegi & Møller, 2012). Therefore, we weighted statistical models by sample size. Finally, we avoided over-representation of taxa with large sample size by using the square-transformed number of prey individuals as a weighting factor.

We used the leveraged residuals and genetic statistics to make illustrations. Leveraged residuals are calculated using the models of phylogenetic regression with and without the variable analysed. Leveraged residuals of

the dependent variable stand for the part of FID that is explained by this variable.

We estimated effect sizes by using Cohen's (1988) guidelines for the magnitude of effects being small (Pearson's $r = 0.10$, explaining 1% of the variance), intermediate ($r = 0.30$, explaining 9% of the variance) or large ($r = 0.50$, explaining 25% of the variance).

Results

Minisatellite band sharing and FID

Mean FID ranged from 4.16 to 76.75 m with a mean of means of 17.59 m (SE = 1.98), $N = 52$ species. Band sharing coefficients ranged from 0.05 to 0.48 with a mean value of 0.21 (SE = 0.01), $N = 52$ species. FID decreased with increasing band sharing coefficients in a phylogenetic analysis across 52 species of birds with an effect size that was intermediate accounting for 9% of the variance (Fig. 1). In a multivariate model that accounted for the effects of potentially confounding variables, there were additional effects of body mass and mean population size on FID, whereas the effect of total breeding area did not reach statistical significance (Table 1A).

Microsatellite genetic variability, heterozygosity and FID

Mean FID ranged from 5.14 to 140.00 m with a mean of means of 28.47 m (SE = 2.45), $N = 111$ species. Microsatellite heterozygosity ranged from 0.21 to 0.94

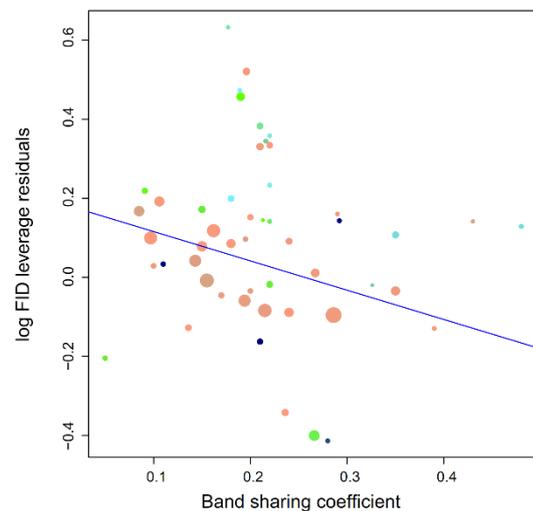


Fig. 1 Log₁₀-transformed flight initiation distance (FID (m)) decreased with increasing band sharing coefficient across 52 species of birds. Symbol sizes are proportional to square-root-transformed sample sizes. The colours represent different species with more closely related species having more similar colours. The line is the linear regression line. The phylogeny is reported in Appendix S2.

Table 1 Models of the relationship between log₁₀-transformed flight initiation distance (FID) and genetic variability and body mass, mean population size and total area of the breeding range, respectively, weighted by sample size for species of birds. The model for band sharing coefficient had the statistics $F_{4,47} = 13.56$, $r^2 = 0.48$, $P < 0.0001$, the model for H_o had the statistics $F_{4,106} = 50.46$, $r^2 = 0.57$, $P < 0.0001$, and the model for inbreeding coefficients had the statistics $F_{4,100} = 46.41$, $r^2 = 0.611$, $P < 0.0001$.

Term	Value	Standard error	d.f.	t	P
(A)					
(Intercept)	1.607	0.609	52	2.638	0.011
			(total)		
Band sharing	-0.618	0.268		-2.309	0.025
log body mass	0.223	0.073		3.068	0.004
log Mean population size	0.080	0.030		-2.648	0.011
log Total area	0.040	0.056		-0.720	0.475
Residual		0.669	47		
(B)					
(Intercept)	-0.414	0.510	111	-0.812	0.419
			(total)		
H_o	0.487	0.140		3.486	0.001
log Body mass	0.278	0.053		5.285	< 0.001
log Mean population size	0.002	0.028		0.084	0.933
log Total area	0.047	0.047		0.994	0.322
Residual		1.014	106		
(C)					
(Intercept)	0.218	0.524	105	0.418	0.677
			(total)		
Inbreeding coefficient	-0.681	0.197		-3.453	< 0.001
log Body mass	0.232	0.055		4.228	< 0.001
log Mean population size	-0.017	0.028		-0.608	0.545
log Total area	0.052	0.047		1.115	0.267
Residual		0.948	100		

with a mean value of 0.60 (SE = 0.01), $N = 111$ species. The correlation between band sharing coefficients and microsatellite heterozygosity was Pearson's $r = -0.22$, $t = -1.30$, $P = 0.20$.

Flight initiation distance increased with increasing heterozygosity in a phylogenetic analysis across species of birds with an effect size that was large and accounted for 25% of the variance (Fig. 2). In a multivariate analysis that controlled statistically for potentially confounding variables, there was an additional partial effect of body mass, whereas population size and total breeding area did not account for a significant proportion of the variance (Table 1B).

Microsatellite genetic variability inbreeding coefficient and FID

Mean FID ranged from 5.14 to 140.00 m with a mean value of 27.93 m (SE = 2.52), $N = 105$ species.

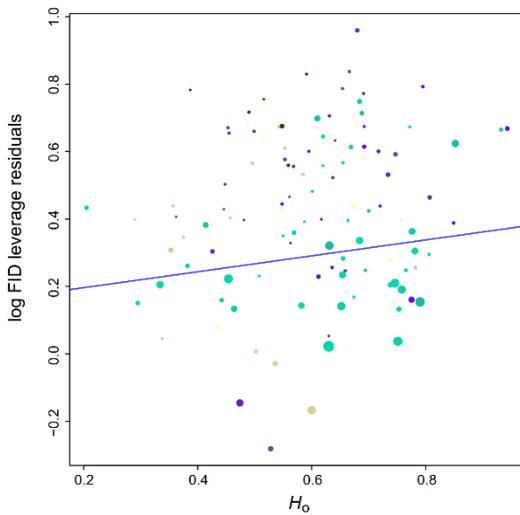


Fig. 2 Log₁₀-transformed flight initiation distance (FID (m)) increased with increasing heterozygosity across 111 species of birds. Symbol sizes are proportional to square-root-transformed sample size. The colours represent different species with more closely related species having more similar colours. The line is the linear regression line. The phylogeny is reported in Appendix S3.

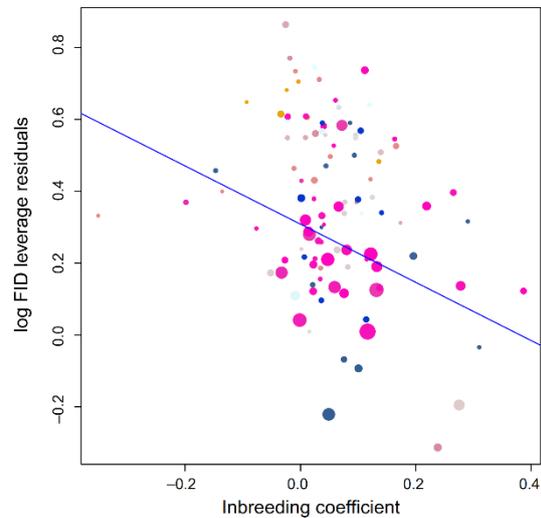


Fig. 3 Log₁₀-transformed flight initiation distance (FID (m)) decreased with increasing inbreeding coefficient across 105 species of birds. Symbol sizes are proportional to square-root-transformed sample size. The colours represent different species with more closely related species having more similar colours. The line is the linear regression line. The phylogeny is reported in Appendix S4.

Inbreeding coefficients ranged from -0.35 to 0.39 with a mean value of 0.06 ($SE = 0.01$), $N = 105$ species. The correlation between band sharing coefficients and inbreeding coefficients was Pearson's $r = -0.16$, $t = -0.90$, $P = 0.38$.

Flight initiation distance decreased with increasing heterozygosity in a phylogenetic analysis across species of birds with an effect size that was large and accounted for 25% of the variance (Fig. 3). In a multivariate analysis that controlled statistically for potentially confounding variables, there was an additional partial effect of body mass, whereas population size and total breeding area did not account for a significant proportion of the variance (Table 1C).

Discussion

The main finding of this study was that mean FID of different species of birds was correlated with band sharing coefficients of minisatellites and heterozygosity and inbreeding coefficients of microsatellites with higher levels of genetic variability being associated with longer FID. These findings were robust to differences in sampling effort and potentially confounding effects of variables such as breeding range, population size and body mass. Likewise, these effects were retained in phylogenetic analyses that accounted for similarity due to the potentially confounding effects of common phylogenetic descent.

We found consistent effects using different measures of genetic variability as reflected by band sharing

coefficients for minisatellites and heterozygosity of microsatellites showing that the results were robust to the specific measures of genetic variability. Bird species differed in terms of sample size because rare species by definition are more difficult to observe, but also to sample for analyses of genetic variation. We took this potential cause of bias into account by weighting estimates of FID by sample size. Band sharing coefficients for minisatellites in different species of birds have previously been shown to be negatively correlated with population size and size of the breeding range (Møller *et al.*, 2008a). Furthermore, species abundance and range size are always positively related (Gaston & Blackburn, 1996) along with a complex interaction with body mass (Haskell *et al.*, 2002). However, these three variables did not confound our conclusions because the relationships between FID and genetic variability were statistically independent of body mass, population size and breeding range size.

One possible assumption of the functional hypotheses attempting to explain molecular genetic variation and the evolution of FID is that high genetic variability for a given species is a proxy of success and appropriate FID contributes to this success. Previous studies have shown that individuals/species with long FID have higher probability of escape from predators than species with short FID (Møller *et al.*, 2008b; Carter *et al.*, 2010). Although only a few intraspecific studies have so far linked FID to genetic variability (e.g. Bize *et al.*, 2012; Carrete *et al.*, 2016), here we have demonstrated based on observations of 52, 105 and 111 bird species,

respectively, that genetic variation shown by both minisatellite and microsatellite markers is correlated with FID. This is consistent with the assumption that long FIDs have survival value when facing a potential predator (Møller *et al.*, 2008b, 2017; Møller, 2014). Species with short FIDs faces more difficulties than species with long FID to reach large effective population size and a high level of genetic variance. Nevertheless, it would be interesting to test for effects of inbreeding on risk-taking behaviour and hence FID in an intraspecific study. We would expect relatively short FID in inbred compared to outbred individuals.

Antipredator behaviour has evolved in response to selection imposed by predators at the level of individual prey. In contrast, genetic variance constitutes an estimate of the variability in genetic variation among individuals within populations. Any trait that is related to effective population size may contribute to genetic variation (Nagylaki, 1998; Wakeley, 1998). For example, mating system, differential mortality of the sexes and any other factor that contributes to variation among individuals to effective population size may affect the amount of standing genetic variation. Distribution range, population size, subspecies richness and mating system have all been shown to contribute to genetic variation in birds although these variables are not explicitly related to effective population size (Møller *et al.*, 2008a). However, we cannot exclude the possibility that socioecological factors other than those just listed may also contribute to effective population size. This is a considerable literature discussing such socioecological factors (e.g. Blumstein, 2002; Giraldeau *et al.*, 2002; Sirot, 2006; Clucas & Marzluff, 2012; Dingemanse *et al.*, 2010). Although we are unaware of any studies showing a link between these factors and genetic variation, we urge further research to address this issue.

The best predictor of variation in free-living species is, in the first place, ecological strategy rather than demography (Romiguier *et al.*, 2014). Our studies suggest that genetic variance is related to FID. Complex spatial patterns of population trends are also generated by the interaction between FID and geographical location (Díaz *et al.*, 2015b). This association suggests that the effect of life-history traits on genetic variance could be part of pace-of-life syndromes (Ricklefs & Wikelski, 2002). Life-history traits of species and demographic dynamics have complex interplay and may contribute to genetic variance (Ellegren & Galtier, 2016).

Many species analysed here have breeding ranges that exceed millions of square kilometres and populations exceeding millions of breeding pairs. The fact that some of these species still show little genetic variability implies that single or multiple bottlenecks must have reduced their populations in the past. There is a close link between heterozygosity and inbreeding coefficients, implying that taxa with low heterozygosity also have high inbreeding coefficients (Wright, 1922). The

relationship between inbreeding coefficients and FID has implications for captive breeding and for management of threatened species under free-living conditions. The most vulnerable individuals, populations and species are likely to be those with the shortest FID, and direct or indirect effects of predation may under such conditions have significant impacts on the development of population sizes. Although such effects may apply to viability, Spottiswoode & Møller (2004) showed a four-fold increase in infertility in bird species with the lowest levels of genetic variability. The reduction in genetic variability can be considered an Allee effect if fecundity, viability or population growth at low population densities contributes to further reductions (Courchamp *et al.*, 1999; Stephens & Sutherland, 1999). Although there is only overall weak evidence of demographic Allee effects across different study organisms (Gregory *et al.*, 2010), this does not preclude the possibility that Allee effects may play a role in the reduction in genetic variability under high predation pressure and hence fear responses to human proximity as reflected by long FID. Note that some of the studied species occupied urban habitats. The decreased FID could be an approved response to the conversion of environment related to human-related habitats (e.g. Fernández-Juricic *et al.*, 2001). A reduction in FID in urban habitats may be advantageous for commensal species if such reductions result in saving of energy (Ydenberg & Dill, 1986; Marzluff *et al.*, 2001).

Behavioural response to predation such as FID may also have implications for population trends outside the context of Allee effects (e.g. LaManna & Martin, 2016) and hence for future threat status of species with little genetic variance. Several studies have shown negative correlations between FID and population trends of bird species in Europe (Møller, 2008; Díaz *et al.*, 2015a). Because short FID implies frequent disturbance by humans, individuals that are subject to frequent and increasing numbers of human approaches will experience a higher level of disturbance and an associated negative energy budget that has to be balanced either by emigration to areas with lower human population density (Carrete & Tella, 2010; Reboló-Ifrán *et al.*, 2015) or by increased rates of ingestion (Blumstein & Daniel, 2005).

The findings that we have reported here have a number of implications for conservation. Cats and rats as the most commonly introduced predators on islands constitute significant threats to endemic species of prey (Jones *et al.*, 2008; Medina *et al.*, 2011) due to absent or weak antipredator defences (Greenway, 1967; Fuller, 2001). The severity of this impact of predators will be particularly costly for bird species with little genetic variation. If there are no further introductions of potential predators, there are no major risks for island faunas. However, mainland species with low levels of genetic variation are likely to be particularly vulnerable to

further population declines caused by predation mainly through the indirect effects of predation on disturbance and altered activity budgets for potential prey. Finally, knowledge about FID in extant populations with a threat status as, for example, reflected by presence in the Red List of threatened species implies that human activity including that by farmers, naturalists and joggers can be managed to minimize or reduce the effects of disturbance for the species in question.

In conclusion, we have demonstrated significant positive associations between a behavioural measure of risk-taking behaviour by birds and various measures of the degree of genetic variability. Higher levels of genetic variability were consistently associated with longer FID, and this association has implications for the management of threatened species, design of nature reserves with public access and captive breeding.

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Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1 Information on mean population size, total breeding distribution area (km²), body mass (g), band sharing coefficient, observed heterozygosity (H_o), and inbreeding coefficient for species of birds.

Appendix S2 The consensus tree for 52 bird species with band sharing coefficient data.

Appendix S3 The consensus tree for 111 bird species with H_o data.

Appendix S4 The consensus tree for 105 bird species with inbreeding coefficient data.

Appendix S5 References used to derive information on heterozygosity and inbreeding coefficients in birds.

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II Antipredator escape distances of common and threatened birds



Original Article

Antipredator escape distances of common and threatened birds

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Most animals keep a safe distance from humans and other potential predators, forcing animals to trade foraging and other critical behaviors against flight with potentially negative consequences for population trends if energy budgets are consistently negative. Animals can adapt to human proximity through habituation or microevolution, and island, domesticated and urbanized animals have all reduced their threshold of fear compared to controls. We tested whether a common cause of threat status is susceptibility to human proximity. We did so by estimating whether 48 pairs of closely related bird species differing in their threat status consistently had longer flight initiation distances (FID, the distance at which the individual takes flight from an approaching human) in the more threatened species. We estimated threat status by relying on existing categorization of threat status by the European Union. Threatened species had consistently longer FID than their closely related species in both parametric and nonparametric tests. Common species were indeed more often recorded during field work while recording FID than were threatened species, the difference being almost 2-fold. This result provides a link between antipredator behavior, human proximity, threat status, and abundance.

Key words: anthropogenic disturbance, flight initiation distance, susceptibility to human proximity, threatened species.

INTRODUCTION

Almost all environments around the world have been affected by humans negatively impacting numerous free-living species (Vitousek, Mooney, et al., 1997; Ceballos et al., 2015). Habitat loss and fragmentation (Andrén, 1994; Haddad et al., 2015), climate change (Houghton et al., 1990; Bellard et al., 2012), various pollutants (McNeely, 1992; Camargo and Alonso, 2006; Verhoeven et al., 2006; Gaston et al., 2013), human consumption (Maurer, 1996; Butchart et al., 2010), introduced species (Vitousek, D'antonio, et al., 1997; Early et al., 2016), and many other human-induced changes have modified the environment for living organisms, reducing the survival prospects of free-living species. Free-living populations may also suffer from anthropogenic disturbance due to the increase in the size of human populations resulting in competition for limiting resources including an insatiable appetite for exploration (nature adventures by humans/field exploration) (e.g., Arroyo and Razin, 2006; Stankowich, 2008). Because all animals acquire food and other limiting resources while keeping a safe distance from predators including humans, animals have to trade acquisition of food and other critical resources against safety (Ydenberg and Dill, 1986).

Animals can adjust to changing levels of disturbance through habituation or microevolutionary change. People have long known that animals on islands have lost or reduced their antipredator behavior as evidenced by decreased flight initiation distances (FID) (Cooper et al., 2014). Birds and mammals also lose their fear responses towards humans and their animals through domestication (e.g., Clutton-Brock, 1992; Broom and Fraser, 2015). As an adaptation to recent urban environments appearing during the last 10,000 years, urban birds became more tame as reflected by their relatively short FID and reductions in relative FID as predicted by the number of generations since urbanization (Møller, 2008c; Weston et al., 2012). Food provisioning especially in urban habitats may further reduce fear responses as compared to their ancestors in rural habitats (Robb et al., 2008; Møller et al., 2015). Because island populations of animals, domesticated animals and urban animals all have lost or reduced their fear of humans, we can infer that animal responses to humans can change rapidly (Samia et al., 2015). Thus, there is reason to believe that current populations of birds and other animals are caught in a transition phase from being more to being less easily disturbed by human activity.

FID can be considered an estimate of risk of real predation. Predation risk is likely to have a concave upward relationship with distance to potential predators, and it increases sharply at short distances (Cooper and Frederick, 2007). Species with relatively short FID run elevated risks of predation by sparrowhawks *Accipiter nisus*

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(Møller et al., 2008) and domestic cats *Felis catus* (Møller et al., 2010), and the risk of getting hit by vehicles (Møller et al., 2011). These relationships remain robust even after controlling for additional factors associated with risk of predation such as body mass and sexual dichromatism. Individuals known to have died from predation had significantly shorter FID than survivors in a population of barn swallows *Hirundo rustica* (Møller, 2014). Thus, longer FIDs are associated with lower predation risk and smaller levels of risk-taking.

Differences in antipredator escape distances within bird species can influence the choice of habitat across the entire range of species (Burger, 1981; Martin and Réale, 2008). The larger the diversity in FID among species the greater the dispersal distances and the larger the number of breeding habitats and total range size (Carrete and Tella, 2010; Møller and Garamszegi, 2012). This difference in terms of variation in FID may have important consequences for populations of free-living animals. Species with long FID on average had declining population trends across Europe (Møller, 2008b; Møller et al., 2014), FID and latitude interacted to generate complex spatial patterns of population trends linked to risk-taking behavior (Díaz et al., 2015).

Here, we test whether this recently evolved change in response to proximity of humans might influence the threat status of species; we used a pairwise comparative method that explicitly investigates to which extent closely related taxa consistently vary in their phenotype (Møller and Birkhead, 1992). Such paired comparisons of values of the dependent variable (FID of pairs of closely related species) should also differ in terms of character state of the independent variable. This comparative approach focuses on the tips of the phylogeny because only closely related taxa are investigated, and it exploits the fact that closely related species by definition share most phenotypic traits due to their common phylogenetic history. Thus, pairs of species differing in their threat status are unlikely to consistently differ in other respects because the majority of their evolutionary history is shared except for recent transitions, which are of greater concern for conservation. This argument even applies to unknown confounding factors that so far have not yet been identified making this a powerful tool for testing phylogenetic hypotheses (e.g., Sol et al., 2002; Svenning and Skov, 2004).

In this study, we compared FID in pairs of closely related species of birds differing in their threat status, but we also tested explicitly whether a measure of relative abundance differed between these 2 categories of species, as predicted by the difference in their threat status according to *Birds in Europe* (Burfield et al., 2004) and *European Red List of Birds* (BirdLife International, 2015). Antipredator behavior of animals as estimated from FID provides a consistent metric of the extent of tolerance to human proximity (Cooper and Blumstein, 2015). If FID at least partially reflected variation in adaptation of wild animals to human proximity, we predicted that mean FID of pairs of closely related species differing in threat status would be consistently longer in the group of species that is more threatened. In a conservation context, a link between antipredator behavior and threat status will help us understand the impact of anthropogenic disturbance on wild species, and it may eventually also help us reduce such effects.

METHODS

FID estimates

We estimated FID across Europe using a standardized process following Blumstein (2006) and Møller (2008b). In brief, we approached foraging or resting birds by walking at a normal speed and recording the distance at which the individual took flight or walked away as horizontal distance. The perching height was recorded if the individual was

positioned in the vegetation. FID was estimated as the hypotenuse of a right-angled triangle and the other 2 sides were horizontal distance and perching height, respectively. We collected FID information from all individuals encountered implying that the number of observations for each species provided information on their relative abundance. The data were collected during February–September 2006–2015 in an area of 100 km² in Orsay (48°42'N, 2°11'E), Ile-de-France, France, an area of 800 km² in Northern Jutland (57°12'N, 10°00'E), Denmark, and an area of 500 km² in Oslo (59° 54'N, 10° 45'E), Norway. Estimates of the length of FID were consistent across studies, countries, years, and seasons (Blumstein, 2006; Møller, 2008a, 2008c; Møller, 2015).

We also used FID information for a direct test of the hypothesis that threatened species should be less commonly encountered than nonthreatened species when collecting data on FID.

Threat status assessment

The threat status of the species was categorized according to either *Birds in Europe: Population estimates, trends and conservation status* (Burfield et al., 2004) or *European Red List of Birds* (BirdLife International, 2015). Each species was assigned to one of 5 categories of decreasing threat status (1, 2, 3, Non and Non^E). A species is categorized as SPEC1 if its status is classified as threatened, near threatened or data deficient under the IUCN Red List Criteria at the global level. Other species whose populations are small and nonmarginal, declining moderately, depleted following earlier declines, or highly localized, are listed as SPEC2 if more than 50% of their global breeding or wintering population or range occur in Europe. They are categorized as SPEC3 if they are not concentrated in Europe. Other species that have a favorable conservation status in Europe are categorized as Non-SPEC and are marked as Non-SPEC^E if they are concentrated in Europe. We chose *Birds in Europe* rather than IUCN Red List so that more species could be included in the analyses. The results based on the 2 sources could help us better understand the impact of anthropogenic disturbance on the status of most species, not just those classified as being extremely threatened. In addition, we included more possible pairs of species by using *European Red List of Birds* (BirdLife International, 2015) in addition to *Birds in Europe*. The threat status of all species in this list was classified into 6 categories Critically Endangered, Endangered, Vulnerable, Near Threatened, and Least Concern according to the IUCN Red List Categories and Criteria. Species receiving different categories were regarded as threatened and relatively less threatened if they were listed under the same categories in *Birds in Europe*.

Comparative analyses

Species belonging to the same genus were defined as close relatives and paired if they were assigned in the Red Lists to 2 different categories of threat status. We identified as many such pairs as possible and used these pairs for a phylogenetically controlled paired analysis (Møller and Birkhead, 1992). Preferably, such pairs of species should be chosen randomly to avoid any conscious or unconscious observer bias affecting the conclusions. When confronted with the case that more than one congener or more than one pair being available in a single genus, we first chose the most closely related common and threatened species according to a random sample of phylogenetic trees (Appendix A). If they were at the same level in the phylogeny, we chose possible species with the largest sample size for FID. Each species was included only once in the analyses.

We made such paired tests for FID and for the relative abundance of species as determined by the sample sizes for FID of the 2 categories of species. We used the natural logarithm of FID and

sample sizes in the analysis to avoid highly skewed distributions. We used R 3.3.1 (R Core Team, 2017) for the Wilcoxon matched pairs signed ranks test and one sample *t*-test.

RESULTS

We were able to identify a total of 48 pairs of bird species differing in threat status and compare their FID (Table 1; Appendix A). Relatively threatened species had longer FID than their closest relatives (mean_{threatened} = 29.608 ± 4.043 m; mean_{common} =

20.498 ± 2.528 m; sign test, *V* = 885, *P* = 0.002; one sample *t*-test, *t* = 2.605, *df* = 47, *P* = 0.012). The distribution of log-transformed mean FID for threatened species and their most closely related nonthreatened species is shown in Figure 1.

The difference still remained the same if we removed the rare species with less than 4 records: relatively threatened species had longer FID than their closest relatives (mean_{threatened} = 18.520 ± 3.097 m; mean_{common} = 12.947 ± 1.785 m; sign test, *V* = 242, *P* = 0.007; one sample *t*-test, *t* = 2.575, *df* = 23, *P* = 0.017). Following elimination of rare species there would be 24 pairs of species left.

Table 1

Mean FID of pairs of bird species, sample size (*n*), the identity of these pairs of species, their threat status, and the difference in their FID

Relatively threatened species	FID (m)	<i>n</i>	EU27	SPEC category	Relatively common species	FID (m)	<i>n</i>	EU27	SPEC category	Difference (FID)
<i>Tetrao tetrix</i>	24.3	6	LC	3	<i>Tetrao urogallus</i>	77.5	1	LC	Non	-53.17
<i>Buteo lagopus</i>	20.1	1	EN	Non	<i>Buteo buteo</i>	60.3	26	LC	Non	-40.22
<i>Mergus serrator</i>	15	2	VU	Non	<i>Mergus merganser</i>	37.5	2	LC	Non	-22.5
<i>Tringa erythropus</i>	23	3	NT	3	<i>Tringa nebularia</i>	36.2	5	LC	Non	-13.2
<i>Charadrius alexandrinus</i>	9.5	6	LC	3	<i>Charadrius hiaticula</i>	21.1	37	LC	Non ^E	-11.64
<i>Gallinago media</i>	15	1	VU	1	<i>Gallinago gallinago</i>	25.8	6	LC	3	-10.83
<i>Passer domesticus</i>	4.3	433	LC	3	<i>Passer hispaniolensis</i>	11.9	7	LC	Non	-7.61
<i>Anas acuta</i>	34.8	1	VU	3	<i>Anas crecca</i>	39.2	22	LC	Non	-4.48
<i>Sturnus vulgaris</i>	11	294	LC	3	<i>Sturnus unicolor</i>	14.3	6	LC	Non ^E	-3.31
<i>Phylloscopus bonelli</i>	5	3	LC	2	<i>Phylloscopus trochilus</i>	7.3	156	LC	Non	-2.33
<i>Emberiza cia</i>	9.4	4	LC	3	<i>Emberiza citrinella</i>	10.3	162	LC	Non ^E	-0.89
<i>Regulus regulus</i>	4.3	56	NT	Non ^E	<i>Regulus ignicapilla</i>	4.8	12	LC	Non ^E	-0.53
<i>Parus montanus</i>	5.6	7	VU	Non	<i>Parus caeruleus</i>	5.4	262	LC	Non ^E	0.19
<i>Turdus pilaris</i>	10.1	131	VU	Non ^E	<i>Turdus philomelos</i>	9.8	157	LC	Non ^E	0.29
<i>Parus cristatus</i>	6.2	34	LC	2	<i>Parus ater</i>	5.8	13	LC	Non	0.37
<i>Parus palustris</i>	6.3	40	LC	3	<i>Parus major</i>	5.9	450	LC	Non	0.48
<i>Aythya ferina</i>	12	1	VU	2	<i>Aythya fuligula</i>	11	37	LC	3	1
<i>Lanius senator</i>	11	6	LC	2	<i>Lanius collurio</i>	10	33	LC	3	1.05
<i>Sylvia undata</i>	10.2	4	NT	2	<i>Sylvia communis</i>	8.6	200	LC	Non ^E	1.61
<i>Turdus iliacus</i>	10.7	39	VU	Non ^E	<i>Turdus merula</i>	8.6	981	LC	Non ^E	2.14
<i>Carduelis flavirostris</i>	8	2	VU	Non	<i>Carduelis spinus</i>	4.8	13	LC	Non ^E	3.16
<i>Hirundo rustica</i>	11.5	147	LC	3	<i>Hirundo daurica</i>	8.1	2	LC	Non	3.37
<i>Carduelis cannabina</i>	10.7	109	LC	2	<i>Carduelis carduelis</i>	7.2	51	LC	Non	3.49
<i>Phoenicurus phoenicurus</i>	12.8	27	LC	2	<i>Phoenicurus ochruros</i>	8.6	38	LC	Non	4.15
<i>Anthus campestris</i>	18.2	2	LC	3	<i>Anthus trivialis</i>	12.4	60	LC	Non	5.84
<i>Miliaria calandra</i>	15.9	111	LC	2	<i>Emberiza schoeniclus</i>	9.7	104	LC	Non	6.18
<i>Larus argentatus</i>	40.1	80	VU	Non ^E	<i>Larus fuscus</i>	33.3	206	LC	Non ^E	6.82
<i>Picus viridis</i>	20.9	54	LC	2	<i>Picus canus</i>	14	3	LC	3	6.9
<i>Anthus pratensis</i>	11.2	146	VU	Non	<i>Anthus spinoletta</i>	4.2	24	LC	Non	7.07
<i>Tringa totanus</i>	27.8	19	VU	2	<i>Tringa glareola</i>	20.3	3	LC	3	7.46
<i>Sylvia hortensis</i>	15	1	LC	3	<i>Sylvia curruca</i>	6.7	59	LC	Non	8.29
<i>Ardea purpurea</i>	50	1	LC	3	<i>Ardea cinerea</i>	39.2	52	LC	Non	10.77
<i>Calidris canutus</i>	26	1	LC	3	<i>Calidris alba</i>	15.1	68	LC	Non	10.91
<i>Branta bernicla</i>	23.5	6	LC	3	<i>Branta leucopsis</i>	12.6	4	LC	Non ^E	10.95
<i>Falco naumanni</i>	44.3	5	LC	1	<i>Falco tinnunculus</i>	32.6	10	LC	3	11.62
<i>Oenanthe leucura</i>	30.4	4	VU	3	<i>Oenanthe oenanthe</i>	17.8	29	LC	3	12.58
<i>Limosa limosa</i>	46.5	1	EN	2	<i>Limosa lapponica</i>	33.3	5	LC	Non	13.25
<i>Anas clypeata</i>	28	1	LC	3	<i>Anas platyrhynchos</i>	9.9	339	LC	Non	18.06
<i>Somateria mollissima</i>	51.3	4	EN	Non ^E	<i>Somateria spectabilis</i>	33	12	NE	Non	18.25
<i>Numenius arquata</i>	57.6	10	VU	2	<i>Numenius phaeopus</i>	37.7	2	LC	Non	19.9
<i>Streptopelia turtur</i>	31	7	NT	3	<i>Streptopelia decaocto</i>	7.5	110	LC	Non	23.51
<i>Gavia stellata</i>	110	3	LC	3	<i>Gavia immer</i>	76.8	1	VU	Non	33.25
<i>Larus canus</i>	54	56	LC	2	<i>Larus ridibundus</i>	14	91	LC	Non ^E	40.07
<i>Anas strepera</i>	55	1	LC	3	<i>Anas penelope</i>	9.5	3	VU	Non	45.5
<i>Cygnus columbianus</i>	78	1	EN	3	<i>Cygnus cygnus</i>	21.7	10	LC	Non ^E	56.3
<i>Podiceps auritus</i>	85	1	VU	3	<i>Podiceps nigricollis</i>	22.6	5	LC	Non	62.4
<i>Fulica cristata</i>	91	2	EN	3	<i>Fulica atra</i>	20.2	19	LC	Non	70.79
<i>Pyrhocorax pyrrhocorax</i>	120	2	LC	3	<i>Pyrhocorax graculus</i>	40	6	LC	Non	80

See Material and Methods for further information. The pairs of species are ordered with respect to the difference in their FID. EN, Endangered; LC, Least Concern; NT, Near Threatened; VU, Vulnerable.

Common species were indeed more often more abundant as suggested by the numbers recorded during field work while recording FID than were threatened species ($\text{mean}_{\text{threatened}} = 2.017 \pm 0.266$ m; $\text{mean}_{\text{common}} = 3.087 \pm 0.248$ m; sign test, $V = 295.5$, $P = 0.0046$; one sample t -test, $t = -3.09$, $df = 47$, $P = 0.0034$), the difference being almost 2-fold.

DISCUSSION

Observations of FID were consistent with the prediction that relatively threatened species had consistently longer FID than closely related species of lower threat status. That was the case in both parametric and nonparametric tests. We also found evidence of nonthreatened species being more abundant than threatened species, as evidenced by the larger number of observations of FID in the former species. These findings are consistent with the hypothesis that threat status of birds is linked to their susceptibility to human proximity, with potential consequences for conservation.

Many potentially confounding factors may contribute to differences in FID between threatened and nonthreatened species, and these factors may include body size (larger species are generally more threatened than small species (Bennett and Owens, 2002)

and larger species have longer FID than smaller species (Møller, 2008b), population size (species with very small populations are generally more threatened for various reasons, partially known as Allee effects (Courchamp et al., 1999)) and range size (species with restricted ranges being more threatened (Purvis et al., 2000; Cardillo et al., 2004)). However, we assume that this alternative explanation is unlikely given that closely related species by definition are similar in terms of most phenotypic variables. For instance, we have tested for differences in body mass for pairs of species differing in conservation status, using a similar analysis, but we did not find a significant difference (sign test, $V = 561$, $P = 0.447$; one sample t -test, $t = -1.411$, $df = 47$, $P = 0.165$). Thus, our results for FID and relative abundance might provide underlying mechanisms for how anthropogenic disturbance contributed to negative population trends (Díaz et al., 2015; Møller, 2008b) and eventually extinction of species.

Species of birds included in the present study differed in sample size, as do all other characteristics of species. Hence, it is unsurprising that sample size has a strong impact on statistical tests as shown consistently in a recent review (Garamszegi and Møller, 2010). Previous studies have shown that there is a strong positive correlation between sample size for FID for different species of birds and

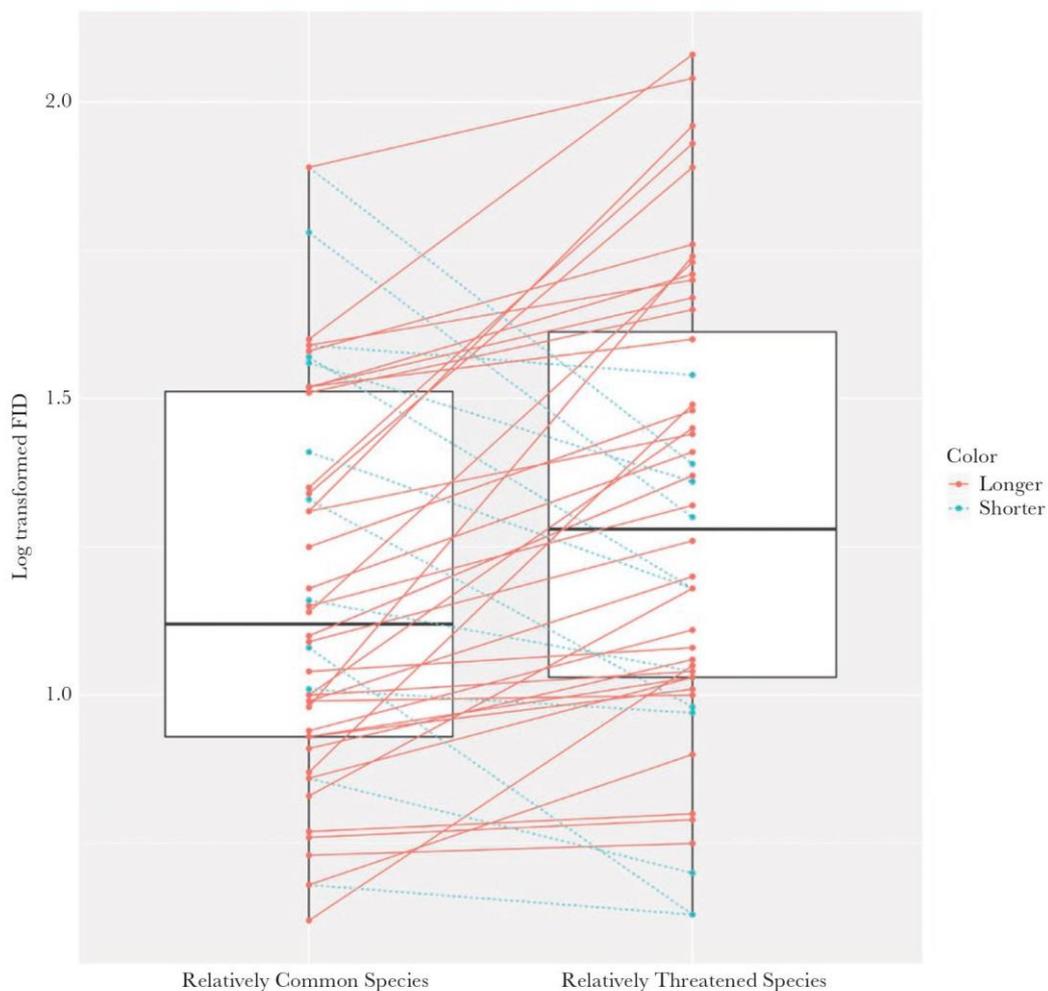


Figure 1

Among 48 pairs of species of birds, 36 were threatened species that had longer FID (m) than their nonthreatened close relatives. Each data point represents one species and all pairs are connected with lines. The colors and line types represent different trends in FID for pairs of species. All species are reported in Table 1 and the phylogeny is reported in Appendix A.

their abundance (Møller et al., 2006; Møller et al., unpublished data). Thus, rare species have fewer observations of FID. In general, there is a strong positive correlation between local and global abundance of animals documented by Brown (1984) and Brown and Lomolino (1998). Therefore, locally rare species are also globally rare. This implies that rare species have few observations of FID, and that exclusion of rare species (using an arbitrary sampling effort of at least 4 observations) will result in rare species as well as uncommon species being excluded from the data set.

Species particularly susceptible to human proximity may be unable to coexist with humans for several reasons. Such species may have to spend more time and energy escaping from potential threats than less susceptible species. Foraging behaviour and related parental care during the breeding season may be affected by human disturbance (Burger, 1991; Verhulst et al., 2001). Human activities alter habitat selection of birds (Fernández-Juricic, 2002; Meager et al., 2012), and antipredator behavior towards human proximity may constrain both spatial and temporal use of suitable habitat (Blumstein et al., 2005). Birds that differentially colonize urban areas are those with short mean FID and large variance in FID in their ancestral rural populations (Møller, 2010). When raptors always have a longer FID than their prey, urban areas become refuges for prey species that are relatively unaffected by human proximity (Møller, 2012). Species with relatively long FID for their body size are unlikely to adjust to anthropogenic disturbance when initially colonizing urban habitats.

The threat status of species may become increasingly critical if the FID of populations or species does not change sufficiently (Runyan and Blumstein, 2004; Carrete and Tella, 2010). The reasons for such a lack of response to increasing human disturbance may be caused by slow change due to microevolution rather than the more rapid habituation as individuals are highly consistent and heritable in the fear responses to humans (Carrete and Tella, 2013; Carrete et al., 2016). When populations are intolerant to human proximity, this may result in the differential elimination of species susceptible to human proximity. Species characterized by large variances in FID would have a higher probability of survival because at least some individuals will be able to cope with high or low levels of human disturbance (Møller, 2010; Blumstein, 2014). Even though there is the potential for long-term habituation to stimuli (Møller, 2008c; Blumstein, 2016), and life history may promote the evolution of long FIDs in some taxa (Blumstein, 2006), increased anthropogenic disturbance may still result in loss of species (Fernández-Juricic, 2002).

The findings reported here suggest that FID is related to conservation status. Admittedly, historical observations have shown that many insular species such as the solitaires *Pezophaps solitaria* and *Threskiornis solitaries*, the dodo *Raphus cucullatus* and many others had exceedingly short flight distances for their large body size, and they all went extinct rapidly when the first humans arrived (Steadman, 1995). A loss of fearfulness and antipredator responses due to human presence may increase prey vulnerability to predators (Geffroy et al., 2015). In fact, our findings indicated that the impact of nonfatal anthropogenic disturbance on free-living populations may become increasingly crucial as a part of human impacts during the last few decades. Relatively long FID among individuals belonging to a given species may be the cause of their vulnerability, which may turn such species into threatened ones due to anthropogenic impact (e.g., Thuiller et al., 2011). Diverse interactive factors at various levels are likely to modulate the impact of humans

on wildlife (Tablado and Jenni, 2015). The link between FID and threat status may help us better understand human impacts on wildlife.

In conclusion, we have shown that bird species with a threat status of greater concern consistently had longer FID compared to closely related species that were not or less threatened. We assumed that threat status categories reliably reflected relative abundance of different species, and our samples of FID did indeed provide support consistent with this assumption because more threatened species had fewer observations of FID than less threatened species.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by (Jiang and Møller, 2017).

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APPENDIX A. PHYLOGENETIC TREE

Appendix A. The phylogenetic tree for paired comparative analyses of FID in bird species differing in their threat status.

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III Evolutionary distinctiveness covaries with anti-predator behavior in bird communities

Evolutionary distinctiveness covaries with anti-predator behavior in bird communities

Evolutionary distinctiveness (ED) reflects the phylogenetic isolation of taxa with high values characterizing species with unique phenotypes that deviate the most from other taxa. Testing for the correlation between ED and behavioral traits under strong selection may help us understand the evolution of ED values. Anti-predator behavior reflecting the interaction between prey and predator is such a factor. We examined the relationship between ED and flight initiation distance (FID, the distance at which an animal takes flight when approached by a human), which signifies an important component of the anti-predator strategy of individuals belonging to any species. Overall, ED was positively related to FID, implying that species that were particularly evolutionarily distinct were also the species that took the smallest risks when encountering predators, and such species were less susceptible to predation. One potentially confounding factor was body mass, which was negatively related to ED and positively related to FID. The migratory status of species was only weakly correlated with ED in a linear model, although we did not find significant relationships between ED and the extent of breeding range or migratory behaviour. This is the first attempt to relate current anti-predator behavior to evolutionary distinctiveness. The results contribute to establishing a link between ED and life-history traits, helping us to understand the evolution of ED and hence allowing for better protection of such species.

Keywords: migratory status, phylogenetic linear regression, waterbird

Introduction

Planet earth is in the midst of an ongoing extinction spiral with extensive loss of species and their associated functions. Some species have specific evolutionary, ecological and morphological traits (Pavoine *et al.* 2005, Redding *et al.* 2010) that result in their extinction causing greater loss than species with common phenotypes. A quantitative measure of genetic or evolutionary uniqueness is evolutionary distinctiveness (ED), based on branch lengths of species and the number of closely related taxa (Isaac *et al.* 2007). ED is expected to capture unique genomes and functions of species and hence reflect an important component of biodiversity (Warren *et al.* 2008, Redding *et al.* 2010). ED values of indigenous species constitute phylogenetic diversity of a local community (Vane-Wright *et al.* 1991). This attribute predicts the function of local ecological assemblages in plant communities (Cadotte *et al.* 2012) and is regarded as an additional component of biodiversity with important significance for conservation (Veron *et al.* 2017).

Among 9993 bird species on earth, ED is distributed very unevenly (Redding and Mooers 2006). Of all bird species, the top 10% most evolutionarily distinct species represents approximately one-third of total phylogenetic diversity (Jetz *et al.* 2014; Fig. 1). The most evolutionary distinct birds include both threatened and isolated species such as giant ibis *Thaumatibis gigantea* and widely distributed common species such as osprey *Pandion haliaetus*, which can be found in almost every environment on earth. The origin of species with high ED through natural selection and other evolutionary processes remains ambiguous. Still we are losing avian phylogenetic diversity in anthropogenically modified habitats (Morelli *et al.* 2016).

Species with high ED could be the result of speciation or extinction among relatives. Many studies have investigated the phylogenetic and geographic distribution of species and concentrated on species with top level ED (e.g. Cadotte and Jonathan Davies 2010, Jetz *et al.* 2014). For example, while mountains are thought to harbor stable local conditions and thus high persistence of species (Fjelds  *et al.* 2012), they show no correlation with high ED (Jetz *et al.* 2014) as in the case of isolated islands (Jetz *et al.* 2012). Still, isolated landmasses exhibit a cluster for the world's top 1,000 (i.e., top 10%) ED species (Jetz *et al.* 2014). Thus, species from different continents may have very different reasons for resistance to evolutionary distinctiveness. Resident species are known or thought to inhabit a given locality throughout the year while migratory birds have seasonal movements from their breeding area to the wintering area. Migrants suffer more potential selective pressures in type of variance habitats, predators, parasites and other species than residents, while residents experience relatively greater geographical isolation during differentiation of

populations (Cox 1985). The breeding range may also contribute to greater ED as species diversity among bird families was positively correlated with geographical range occupied by each family (Owens *et al.* 1999). A large geographical range increases diversification rates as a buffer from relatively localized environmental disturbances (Cardillo *et al.* 2003).

Most conservation concern is put on the world's most evolutionarily distinct species (e.g. Jetz *et al.* 2014, Veron *et al.* 2017), raising particular concerns for isolated landmasses including Australia and New Zealand. Simultaneously, the over-all phylogenetic distinctiveness in urban areas is decreasing across the world (Morelli *et al.* 2016, Sol *et al.* 2017). Uncovering relevant components of species with high ED scores would help us understand the causes, and this knowledge may have a key effect on protection of species at a global scale.

One possible commonality for high-ED species is anti-predator behavior. Predation imposes strong natural selection on most animal species, and anti-predator behavior affects the ability to avoid predation for prey (Caro 2005). High ED species may once have had close relatives that went extinct in the process and became the only species left in a given clade. Originality or possible irreplaceability of species in ecological niches and a unique role in ecosystems may result in only individuals with effective anti-predator behavior surviving or surviving disproportionately. Appropriate escape decisions should balance the costs from lost foraging or mating opportunities, and the benefits of escape from reduced predation risk (Cooper and Blumstein 2015). Such anti-predator behavior should affect the ability to avoid predation and effective anti-predator behavior should therefore contribute to high ED values of certain species.

Numerous anti-predator behavior metrics exist such as color resemblance, alarm calls, warning signals and escape behavior (Caro 2005), and the origin and the maintenance of this diversity begs an explanation. Unlike other anti-predator behavior with potential follow-up strategies in the case of failure, escape behavior is the last line of defense (Cooper and Blumstein 2015). It is of particular importance for survival. Flight initiation distance (FID), measured as the distance at which an animal flees when approached by a human (Blumstein 2003, Møller *et al.* 2008), is a reliable metric for monitoring escape behavior (Blumstein 2016). In studies of individually marked individuals, FID is highly repeatable (Carrete and Tella 2010, 2013) and heritable (Dall *et al.* 2004, Blumstein *et al.* 2010, Møller and Nielsen 2010, Bize *et al.* 2012) and should also be subject to strong selection (Abrams 2000).

Waterbirds have similar life-cycles and are ecologically homogeneous with respect to the use of habitats and avoidance of potential predators compared with other taxa (Lack 1974). They are more likely to share similar adaptive evolution in relatively similar aquatic

environments as reflected by adaptive convergence (Reznick and Ghalambor 2001) and speciation (Schluter 2001) are partially environmentally dependent. Aquatic environments show little variability in terms of habitat differences and the degree to which they early detect predators (Caro 2005). That is the case despite scientists only documenting small effect of open habitats (Blumstein 2006) and habitat complexity (Møller and Erritzøe 2010) on flightiness. Thus, waterbirds constitute a relatively uniform community of species.

The objective of this study was to investigate the association between evolutionary distinctiveness and anti-predator behavior. Because species with long FID have high survival rates (Møller and Garamszegi 2012), and because they are particularly able to escape predation (Møller *et al.* 2008), we would expect a positive relationship between ED and FID. We also included three potential confounding factors affecting this association: body mass because large-sized species are better able to escape predation (Møller and Garamszegi 2012), migratory status because migrants interact with relatively more variable local species and experience different environmental conditions, while different resident populations are more isolated (Cox 1985) and the size of the breeding range because high species diversity in a certain family is strongly positively associated with large geographical ranges (Owens *et al.* 1999), which represent morphological traits, life-style and geographical range, respectively. Accounting for these correlations is not only essential for explaining the relationship between life-history and evolution, but also critical for assigning a prospective conservation value in different species.

Material and Methods

Evolutionary distinctiveness

ED score for each species was calculated at each node between the tips and root for the species in different orders (Isaac *et al.* 2007), based on species' branch length and number of closely related taxa (Faith 1992). We used published ED scores (Jetz *et al.* 2014) for birds as this index is robust to taxonomic changes (Isaac *et al.* 2007) including the effect of phylogenetic uncertainties (Sol *et al.* 2017).

Recording flight initiation distance

FID data were collected in an area of 800 km² in Northern Jutland (57°12'N, 10°00'E), Denmark from 2006-2016 combined with additional data collected in Spain, France, Iceland,

Norway and Ukraine under a standard protocol following Blumstein (2006) and Møller (2008). FID was recorded by approaching foraging or resting birds by walking at a normal speed and recording the distance at which the individual took flight or walked away. Few individuals were resting above the ground level. In these cases, the perching height was recorded and FID was estimated as the Euclidian distance and the other two sides were horizontal distance and the perching height, respectively. All estimates were collected in rural habitats to avoid any potential inference between habitat dimension and FID (Møller 2012, Samia *et al.* 2017). Only water birds with similar habitat openness were considered because distance to refuge affects FID (Dill and Houtman 1989), and species may develop different strategies under various circumstances (Kappeler *et al.* 2013).

Additional data

Information on body mass (g) of species was extracted from Dunning (2007). A mean value was used if the body masses of males and females were provided separately. Information on the breeding area of migratory and resident species estimated as the global range of the breeding area (in km²) was collected from Birdlife International (2017). We also scored species as resident or migratory. When species had variable migratory status across its geographical range, we recorded migratory behavior dependent on the population actually studied. All information is provided in the Appendix A.

Comparative analyses

All analyses were made with R 3.4.0 (R Core Team 2017). We log₁₀-transformed body mass and breeding area to obtain variables that were normally distributed and log₁₀-transformed evolutionary distinctiveness to obtain normal distribution of the residuals, allowing the use of parametric statistics. Models were weighted by sample size (the number of individuals) to account for the fact that sample sizes differed among taxa, giving each datum a weight that reflects its degree of precision due to sampling effort (Sokal and Rohlf 1995) and avoiding any bias in sampling (Garamszegi *et al.* 2012). We avoided over-representation of taxa with large sample sizes by using the square-root transformed number of individuals as a weighting factor. FID increases consistently with body mass (Blumstein 2006, Fernández-Juricic *et al.* 2006, Møller 2008b, 2015; effect sizes range from 0.04 to 0.96 with a mean of 0.45). We calculated the residuals of a log-log linear regression of FID against body mass (linear regression weighted by sample size, $r^2 = 0.18$, $F_{1, 76} = 16.5$, $P = 0.0001$). We used

residuals as a measure of relative FID. Because the comparative analysis concerned interspecific variation of trait values and the potential correlations could be subject to evolutionary forces and due to common ancestor (Garamszegi 2014), we used both generalized linear model and phylogenetic generalized linear model using the libraries *ape* (Paradis *et al.* 2004) and *nlme* (Pinheiro *et al.* 2017). We extracted the phylogenetic relationship for 78 species from the phylogeny available on line (Jetz *et al.* 2012, 2014) and obtained consensus phylogenies from the downloaded 100 trees with Mesquite 3.31 (Maddison and Maddison 2017).

Results

A total of 48 migratory and 30 resident water birds were investigated. Evolutionary distinctiveness scores ranged from 1.18 (*Anas platyrhynchos*) to 49.48 (*Gavia stellata*) (Fig. 2) showing a pattern similar to that of birds in general. A generalized linear model showed that ED score was positively related to relative FID (Table 1, Fig. 3). Similarly, a phylogenetic generalized linear model showed that ED was negatively related to body mass (Table 1, Fig. 4). Migratory status was weakly negatively related to ED in the linear model, although the significance of this relationship disappeared in the phylogenetic model (Table 1, Fig. 5). We found no significant correlation between ED and breeding range in either model (Table 1). These results imply that species with large ED are also those that take smaller risks when confronted with potential predators.

Discussion

The main finding of this study was a positive association between evolutionary distinctiveness and flight initiation distance. This finding implies that an important component of biodiversity is related to anti-predator behavior, that ED has evolved in the context of predator-prey interactions, and that FID must have coevolved with ED across evolutionary time scales. This makes sense because coevolutionary interactions between predators and their prey have played a significant role in the evolution of clades of predators and prey (Vermeij 1987, Jablonski 2008, Rabosky 2013). This is the first study showing that the current anti-predator behavior is correlated with ED scores, which reflects evolutionary history. This result was robust to differences in sampling effort and the potentially confounding effects of body mass, migratory status, the extent breeding ranges and similarity among taxa due to common phylogenetic descent.

The positive relationship between ED and FID implies that “ancestral” species with a relatively long FID would have an effective anti-predator behavior when encountering a predator (Møller and Garamszegi 2012). However, this does not provide evidence that distinct species are predictably on their way to extinction as a result of their behavior and ecology (Erwin 1991). Species with high ED could have rare and derived characteristics, but their current characteristics do not make them less likely to contribute to the future ecological landscape (Redding *et al.* 2010). On the contrary, species with relatively long FID could have contributed to the formation of their high ED scores, as suggested by lower susceptibility to predation by different species of predators in prey species with long FID (Møller *et al.* 2008, 2016, Møller and Garamszegi 2012). In other words, FID is a major and reliable predictor of survival prospects.

The presence of predators may play an important role in maintaining efficient antipredator behavior (Blumstein 2002, Møller *et al.* 2016). Here we have shown that species with relatively high ED values had relatively long FID. As an example, species living on predator-free islands consistently show reduced FID compared to their mainland relatives (Cooper *et al.* 2014). Because of the absence of predators and the absence of anti-predator behavior on islands, human colonization and invasive alien species on islands have accounted for numerous extinctions, mainly among edemic island species (McNeely 1992, Veron *et al.* 2017). Thus, the absence of predators has made island communities vulnerable to predation. Therefore, islands with ‘tame’ species should be priorities for preserving evolutionary diversity (Lovette 2014) because of the potentially high evolutionary diversity on such isolated landmasses (Jetz *et al.* 2014, Tucker *et al.* 2017).

Body mass was significantly negatively related to ED score and positively related to FID (review in Møller 2015). Body mass has always shown mixed relationships with rates of speciation and extinction, which are probably context dependent (Jablonski 2008). Although species with larger body mass had evolutionary rates marginally slower than those with smaller mass (Nunn and Stanley 1998, Gillman *et al.* 2012), they are less abundant (Rossberg *et al.* 2008) and have smaller clutch sizes (Jetz *et al.* 2008). Relative abundance and encounter rate with individuals from other populations can influence the opportunity for behavioral isolation (Butlin *et al.* 2012) and affect the diversity of close relatives. Still, large-bodied birds tend to be more at risk from extinction than small-bodied species (Gaston and Blackburn 1995). Thus, the negative correlation between ED and body mass reflects the complex relationship between body mass and taxonomic diversity (Orme *et al.* 2002). Although relatively long FID for a given body mass indicates a lower risk of predation, it should not affect the relationship between body mass and ED across species. Large species tend to have long FID mostly to make up for their reduced escape abilities (Tobalske 2016).

Migratory birds have slightly larger ED values than resident birds although not significantly so in the phylogenetic regression. This result was unexpected because migrants are exposed to a greater variety of habitats, predators, parasites and other species than residents. Their interaction with local species and experience under different environmental conditions should contribute to small levels of ED. Nevertheless, geographical gaps could both prevent (Jetz *et al.* 2014) or promote speciation (Jetz *et al.* 2012). Seasonal migration under variable predation risks (Wilson 1991) could restrict migratory birds to specific environments throughout life (Bensch 1999), especially because migratory birds are highly integrated at various levels, e.g. morphological, sensory, physiological and behavioral (Vágási *et al.* 2016). While migratory species are significantly less likely to have a large range and colonize new breeding areas than resident species (Bensch 1999), bird species with the largest ranges are indeed residents (Tokeshi 1996), that have a greater probability of speciation (Gaston 1998) and probably small ED values. The correlation between ED and migration disappeared after controlling for the phylogenetic relationship, which could be explained by the fact that sedentary species are more likely to maintain their migratory behavior when speciating (Rolland *et al.* 2014), even though a strong phylogenetic component with regard to migratory adaptations is unlikely (Helbig 2003).

The results presented here are based on both migratory and resident water birds across Europe. The distribution of ED values of 78 water birds is similar with that of all bird species (Fig. 1 and 2). Thus the correlation between ED and antipredator behavior is general. Nevertheless, many top-ED species are isolated on other continents (Jetz *et al.* 2014) including many islands where predation risk is either absent or negligible (MacArthur and Wilson 1967) with leveraged food resources (Ebenman and Nilsson 1982). Resident species on islands have shown large differences in morphological and behavioral traits compared with mainland species (e.g. Blumstein 2002), which may result from differences in risk of predation (Lima 2009) and food abundance (Ebenman and Nilsson 1982). It would be interesting to investigate the relationship between ED and FID for such species.

Bird species with relatively high ED scores did not have a consistently large breeding range compared to species with low ED. This is consistent with a study for top-10% ED species by Jetz *et al.* (2014). Although habitat remnants and isolation have been cited as key factors supporting high endemism (Kier *et al.* 2009), and low-ED species are clearly not relict or have diverged recently (Jetz *et al.* 2012), there may be other important mechanisms for the evolution of species with high ED.

Although species with relatively long FID suffer less from predation (Møller *et al.* 2008), habitats affected by humans, especially urban habitats, favour species (Møller 2012) and

individuals (Carrete and Tella 2011) with relatively short FID. Thus species with high ED will be under strong selection in urban environments. This is consistent with the negative impact of urban environments on the evolutionary uniqueness of birds (Morelli *et al.* 2016). However, the rate of speciation decreased with clade age (Ricklefs 2006), which may increase ED. We should pay increased attention to the protection of high-ED species since such species with consistently long FID are more likely to be threatened than their close relatives (Jiang and Møller 2017).

In conclusion, we have demonstrated a significant positive relationship between ED and FID, even when controlling statistically for potentially confounding variables. This paper constitutes the first attempt to associate current behavior with evolutionary distinctiveness. The results contribute to our understanding of the link between ED and life-history, and they may help us understand the evolution of species with high ED.

Supplementary Material

Further details on the data sets used (Appendix A) are available on-line.

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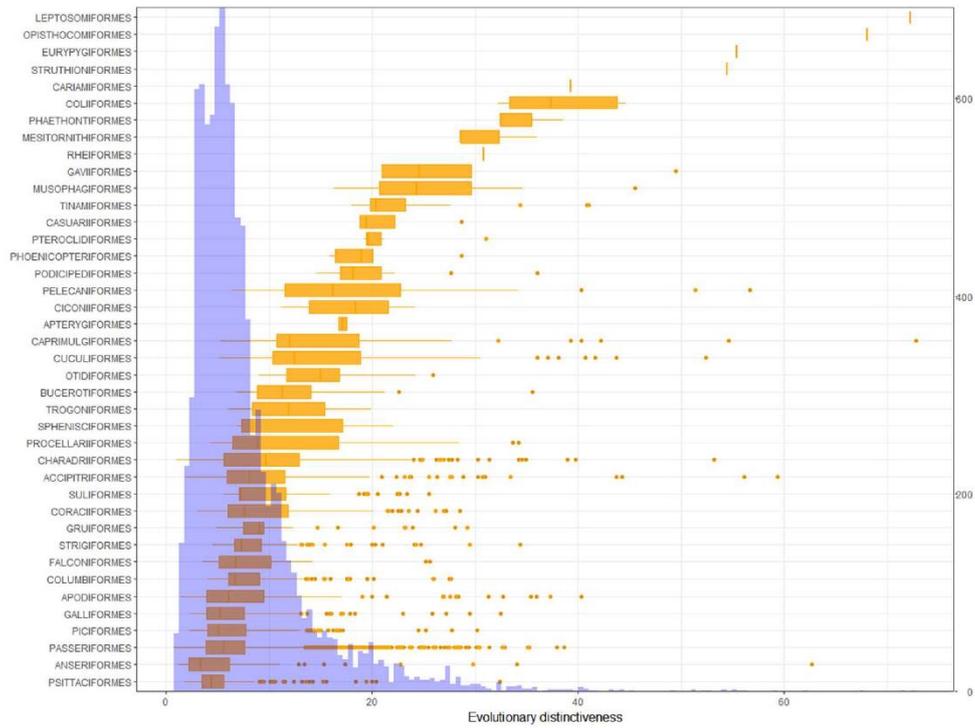


Fig. 1 Histogram of the distribution of evolutionary distinctiveness (ED) for all 9,993 bird species. The right y-axis is the number of species. The boxplots show variation (medians, quartiles, 5- and 95-percentiles and outliers) for each order listed on the left y-axis. Modified from Jetz et al. (2014).

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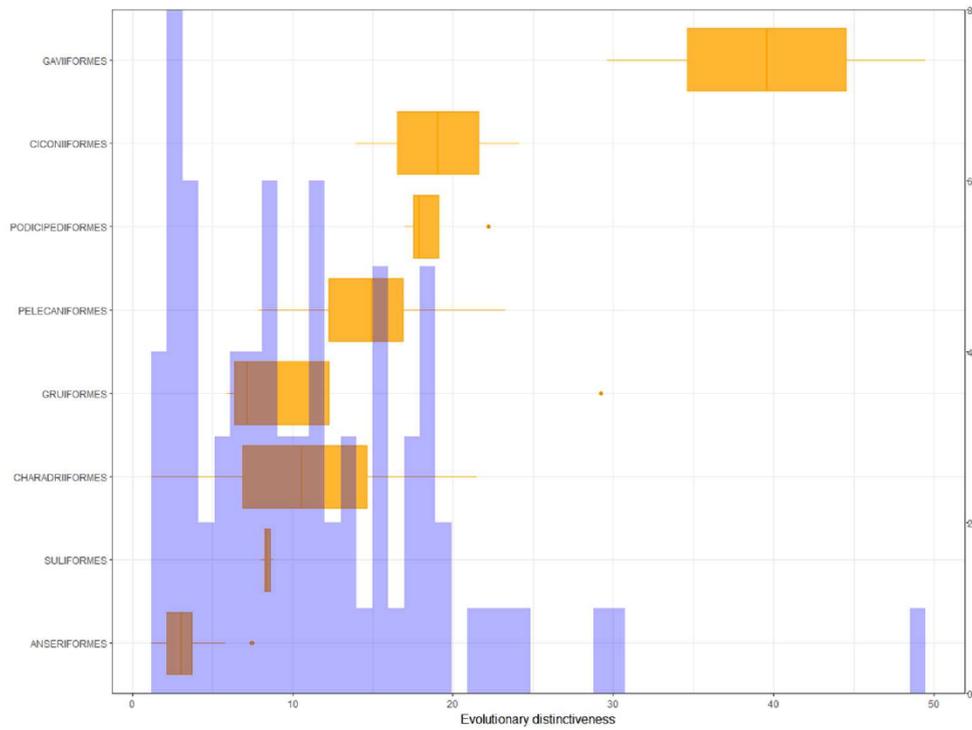


Fig. 2 Histogram of the distribution of evolutionary distinctiveness (ED) for 78 water birds included in the present study. The right y-axis is the number of species. The boxplots show the variation (medians, quartiles, 5- and 95-percentiles and outliers) for each order listed on the left y-axis.

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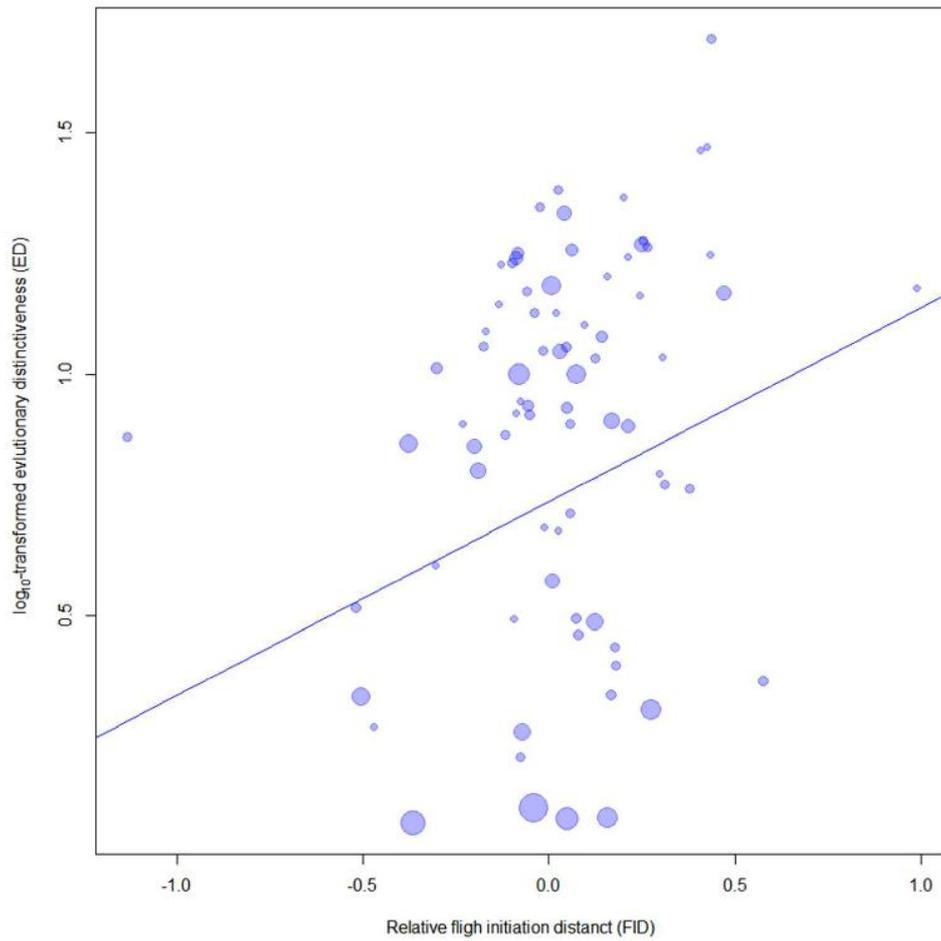


Fig. 3 Evolutionary distinctiveness (ED) increased with increasing relative flight initiation distance (FID (m)) across 78 species of European water birds. Each point represents one species. Symbol sizes are proportional to square-root transformed sample sizes. The line is the linear regression line.

238x238mm (96 x 96 DPI)

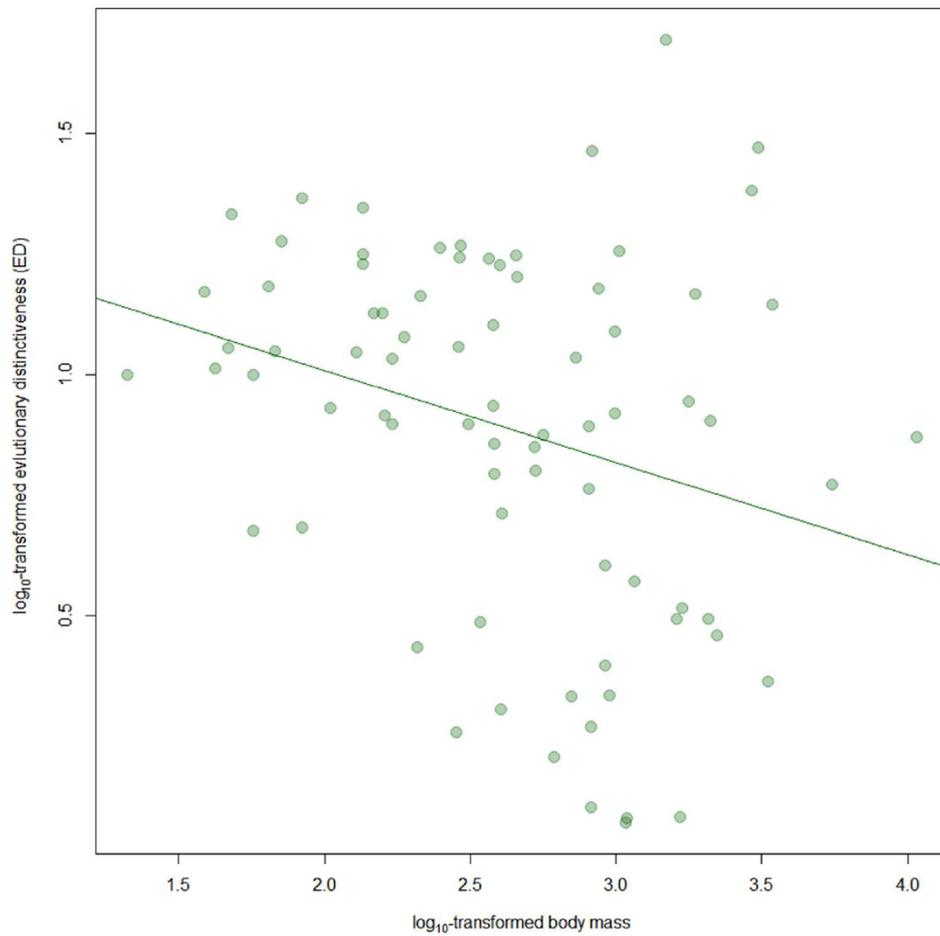


Fig. 4 Evolutionary distinctiveness (ED) decreased with increasing log₁₀-transformed body mass (g) across 78 species of European water birds. Each point represents one species. The line is the linear regression line.

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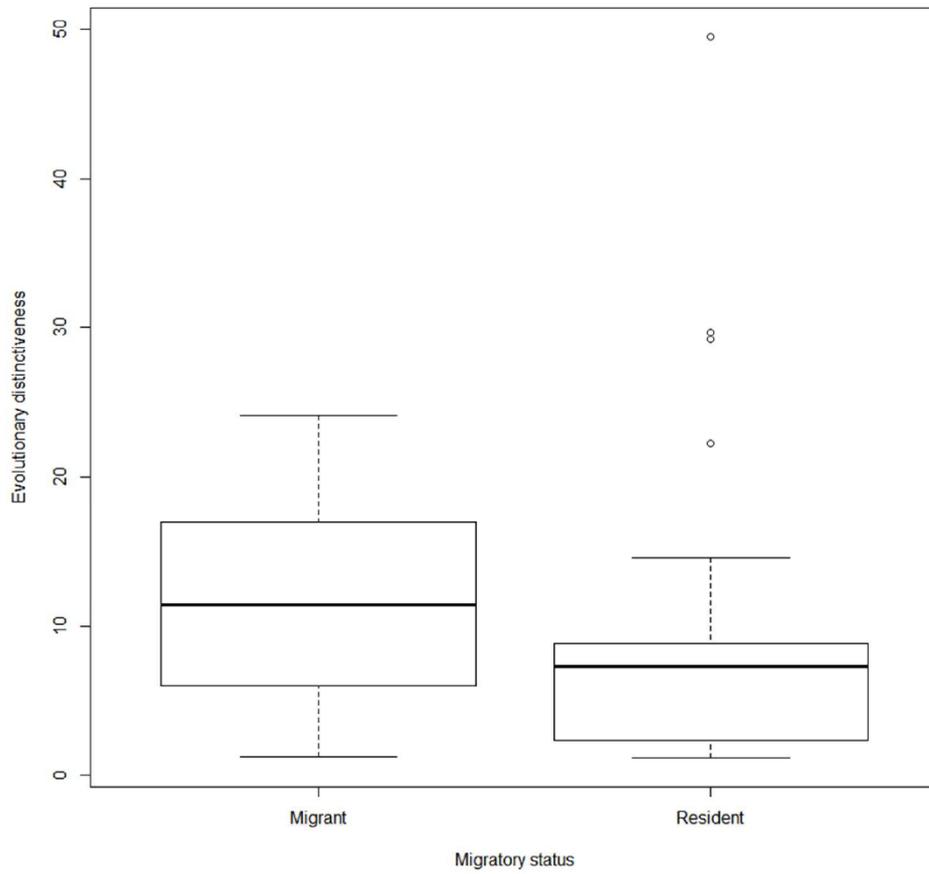


Fig. 5 Among 78 species of birds, 48 migratory species had relatively larger evolutionary distinctiveness ED scores than 30 resident species. Box plots show medians, quartiles and 5- and 95-percentiles.

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Table 1 Models of the relationship between \log_{10} -transformed evolutionary distinctiveness (ED) and relative FID, \log_{10} -transformed body mass (g) and \log_{10} -transformed breeding range (km^2), respectively, weighted by sample size for species of birds. Relative FID is the residual of linear regression of \log_{10} -transformed flight initiation distance (FID, m) on \log_{10} -transformed body mass (g) weighted by sample size for each species. (A) The linear model had the statistics $\text{AIC} = 95.038$, $F_{4, 73} = 8.916$, $r^2 = 0.328$, $P < 0.001$. (B) The phylogenetic generalized linear model had the statistics $\text{AIC} = 38.180$, $F_{4, 73} = 3.074$, $r^2 = 0.112$, $P < 0.001$.

Term	Estimate	Standard Error	d.f.	<i>F</i>	<i>P</i>
(A)					
(Intercept)	0.080	0.759	78 (total)		
Relative FID	0.364	0.171	1	5.739	0.019
\log_{10} -transformed body mass	-0.282	0.083	1	21.193	< 0.001
\log_{10} -transformed range	0.198	0.099	1	2.191	0.143
Migratory status	-0.247	0.096	1	6.542	0.013
(B)					
(Intercept)	0.790	0.325	78 (total)		
Relative FID	0.211	3.136	1	13.398	0.001
\log_{10} -transformed body mass	-0.297	1.517	1	22.597	< 0.001
\log_{10} -transformed range	0.042	1.813	1	2.327	0.132
Migratory status	0.041	1.769	1	2.497	0.118

IV Flight initiation distance is correlated with oxidative stress in birds

Flight initiation distance is correlated with oxidative stress in birds

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Abstract

Oxidative stress is closely related to life-history and ecological traits. All animals flee from potential predators including humans thereby incurring metabolic costs. Oxidative stress arises from the production of free radicals and thereby plays a core role in the evolution of optimal investment trade-offs between reproduction and survival. Oxidative stress is the outcome of metabolism and it is produced by a number of stressful events. Predators constitute an important component of stress in the daily life of prey. Frequent flights from potential predators are energetically expensive and may reach more than 20 times basal metabolic rate, thereby contributing to the production of free radicals and hence oxidative stress. The distance between animals and potential predators when a prey individual takes flight is defined as the flight initiation distance (FID). A relatively short FID indicates comparatively frequent flights. Here we show for the first time that free-living birds with relatively short FID for their body mass experienced more peroxidative damage to lipids (malondialdehyde, MDA), and that they had an up-regulated component of antioxidant capacity (uric acid, UA). These relationships were mediated through relationships with body mass. Brain size was positively related to the level of UA but also to behavioral anti-predator responses. Therefore, we can conclude that anti-predator behavioral strategies of birds have at least partially evolved as a means of managing oxidative stress.

Keywords: antioxidant defenses; birds; non-lethal effect; oxidative damage; predation.

Introduction

Predation constitutes a powerful cause of selection. Direct lethal effects of predation are important, but even more so are indirect non-lethal effects (Caro, 2005). The latter results from disturbance by predators and hence can affect habitat choice, sociality, diet and physiology (Lima, 1998; Cresswell, 2008; Cooper & Blumstein, 2015). Hence indirect effects of predation are often much more important than direct lethal effects (e.g. Creel & Christianson, 2008).

Stressful events constitute important ecological and evolutionary forces modulating adaptive responses in natural populations (Buchanan, 2000), and different species have adopted various behavioral strategies to cope with such stress (Korte *et al.*, 2005). As a case in point, oxidative stress has been found to be closely related to life-history and ecological traits (Costantini, 2008; Selman *et al.*, 2012). Oxidative stress has attracted much attention recently because it plays a core role in the evolution of optimal investment patterns between reproduction and survival and other fitness components (Costantini *et al.*, 2010; Speakman *et al.*, 2015).

Numerous processes generate changes in oxidative balance. Antioxidant defenses are decreased by high investment in current reproduction which is paid off in terms of reduced future reproduction and increased mortality (Alonso-Alvarez *et al.*, 2004, 2006). For example, oxidative stress may be a physiological cost associated with immune response based on a meta-analysis across 16 studies of 10 bird species (Costantini & Møller, 2009). Managing oxidative stress is a prominent determinant of life histories, and oxidative stress itself is likely a mediator of life history trade-offs (Monaghan *et al.*, 2009).

Strenuous physical activity can increase oxidative stress (Herrero & Barja, 1997), and many studies of oxidative stress and physical activity have focused on migratory birds. Although long flights may not seem to influence immune responses for long-distance migrant bird (Møller *et al.*, 2004; Hasselquist *et al.*, 2007; Møller & Szép, 2011), they cause oxidative stress (Costantini *et al.*, 2008), and birds up-regulate their antioxidant capacity following stress during endurance flight (Jenni-Eiermann *et al.*, 2014). Thus, physical activity is an important potential cause of oxidative stress. Surprisingly, no study has examined how oxidative stress is related to anti-predator behavior, a central organizing feature in life history and the trade-off between acquisition of energy and predator avoidance (Houston *et al.*, 1993).

Individuals optimize the costs of the distance to potential predators balancing these against the costs of flight (Ydenberg & Dill, 1986). Flight initiation distance (FID) is the distance at which an individual takes flight/walks from a potential predator, and hence it reflects this

important life history compromise. For example, the risk of predation by sparrowhawks *Accipiter nisus* increases with decreasing FID across species (Møller *et al.*, 2008). Likewise, individual barn swallows *Hirundo rustica* with short FID run higher risks of falling prey to a predator than conspecifics with long FID (Møller, 2014). Thus species with relatively long FID for their body size enjoy a leveraged safety. However, they are also more easily disturbed by potential predators compared to species with relatively short FID. Short and brief aerial flapping flight is metabolically costly, and it may reach 23 times basal metabolic rate in robins *Erithacus rubecula* (Tatner & Bryant, 1986), which would inevitably increase oxidative stress.

Brains play a key role in predator-prey interactions (Møller, 2015; Samia *et al.*, 2015) as animals use cognitive abilities for assessing the behavior of predators (Tyrrell & Fernández-Juricic, 2015). A range of cognitive benefits has been associated with relatively large brain size (Sol, 2009). Møller and Erritzøe (2014) found that birds with relatively large brains for their body size avoid the rush when a predator approached. Thus they make the least expensive escape decision after assessment and monitoring of the threat of predation thereby reducing the energy costs of flight (Samia & Blumstein, 2015). However, brain sizes may constitute a trade-off between the costs of brain tissue, for example in terms of antioxidants, and the benefits of increased cognitive abilities, given that neural tissue is energetically expensive (Isler & van Schaik, 2006) and demands large amounts of antioxidants (Romero *et al.*, 1991; Galván & Møller, 2011). Individuals may adapt to the costly development of a large brain. Compared with small-brained birds, birds with relatively large brains for their body size may evolve improved resistance to oxidative stress, as they suffer less oxidative damage to lipids and exhibit higher total non-enzymatic antioxidant capacity (Vágási *et al.*, 2016).

The objectives of this study were to test the relationship between FID and oxidative stress under field conditions and to determine how brain size and body mass mediate the relationship between these two factors. A marker of peroxidative damage to lipids (malondialdehyde, MDA) and two markers of antioxidant capacity, total antioxidant status (TAS) and plasma uric acid (UA), were used, relying on a unique and valuable public database (Vágási *et al.*, 2016). As frequent flight take-offs result in high energy consumption (Tatner & Bryant, 1986), and high levels of oxidative stress, we predicted that relatively long FID predisposed certain bird species to elevated oxidative damage (a high MDA level) and/or an elevated antioxidant level (TAS/UA level). Furthermore, we predicted that a relatively large brain reduced oxidative stress to the brain due to both less energy demanding behavior (relatively short FID; Møller & Erritzøe, 2014) and an efficient defensive machinery against oxidative stress (relatively high TAS/UA level (Vágási *et al.*, 2016)).

Materials and methods

Flight initiation distances

FID data were mainly collected by Anders Pape Møller in an area of 100 km² in Orsay (48°42'N, 2°11'E), France and an area of 800 km² in Northern Jutland (57°12'N, 10°00'E), Denmark during February-September 2006-2016, combined with fewer data from Spain, Norway, Finland, Ukraine and Iceland using a standard protocol (Blumstein, 2006; Møller, 2012). In brief, we approached an individual bird from a distance of 30 m or more and recorded the horizontal distance when the focal bird was moving away either by foot or flight in response to the approaching human. We also recorded the perching height of the bird above the ground. FID was estimated as the Pythagorean distance of the horizontal distance and perching height. A total of 6339 estimates of FID from 72 species with information on redox state were selected from all the records collected.

Redox state markers

Information on three oxidative stress markers (malondialdehyde, MDA, total antioxidant status, TAS and uric acid, UA) was obtained from a previously assembled data set (Vágási *et al.*, 2016). MDA is a widely used marker of oxidative stress which results from lipid peroxidation of polyunsaturated fatty acids (Del Rio *et al.*, 2005). TAS describes the non-enzymatic antioxidant defense on the dynamic equilibrium between pro-oxidants and antioxidants in the plasma compartment (Ghiselli *et al.*, 2000). UA is a potent antioxidant for birds (Tsahar *et al.*, 2006) and has been found to demonstrate substantial interspecific differences in constitutive antioxidant capacity across 92 bird species (Cohen *et al.*, 2007). Despite concerns about intraspecific variation, this variation can be neglected in comparisons among species as the redox state markers were found to be species-specific both for this dataset (Vágási *et al.*, 2016) and previous studies (Cohen *et al.*, 2008).

Brain mass and body mass

Information on brain mass came from an extensive database on birds from Denmark recorded by J. Errizøe in a consistent way during 1960-2013 (Møller & Errizøe, 2014). Previous analyses have shown a high degree of consistency between mean estimates based on this database (Garamszegi *et al.*, 2002) and other databases (Samia *et al.*, 2015). Brain mass was strongly positively correlated with body mass (log₁₀-transformed brain size strongly correlated with log₁₀-transformed body mass, $r^2 = 0.85$, $P < 0.01$). However, multiple regression is the best approach to control for undesirable confounding effects

among correlated covariates. Consequently, we used body mass and brain mass in the same model to control for these confounding effects. Information on body mass was extracted from Dunning (2007). If both male and female body mass were provided, we used the average value. The entire data set is reported in supplementary information Appendix S1.

Comparative analyses

To model the relationship between FID and oxidative stress, we used phylogenetic generalized least square (PGLS) regression models (Garamszegi, 2014). PGLS models avoid the problem of statistical dependence in comparative analyses due to phylogenetic relatedness between species. PGLS models were implemented in packages *ape* (Paradis *et al.*, 2004) and *nlme* (Pinheiro *et al.*, 2016) and the function *gls* with correlation equaling the consensus tree. We \log_{10} -transformed FID, brain size and body mass to obtain variables that follow normal distributions allowing for the use of parametric statistics. We extracted the phylogenetic relationship for all 72 species from a phylogeny available online (Jetz *et al.*, 2012) and obtained a consensus phylogeny from 1000 trees with Mesquite 3.31 (Maddison & Maddison, 2017). We separately analyzed MDA, TAS and UA in the phylogenetic analysis since the species were slightly different.

It is difficult to examine relationships between more than two traits, especially when any trait can contribute to another, or the other way around, and potential correlations can also result in indirect complex relationships between study variables. To test whether the covariances between FID and redox state markers were caused by their common association with body mass, we used phylogenetic path analysis. Path analysis is a powerful statistical method to resolve the complex natural systems in a single causal network and analyze the relative importance of alternative causal models (Shipley, 2000). Phylogenetic path analysis may help verify if the covariance could be a potential causal relationship as well as controlling for non-independence due to a common ancestor (Gonzalez-Voyer & von Hardenberg, 2014). The structure of the phylogenetic path analysis was designed based on previous knowledge of the variables and also on hypotheses to be tested. For instance, oxidative stress may impose an important physiological cost on intense physical activity (Costantini, 2008). Large-brained birds suffer less oxidative damage (Vágási *et al.*, 2016). Relatively large brain size is associated with better cognitive ability (Møller, 2015) and potentially affects anti-predator behavior (Samia *et al.*, 2015). The minimal set of conditional independencies for each path model was tested using PGLS models in the package *caper* (Orme *et al.*, 2013). Path models for the data were estimated via the C value. A significant C statistic indicates that the model is a poor fit to the data. To compare the different path models and identify the most likely causal scenarios, we used the C-statistic

information criterion (CICc; similar to the Akaike information criterion). Standardized path coefficients were calculated for all relationships in the best model using PGLS analyses on standardized variables (mean of 0 and SD of 1). Our final path analyses were made up of three PGLS models. All statistical analyses were carried out in R 3.4.2 (R Core Team, 2017).

Results

Mean FID ranged from 3.91 to 75.76 m with a mean of means of 13.49 m (SE = 1.26), N = 82 species (6506 individuals). The level of MDA ranged from 2.51 to 7.27 $\mu\text{g/mL}$ plasma with a mean value of 4.95 (SE = 0.14), N = 72 species. The level of TAS ranged from 0.44 to 3.99 mM Trolox with a mean value of 2.28 (SE = 0.07), N = 72 species. The level of UA ranged from 6.74 to 37.35 mg/dL plasma with a mean value of 20.66 (SE = 0.66), N = 71 species. The entire data set is reported in Electronic Supplementary Material Appendix S1.

The levels of MDA and UA increased with increasing FID and brain size in a phylogenetic generalized least square analysis across 72 and 71 species of birds respectively (Figs. 1-2, detailed model in Table 1A and 1C). In the multivariate model, we did not find a significant relationship between TAS and FID/brain size (Table 1B). These results were robust to potentially confounding variables, body mass, sample size and similarity due to common phylogenetic descent.

The best phylogenetic path models suggested that body mass had a significant direct effect on oxidative stress, FID and brain size (Fig. 3). FID mostly affected the levels of MDA and UA indirectly through their relationship with body mass (Fig. 3). Brain size mostly affected the levels of MDA indirectly through its relationship with body mass (Fig. 3A), but significantly directly affected UA (Fig. 3B). Phylogenetic path analyses showed relative consistency in path coefficients across two different oxidative stress variables, MDA and UA. FID and brain size did not show any significant path correlation in either path analysis, although brain size showed a potential effect on FID in the path models with MDA (estimate = -0.212, $P = 0.509$).

Discussion

The main finding of this study was that mean flight initiation distance of different species of birds was positively correlated with species-specific MDA and UA levels and mediated through their relationship with body mass. This result was robust to differences in sample size and similarity due to common phylogenetic descent. It suggests that frequent take-offs

during flight from a given number of potential predators could be a mechanism that affects the concentration of pro-oxidants, and it could select for an elevated level of antioxidants.

A few studies have investigated the physiological mechanisms of escape. Some have considered the physiological costs of monitoring (Cooper & Blumstein, 2014), while others have focused on initiated flights finding that FID, after adjustment for body mass, increased with increasing basal metabolic rate (BMR) across 76 bird species (Møller, 2009). This is presumably because predation risk imposes selection favoring wariness requiring higher BMR as a compensation. Species that allow close proximity of a potential predator have high hematocrit for their body size, which represents the ability for high oxygen transport allowing for high performance during rapid take-offs (Møller *et al.*, 2013). As a measurement of trade-off between risk of predation and other activities, FID is consistent among different conditions (Ydenberg & Dill, 1986; Giraldeau & Caraco, 2000; Carrete & Tella, 2010). Although a flush caused by a brief approach by a potential predator may last only a few seconds, the accumulated effect can still be substantial because even brief aerial flapping flight may result in 23 times basal metabolic rate in robins (Tatner & Bryant, 1986). For a given abundance of potential predators, individual prey with relatively long FID should experience greater accumulated energy costs than individuals with short FID because they are more easily disturbed. Species with long FIDs for their body size also developed relatively large wing areas and large aspect ratios, and hence relatively low costs of flight and maneuverability (Møller *et al.*, 2013), expected as a consequence of selection caused by the energetic costs of FID. Thus early flight from predators is not only energetically expensive, but also associated with higher oxidative stress. It would be inspiring and important to include indicators of oxidative stress into such analyses considering anti-predator behavior.

The degree of lipid peroxidative damage measured as MDA and nonenzymatic antioxidant defense mechanism represented by UA showed consistency in their correlation with body mass and FID. Previous study of seven bird species found that cardiac muscle malondialdehyde concentration was negatively related to body mass (Szabó *et al.*, 2006), indicating a progressive myocardial lipid peroxidation in smaller-bodied species. These results are consistent with the fact that high antioxidant levels may reflect less control of free radical production (Barja, 2004), and effective control is a function of lowered membrane gradients rather than upregulating antioxidants (Cohen *et al.*, 2008). However, we did not find a significant correlation between TAS and FID, or body mass or brain size. This could be due to the synergistic and antagonistic interactions among different constituents of non-enzymatic antioxidants (Monaghan *et al.*, 2009), and that adaptation could be an alternative explanation for high antioxidant defense levels (Clausen *et al.*, 2010).

Including different indicators of oxidative stress (two out of four components: free radical production, antioxidant defenses, oxidative damage and repair mechanisms) provide relatively more information (Monaghan *et al.*, 2009) on the relationship between FID and the levels of oxidative stress. For instance, while MDA level reflects oxidative damage among individuals of a given species, UA represents different mechanisms of antioxidant defense and TAS describes total antioxidant status of individuals of a given species.

Although brain size is positively related to MDA, and neural tissue is energetically expensive and demands antioxidants (Isler & van Schaik, 2006), we did not find a direct correlation between brain size and MDA in the phylogenetic path analysis. Rather, brain size only directly increased UA level. This result partially supports the ‘oxidation avoidance’ hypothesis proposed by Vágási *et al.* (2016) that species with relatively large investment in the brain also allocate more to self-maintenance including an efficient antioxidant defense machinery.

We did not find a direct significant path correlation between brain size and FID. Brain size is identified as a major determinant of avian escape strategy (Samia *et al.*, 2015), but that could be explained by associated cognitive functions (reviewed by Sol, 2009). For instance, larger brains help birds respond to novel conditions by enhancing their propensity to innovate rather than indirectly through non-cognitive mechanisms (Sol *et al.*, 2005). The decisive role of brain size could also be explained through its coevolution with relative eye size in birds in response to nocturnal activity and, at least partly, to capture of mobile prey (Garamszegi *et al.*, 2002). Species with higher visual acuity are able to detect a predator model from farther away (Fernández-Juricic & Kowalski, 2011), and species that flee at longer distances from an approaching potential predator have relatively large eyes for their body size (Møller & Erritzøe, 2010).

Sudden take-offs from a potential predator are costly (Tatner & Bryant, 1986), and it is associated with oxidative stress. As an important part of an individual’s daily life, anti-predator behavior measured as FID contributes to the level of oxidative stress. Oxidative stress from extended flights have long been neglected until recent studies found that flying birds experience oxidative stress during long distance migration (Costantini *et al.*, 2007, 2008). Migrants seek to balance different options to achieve optimum strategies for coping with energy consumption during migration (Hedenström & Ålerstam, 1997). They experience oxidative stress during endurance flight and increase their antioxidant capacity to cope with this stress (Jenni-Eiermann *et al.*, 2014). Management of oxidative stress is likely to be a major determinant of life histories (Hulbert *et al.*, 2007). Understanding the

association between physiological stress, caused by unpredictable and detrimental stimuli, can help us better interpret ecological field studies (Romero, 2004).

In conclusion, we show for the first time that free-living birds with relatively short FID for their body mass experienced more peroxidative damage to lipids (malondialdehyde, MDA), and such species had an elevated component of antioxidant capacity (uric acid, UA). These relationships were mostly mediated through the relationship between FID and body mass.

Conflicts of interest

We declare that we have no conflicts of interest.

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Figure legends:

Fig. 1 Concentration of MDA (a) and UA (b) increased with increasing \log_{10} -transformed flight initiation distance (FID (m)) across 72 and 71 species of birds, respectively. Symbol sizes are proportional to square-root transformed sample sizes. The lines are the linear regression lines.

Fig. 2 MDA (a) and UA concentration (b) increased with increasing \log_{10} -transformed brain size across 72 and 71 species of birds, respectively. Symbol sizes are proportional to square-root transformed sample sizes. The lines are the linear regression lines.

Fig. 3 Phylogenetic path models averaged over all tested models for (a) concentrations of MDA and (b) UA. The arrows represent a causal effect of one variable on another. The width of the arrows reflects the magnitude of standardized path coefficients (estimate written next to the corresponding arrow). Blue arrows indicate significant positive effects, red arrows significant negative effects and dotted lines non-significant effects. Flight initiation distance, brain size and body mass are all \log_{10} -transformed.

Fig. 1

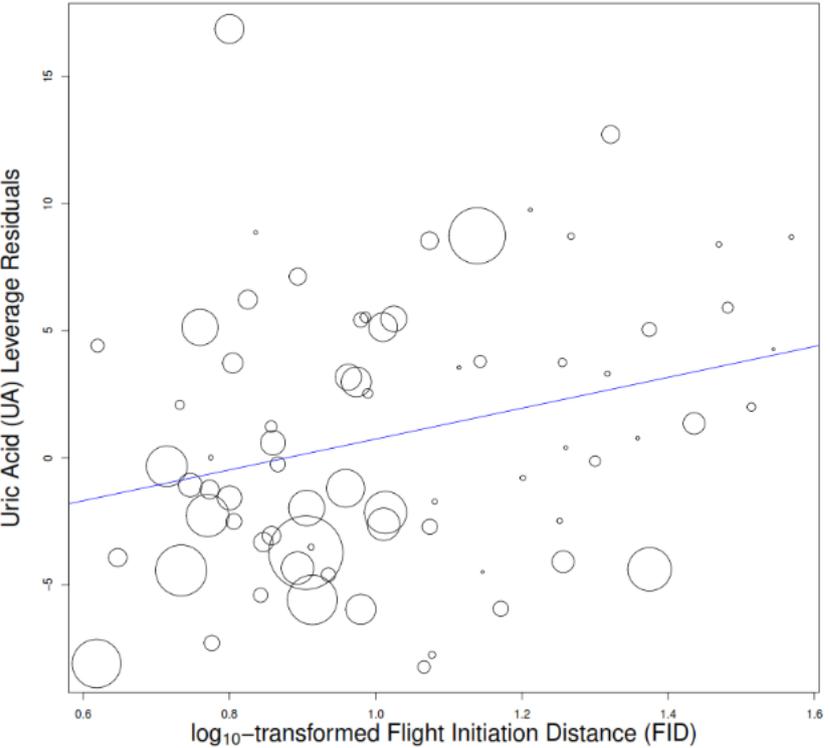
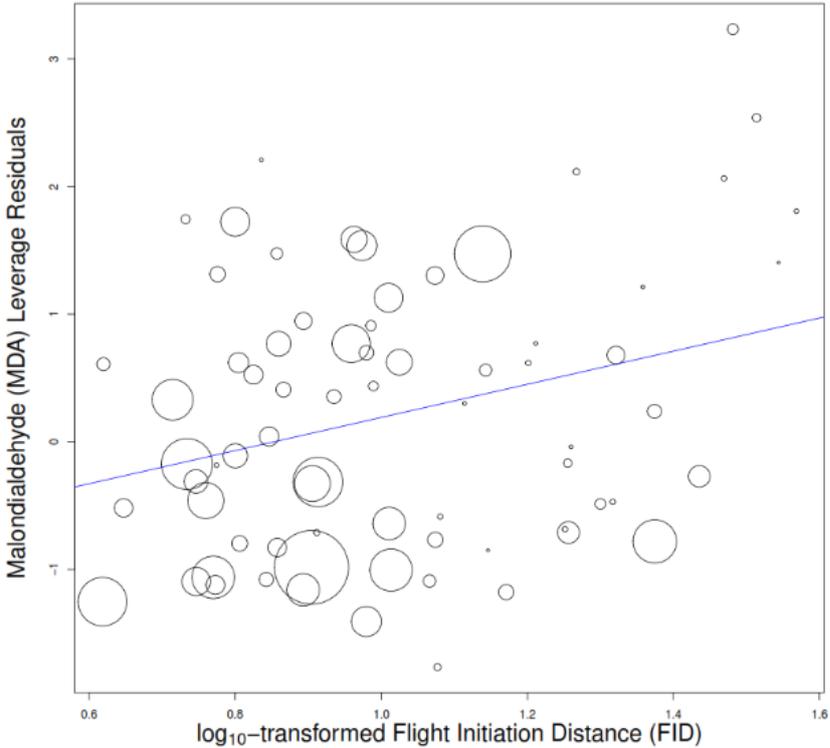


Fig. 2

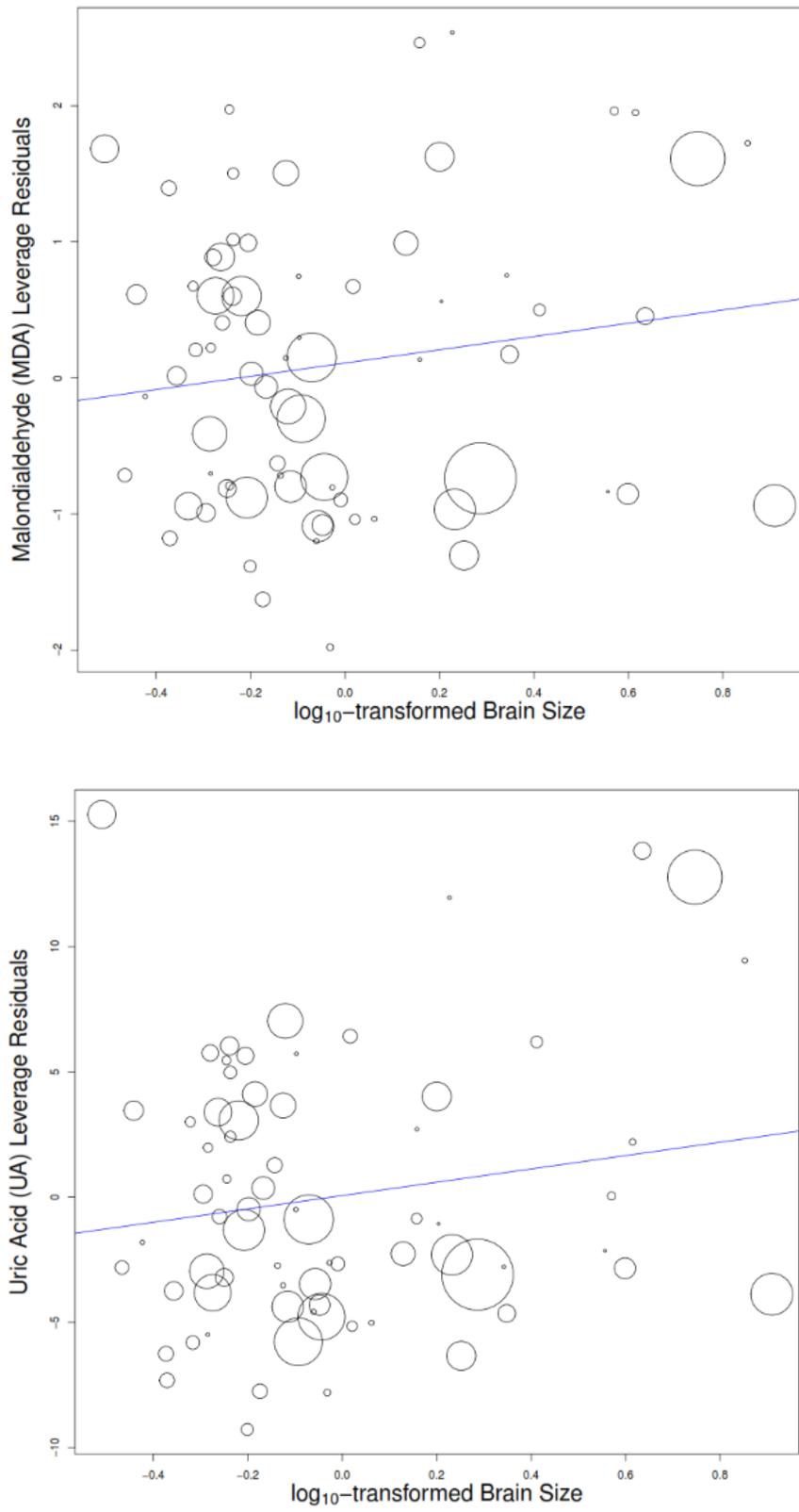


Fig. 3

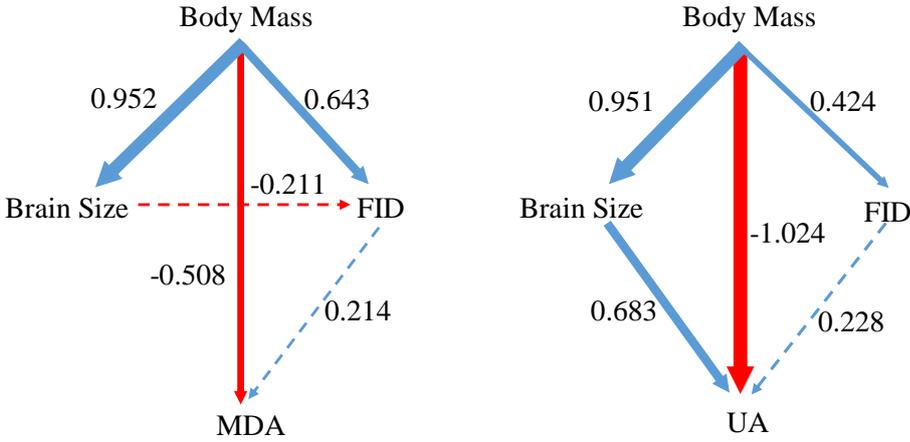


Table 1 PGLS models of the relationship between \log_{10} -transformed flight initiation distance (FID), oxidative damage/antioxidant level, brain size and body mass, respectively, weighted by sample size for species of birds. The model for malondialdehyde (MDA) had the statistics $F_{3,68} = 4.53$, $r^2 = 0.12$, $P < 0.0001$, the model for total antioxidant status (TAS) had the statistics $F_{3,68} = 2.83$, $r^2 = 0.01$, $P = 0.7398$ and the model for uric acid (UA) had the statistics $F_{3,67} = 5.03$, $r^2 = 0.18$, $P < 0.0001$. P -values in bold font are statistically significant at the 0.05 level.

Response	Predictor	Value	Standard Error	t	P
MDA	(Intercept)	10.129	1.867	5.425	0.000
	Brain Size	3.440	1.628	2.113	0.038
	Body Mass	-4.400	1.215	-3.621	0.001
	FID	1.780	0.737	2.414	0.019
TAS	(Intercept)	2.617	0.982	2.665	0.010
	Brain Size	0.500	0.856	0.584	0.561
	Body Mass	-0.414	0.639	-0.648	0.519
	FID	0.348	0.388	0.898	0.373
UA	(Intercept)	57.172	11.966	4.778	0.000
	Brain Size	35.150	10.342	3.399	0.001
	Body Mass	-31.411	7.782	-4.037	0.000
	FID	14.776	4.676	3.160	0.002

V Contagious fear: Flight initiation distance increases with flock size in gregarious birds

Contagious fear: Flight initiation distance increases with flock size in gregarious birds

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Abstract

This study demonstrates that the social behavior of bird species changes the way those birds respond to perceived threats. We found that social birds react to a potential predator quickly (longer flight initiation distance defined as the distance at which a focal bird takes flight when approached by a human) when aggregated in large flocks. These conclusions support a higher vigilance by effect of many eyes scanning in gregarious birds, suggesting that sociality may be a key factor in the evolution of anti-predator behaviors, especially in changing habitats, as urban areas.

Keywords: birds; dilution effect; fear-response; FID; gregariousness; human disturbance; social interactions; vigilance.

Introduction

Flight initiation distance (FID) is defined as the distance at which animals take flight from approaching threats (Hediger, 1934; Blumstein, 2003). This behavioral trait has been used as a surrogate for anti-predator or fear-avoidance behavior in many ecological studies (e.g. Møller 2008a; Weston *et al.* 2012; Legagneux and Ducatez 2013; Møller *et al.* 2013). However, the majority of studies of escape behavior in birds focused on the influence of external or interspecific factors affecting behavioral responses: the direction of approach by predators (Møller and Tryjanowski 2014), intruder starting distance (Blumstein, 2003), population density (Mikula, 2014), urbanization (Samia *et al.*, 2017), road speed limits (Legagneux & Ducatez, 2013), insular distribution (Cooper *et al.*, 2014), predator–prey interactions (Møller, 2008b), spatial gradients of predator abundance (Díaz *et al.*, 2013) or daytime and season when FID was measured (Piratelli *et al.*, 2015).

Currently we know that large species have long FIDs, because larger species need more time to get airborne and hence avoid capture (Hemmingsen, 1951; Fernández-Juricic *et al.*, 2006; Møller, 2008c; Weston *et al.*, 2012). We know that birds from rural areas tend to escape earlier than birds from urban areas, being less tolerant of humans, probably because urban birds live under lower predation risk than their rural counterparts (Møller, 2015; Samia *et al.*, 2017). Finally, we know that behavioral responses of animals to human approach such as FID can be useful for conservation purposes, namely management of disturbance, especially in human-dominated environments (Weston *et al.*, 2012). But we know very little about the intraspecific factors which can be involved in any variation in FID. Group size has also been suggested to be another important prey trait that influences escape decisions (Samia *et al.*, 2017). But this study, even if considering explicitly the relation between FID and the number of individuals of the same species around a focal individual, mainly focused on comparisons between habitats rather than flock sizes in gregarious and non-gregarious species. Møller (2015) reviewed the literature on FID in birds and showed that sociality (directly related to group size) had an intermediate mean effect size of 0.26 on FID. There is even less information available for other classes of animals (Cooper & Blumstein, 2015). The effect of flock size on animal fear is important, because fear responses link individual behavior to social factors, such as the number of conspecifics in a flock, opening the perspective for possible cascade effects on fear reactions in birds.

Under classical ecological models of predation risk, which predict a decrease in individual risk when group size increases (Pulliam, 1973; Alexander, 1974), we would expect a reduction in FID among individuals in large groups through the dilution effect (Pulliam, 1973; Roberts, 1996; Fernández-Juricic *et al.*, 2002). However, the opposite response could

also be expected (increasing FID with increasing flock size) because of the social transmission of fear responses (Griffin, 2004), and early detection of predators in large groups (Stankowich & Blumstein, 2005; Hingee & Magrath, 2009). Awareness or nervous reactions can be positively related to flock size because of the higher vigilance (effect of many eyes scanning for predators) (Pulliam, 1973). Thus, under threat, individuals in large flocks should react more rapidly than solitary individuals or individuals in small groups, as a consequence of cascade effects or contagious alertness.

Despite that the literature on fear responses and sociality is limited, cooperative breeders were shown to be more nervous than species with other breeding systems (Blumstein, 2006), which would support the second hypothesis. In fact, a ground-breaking study conducted by Laursen et al. (2005) reported intermediate to large effect sizes for intraspecific relationships between FID and flock size in different species of waterbirds with FID being longer for larger flocks. These findings are inconsistent with dilution effects, because if each individual in a flock enjoyed a smaller risk, we should expect a shorter FID in larger flocks. In contrast, the results are consistent with effects of many eyes scanning for the presence of a predator, although differences in phenotypic composition of differently sized flocks may be an alternative explanation for these findings. Effect sizes for the interspecific relationship between FID and coloniality were all small (Møller, 2008c). Finally, Tätte et al. (2017) showed that flock size predicts FID, but not the distance fled, implying that it is the perception of risk rather than the actual distance moved during an escape that is the determinant of differences in FID among flocks of different size.

Gregariousness is common in nature and can be defined as the tendency to live in flocks (Miller, 1922). A flock is a term used to define any aggregation of homogenous individuals, regardless of size or density (Emlen, 1952). As pointed out by Miller in 1922, probably the most obvious advantage of gregarious behavior in birds is that it affords a multiplicity of eyes, increasing the chance of sighting a potential predator. Then, any defensive measures can be taken early, increasing the probabilities of success of escape against the risk (Miller, 1922).

We hypothesized that FID in response to human approach would be longer in more social species. The ecological rationale for this expectation is that vigilance and FID increases with group size because of the many eyes effect, and a nervous state can be transmitted more easily when there are many individuals in a flock. However, this process should be more predominant in social or gregarious than in solitary species, because gregarious species may be better at exchanging information with other individuals in the group than non-gregarious species. As a consequence, the aim of this study was to test if FID in birds increases with

the number of conspecifics (flock size), focusing on differences between gregarious and non-gregarious species.

Methods

Study area and flight initiation distance

Data were collected during April-September 2015 using a standard protocol (Blumstein, 2006; Samia *et al.*, 2017). Data were collected in urban and adjacent rural areas of eight cities in eight European countries: Czech Republic, Denmark, Estonia, Finland, France, Hungary, Poland, and Spain (Fig. 1; ESM, Table S1). We used a paired study design with one urban and one rural site (habitat type) in each study location. The distance between each pair of urban and rural site was always shorter than 20 km. The sites classified as “urban” were characterized by areas with multi-story buildings or by areas with single-family houses (suburban areas). The sites classified as “rural” were areas dominated by open farmland with scattered houses (Samia *et al.*, 2017). For the definition of urban and rural habitats we followed the definitions provided in Marzluff *et al.* (2001). Urban habitats were defined as areas with at least 50% of built-up area, building density >10 buildings/ha and, a residential human density >10 humans/ha. Rural habitats were defined as the areas with 5–20% built-up areas, a building density <2.5 buildings/ha, and residential human density between 1 and 10 humans/ha (Marzluff *et al.*, 2001). Observers used binoculars to identify birds that were foraging or engaged in “relaxed behavior” (i.e., roosting or preening). Highly vigilant or obviously alarmed individuals were not approached. Furthermore, data from breeding sites (e.g. from gull colonies) or anthropogenic feeding sites (e.g. rubbish dumps) were not collected. Each individual bird was approached in a straight line by the observer walking at a constant speed (0.5m/s).

Flight initiation distance (FID) was measured as the distance between the observer and the point where the individual bird began to flee (see more details in Samia *et al.* 2017). Only bird species detected on the ground were considered. Sol *et al.* (2017) showed that species with more than 10 recorded cases per study site provided reliable estimates of FID. Here, applying a more conservative approach and trying to focus on the most common species, we only selected bird species with more than 50 observations of FID, so also any potential effect of starting distance should be considerably alleviated.

Flock size was defined as the number of aggregated individuals of the same species, implying that individuals in flocks are closer to each other than individuals that are not in flocks.

Ecological variables: Trophic guild, body mass and gregariousness

For each bird species recorded in this study, we included the following information: trophic guild or diet (main type of food consumed, following the bird traits of feeding ecology provided in Pearman *et al.* (2014)). All species were classified in five main categories as, granivorous, granivorous-insectivorous, insectivorous, carnivorous and carrion-eater (ESM, Table S2). Body mass for each species was obtained from the same source (Pearman *et al.*, 2014) and this variable was log-transformed to fit normality.

All bird species were classified as gregarious or non-gregarious during the breeding and the non-breeding season, using information from the Handbook of the Birds of the Western Palearctic (Cramp & Perrins, 1994) (ESM, Table S2). Birds were classified as “gregarious” when species have shown gregarious activities at least in one period of the year (breeding or non-breeding period) (ESM, Table S2). There was a positive correlation between the gregariousness during these two periods (Kendall rank order correlation $\tau = 0.40$, $P = 0.020$), implying that species that were gregarious during breeding also tended to be gregarious during the non-breeding season. We decided to group breeding and non-breeding gregarious species, because we assumed that cognitive capacity for gregariousness, i.e., the capacity to communicate with other individuals from the same species, is a species-specific trait that may manifest either during breeding or wintering periods but is present all the time.

Bird species were finally classified in quantiles on the basis of their body mass using the ‘ggtool’ package for R (Warnes *et al.*, 2015). The classification of bird species with respect to body mass quantiles was used in some statistical analyses, in order to make easier the comparison of bird species of different size.

Statistical analyses

The average values of FID and flock size between groups based on species-specific gregariousness were compared using the standard nonparametric Wilcoxon test (Triola, 2012).

We used Generalized Linear Mixed Models (GLMM) (Bolker *et al.*, 2009) to analyze the changes in FID behavior of bird species in relation to flock size. Models were fitted separately for non-gregarious and gregarious bird species, using the package ‘lme4’ (Bates *et al.*, 2015). We found that FID (response variable) was normally distributed, after having explored the distribution of the variable (Box & Cox, 1964) using the package ‘MASS’

(Venables & Ripley, 2002). Two series of models were run: First controlling for the phylogenetic signal among species and then non-phylogenetic models using flock size as a fixed factor and other variables as random factors.

In the phylogenetic models, to control for the phylogenetic relationship among species, we used phylogenetic generalized least square (PGLS) on regression models to analyze the changes in FID behavior of bird species in relation to flock size. Models were fitted separately for non-gregarious and gregarious bird species, using the package ‘ape’ (Paradis *et al.*, 2004), ‘nlme’ (Pinheiro *et al.*, 2017) and the function `gls` with correlation equals consensus tree. We extracted the phylogenetic relationship for all bird species from the phylogeny available on line (Jetz *et al.* 2012, 2014) and obtained consensus phylogenies for both gregarious and non-gregarious species from 100 random trees with Mesquite (Maddison & Maddison, 2017). Different populations of the same species from different countries and habitats were defined with a relatively different branch length of 1E-19 just to fit the models. We weighted models by sample size (Garamszegi & Møller, 2010; Garamszegi, 2014).

In the non-phylogenetic models, flock size and habitat were entered as predictor variables, while the cities, body mass quantiles, diet type and bird species were all included as random factors. The use of random factors permits to focus on the main effects of focused predictors (flock size and habitat), removing any potential effect associated to other factors. The inclusion of the cities controlled for possible consistent differences among cities where data were collected, while inclusion of body mass quantiles reduced any effect associated with a strong correlation between FID and body mass (Møller *et al.*, 2016). Moreover, because there were multiple observations for each species, and because a shared evolutionary history makes data statistically dependent (Garamszegi & Møller, 2011), the addition of species as random factor alleviates any potential bias related to phylogenetic dependence among species. An additional GLMM with the same structure as for gregarious birds was run, considering only gregarious species, which have flocks smaller than 11 individuals (equal to the maximum number of individuals recorded for non-gregarious birds).

Because AIC_c converges to AIC with larger sample sizes, it is recommended to always use AIC_c to select the best model (Burnham & Anderson, 2002). When comparing a series of models, the one with the lowest AIC_c is considered to be the most parsimonious or best model. We also calculated an Akaike weight (w_i), or model probability, for each model, considering that the w_i sum to 1 for the whole set of models. The w_i is the probability that model i would be selected as the best-fitting model if the data were collected again under identical circumstances (Burnham & Anderson, 2002). The model selection and multimodel

inference was performed using the package ‘AICcmodavg’ in R (Mazerolle, 2016). The best model was selected considering both lowest AIC_c and large Akaike weights, because this model had the strongest support for data (Mazerolle, 2016). Model averaging was used to obtain parameter estimates for all variables entered in the models. The model averaging calculation was done on the most parsimonious models (Grueber *et al.*, 2011), using the package ‘MuMIN’ for R (Bartoń, 2013). The confidence intervals for the significant variables in each model were calculated by the Wald method using the package ‘MASS’ (Venables & Ripley, 2002).

All statistical tests were performed with R software (R Core Team, 2017).

Results

From a total of 9,871 observations from eight different European countries (Fig. 1; ESM, Table S1) we filtered 7,768 observations of 35 bird species with sample size of FID available for more than 50 observations (ESM, Table S2).

In the initial exploration of data, FID was strongly positively correlated with body mass, in each category of trophic guild, with more pronounced slopes for insectivorous, carrion-eaters and granivorous-insectivorous birds than other categories (Fig. 2).

The average FID was slightly longer in gregarious than in non-gregarious birds (12.2 m and 10.4 m, respectively; $t = -6.9$, $df = 4307.4$, $p = 5.7e-12$; ESM, Fig. S1). The average flock size was larger in gregarious than in non-gregarious birds (2.3 and 1.1, respectively; $t = -17.6$, $df = 6058.5$, $p < 2.2e-16$; ESM, Fig. S1).

When considering separately the two categories of gregariousness of bird species, flock size was not significantly related to FID for non-gregarious species (Fig. 3), while it was strongly positively correlated with the number of individuals in a flock for gregarious birds (Fig. 4), in all models (Tables 1 and 2). Additionally, in the phylogenetic model, FID was negatively correlated with urban habitat for both gregarious and non-gregarious species, while it was positively correlated with body mass for both gregarious and non-gregarious birds. Latitude was negatively associated with FID for non-gregarious birds, while was only slightly positively associated to FID for gregarious birds. Finally, we found a negative association between FID and insectivorous diet for gregarious birds (Table 1).

The second modeling procedure, based on non-phylogenetic models, confirmed that the positive and significant association between FID and flock size verified for gregarious birds was valid even independently of body mass, diet or bird species considered (Table 2).

Furthermore, FID for both gregarious and non-gregarious bird species was negatively associated with urban habitats. The list of evaluated models, with the number of predictors considered, delta AIC values and AIC weights for each one is provided in Table S3 of the Electronic Supplementary Material.

The same significant positive association between FID and flock size was confirmed when standardizing the analyses to similar range of flock sizes for both gregarious and non-gregarious species, i.e., focusing only on gregarious bird species with flocks smaller than 11 individuals (ESM, Table S4). Additionally, the pattern was persistent even when modeling separately the six more frequent gregarious bird species: *Columba livia*, *Columba palumbus*, *Corvus monedula*, *Corvus frugilegus*, *Passer domesticus*, *Sturnus vulgaris* (ESM, Table S5).

Discussion

The main finding of this study was that FID increased with flock size in gregarious species, while that was not the case in non-gregarious species. This pattern was persistent even within species, when focusing on individuals of the six more frequent gregarious birds. Interestingly, these effects were independent of body mass and geographic area where data were collected (city), as well as the phylogenetic signal among species. Indeed Møller (2015) in a meta-analysis of all studies of FID in birds showed a mean effect size estimated as Pearson's product-moment correlation coefficient of 0.39 for body mass thus accounting for 15% of the variance, 0.62 for urbanization (urban vs. rural) accounting for 38% of the variance and 0.26 for sociality only accounting for 7% of the variance. In fact, the effect size of 0.24 reported for gregarious species was very similar to that of 0.26 for sociality reported by Møller (2015). Type of diet was unrelated to the FID of non-gregarious birds in the present study, while in gregarious birds we found that insectivorous species tend to have the shortest FID. Additionally, we found a positive association between FID and body mass (especially marked in non-gregarious species), and we confirmed in all models that FID tends to decrease with urban habitat when compared with rural areas. These two results are confirming previous studies (Weston *et al.*, 2012; Díaz *et al.*, 2013; Møller *et al.*, 2016; Samia *et al.*, 2017). The association between FID and latitude showed a less clear pattern. Finally, the positive correlation between FID and body mass showed a more pronounced slope for insectivorous, carrion-eaters and granivorous-insectivorous birds than other categories. These effects can be explained by the fact that gregariousness is more prominent in species relying on unpredictable food supply such as superabundant carrion and insects

rather than evenly dispersed food (Lack, 1968). Therefore, we expect the association between FID and body mass to be more pronounced in more gregarious species.

The current study tests the two hypotheses listed in the Introduction; the dilution effect (Stankowich & Blumstein, 2005) and the many eyes effect (Stankowich & Blumstein, 2005; Hingee & Magrath, 2009). Indeed, larger flocks have more individuals scanning for predators, but larger flocks also result in stronger dilution effects because the risk is smaller for each individual in a larger flock. Here, using mainly Passeriformes, we have shown a clear positive relationship between FID and flock size, which supports the many eyes effect hypothesis. A similar general pattern was previously reported by Laursen et al. (2005) for waterbirds, while other study suggested no influence of flock size on FID for the particular case of black swans *Cygnus atratus* (Guay et al., 2013).

The present study of mainly passerine birds compares well with that by Laursen et al. (2005) for waterbirds comprised of geese, ducks, waders and gulls. In fact, both studies have very similar effect sizes despite the taxa being completely different and the association with urbanization being restricted to the present study. However, hunting activities affected FID in the study by Laursen et al. (2005), but not in the present study. Indeed Laursen et al. (2005) showed an effect of flock size on FID for nine waterbird species in fall, when hunting is common, while only two species showed a significant relationship between FID and flock size in spring when hunting ceased.

Longer FID in larger flocks of a given species implies that individuals on average run a higher risk in small flocks. This could either be due to such larger flocks being composed of individuals of lower phenotypic quality, or that individuals in small flocks with short FID run higher risks of mortality. Indeed, Møller (2014) has shown that barn swallow *Hirundo rustica* individuals with short FID are more likely to be caught by sparrowhawks *Accipiter nisus*. In addition, bird species with shorter FID were more vulnerable to get caught by raptors (Møller et al. 2008) or cats *Felis catus* (Møller et al. 2010) and to be killed by cars (Møller et al. 2011). We are unaware of any other studies showing such effects.

We classified the species as gregarious or not because we assumed that gregarious species would encounter conspecifics more often than non-gregarious species (Emlen, 1952). For this reason, we can hypothesize that individuals of gregarious species are better adapted at exchanging information with each other than are individuals of non-gregarious species. Thus, individuals belonging to gregarious species would experience a trade-off between foraging (or resting) under the safety of the presence of many conspecifics and having long FIDs, or having short FIDs in the presence of few conspecifics (Laursen et al., 2005). Accordingly, FID was only positively related to flock size in gregarious, but not in non-

gregarious species (Figs. 3 and 4). Thus, the effect of sociality on FID was only obvious in gregarious species, while the effect for non-gregarious species was close to zero. However, a potential alternative explanation for this pattern is that relatively small flocks of non-gregarious species might not be effective in increasing detection of predators as large flocks. Therefore, we compared FID for gregarious bird species with FID for small flocks (these flocks should be more similar to the small flocks of non-gregarious species) (ESM, Table S3), confirming the same positive association between FID and flock size. An additional confirmation of the robustness of this result is that using two different modelling approaches the pattern of this positive and significant association was the same. Therefore, the association between FID and flock size was restricted to gregarious bird species.

We explicitly recorded FID observations in urban and rural habitats. While previous studies have shown consistently longer FIDs in rural than in urban habitats (e.g. Samia *et al.* 2017), we are only aware of a single other study investigating the independent effects of rural vs. urban habitats and flock size on FID (Tätte *et al.*, 2018). The latter study also found a similar effect of flock size in rural and urban habitats.

The present study suggests a number of future prospects. For instance, we can point out that every future study on the FID of gregarious birds has to explicitly consider the number of individuals around the bird observed. We hypothesize that experimental change in sociality will have effects on FID. Indeed, Laursen *et al.* (2016) have shown that flock size changes adaptively in response to intense hunting. We predicted that such changes in immediate risk will be accompanied by similarly directed changes in FID. Finally, we hypothesize that changes in flock size can be experimentally manipulated by changing food availability with consequences for change in FID.

In conclusion, we have shown that FID increases with flock size, but only in gregarious, and not in non-gregarious species. These findings imply a role of sociality for risk taking behavior and hence for social organization. Our conclusions have broad biological implications, especially considering the role of sociality and gregariousness as possible factor facilitating animals to colonize urban environments and to adapt to these human-impacted environments.

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Table 1. Results of phylogenetic generalized linear regression model (PGLS), accounting for variation in flight initiation distance (FID) in relation to flock size, habitat (urban or rural), latitude, body mass and diet in non-gregarious and gregarious bird species, based on data from eight European countries, weighted by sample size for species of birds. The model for non-gregarious birds had the statistics $F_{7,184} = -35.931$, $r^2 = 0.187$, $P < 0.0001$ and the model for gregarious birds had the statistics $F_{7, 946} = -23.325$, $r^2 = 0.128$, $P < 0.0001$. Abbreviations: SE, standard error. Significant variables are highlighted in bold.

Variables	Estimate	SE	d.f.	F	P
Non-gregarious birds			192		
(Intercept)	7.808	7.375	(total)	278.663	<.0001
Flock	-0.236	1.147	1	0.611	0.435
Latitude	-0.151	0.065	1	9.313	0.003
Habitat (urban)	-6.306	0.712	1	73.256	<.0001
Log (body mass)	7.420	2.426	1	7.972	0.005
Diet			3	1.585	0.195
Gregarious birds			954		
(Intercept)	15.278	2.772	(total)	864.211	<.0001
Flock	0.380	0.040	1	94.821	<.0001
Latitude	0.006	0.027	1	4.327	0.038
Habitat (urban)	-6.482	0.464	1	187.71	<.0001
Log (body mass)	0.950	0.988	1	15.938	0.0001
Diet (insectivorous)			3	4.941	0.002

Table 2. Results of Generalized Linear Mixed Models (non-phylogenetic models), accounting for variation in flight initiation distance (FID) in relation to flock size and habitat (urban or rural) in non-gregarious and gregarious bird species, based on data from eight European countries. The full model is based on 2014 observations for non-gregarious and 5754 observations for gregarious birds. Random effects were entered in the models: city (groups = 8), quantiles for body mass (groups = 4 for non-gregarious, 5 for gregarious birds), diet (groups = 4) and bird species (groups = 10 for non-gregarious, 23 for gregarious). Abbreviations: ES, estimate; CI, 95% confidence interval (lower / upper values); SE, standard error; t statistic and p-value. Significant variables are highlighted in bold.

Variables	Estimate	CI	SE	t	p
Non-gregarious birds					
(Intercept)	17.711	11.713 / 23.709	3.060	5.787	2e-05
Flock size	-0.015	-0.814 / 0.783	0.407	-0.038	0.969
Habitat (urban)	-5.860	-6.699 / -5.021	0.428	-13.679	2e-16
Gregarious birds					
(Intercept)	15.931	11.098 / 20.763	2.465	6.426	2e-05
Flock size	0.338	0.284 / 0.393	0.028	12.124	2e-16
Habitat (urban)	-6.154	-6.715 / -5.593	0.286	-21.499	0.961

Figure legends

Figure 1. Location of study sites across 12 European cities. Each site contained one urban and one nearby rural location.

Figure 2. Linear regression lines between flight initiation distance (FID, m) and log-transformed body mass (g) in all birds recorded in this study, belonging to different trophic guilds in eight European countries. Colors indicate the diet (ESM, Table S2). Envelopes around lines are 95% confidence intervals.

Figure 3. Linear regression lines between flight initiation distance (FID, m) and flock size in non-gregarious bird species from rural and urban environments in eight European countries species. Colors indicate bird family, and circle size is proportional to body mass of birds (g). Envelopes around lines are 95% confidence intervals.

Figure 4. Linear regression lines between flight initiation distance (FID, m) and flock size in gregarious bird species from rural and urban environments in eight European countries. Colors indicate bird family, and circle size is proportional to body mass of birds (g). Envelopes around lines are 95% confidence intervals.

Fig. 1

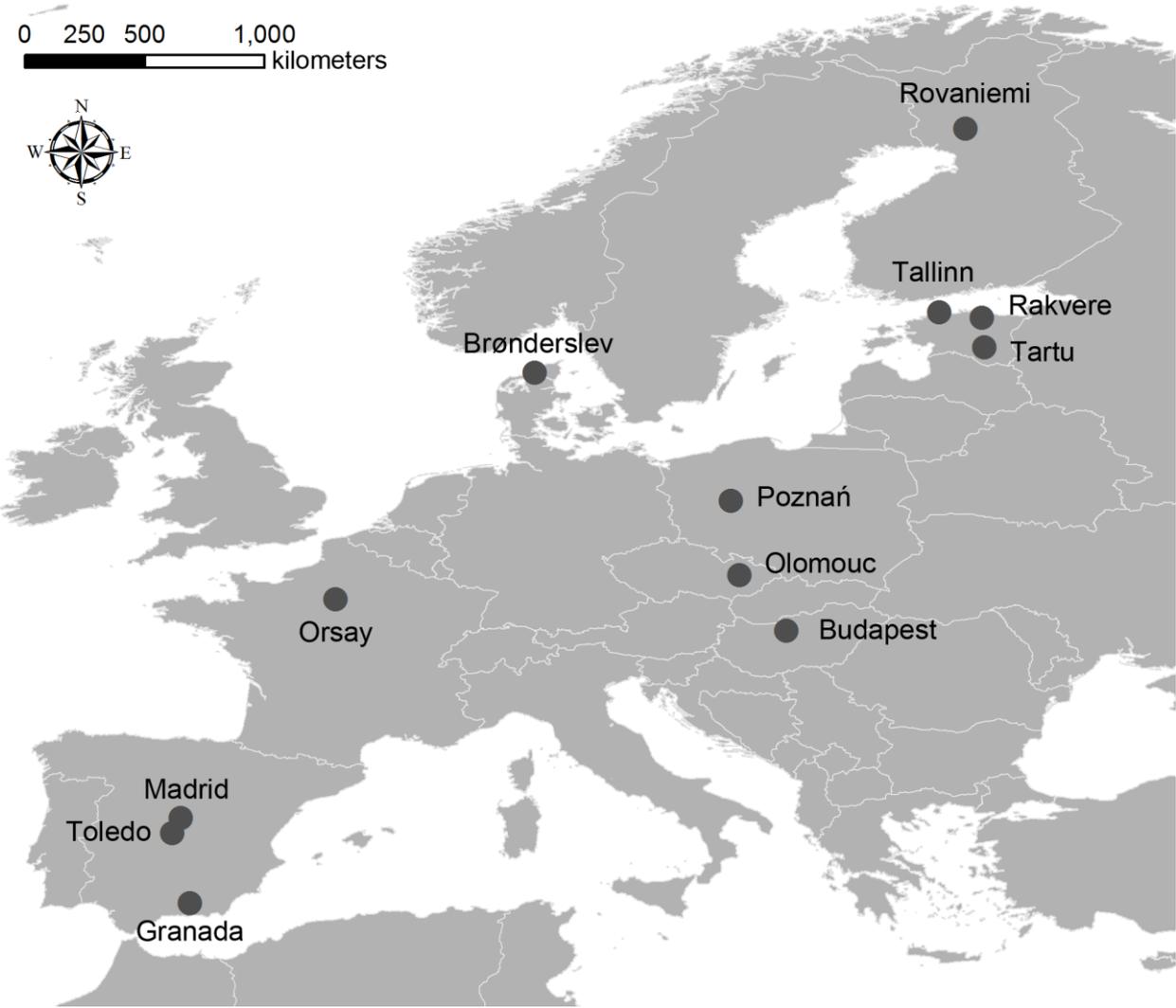


Fig. 2

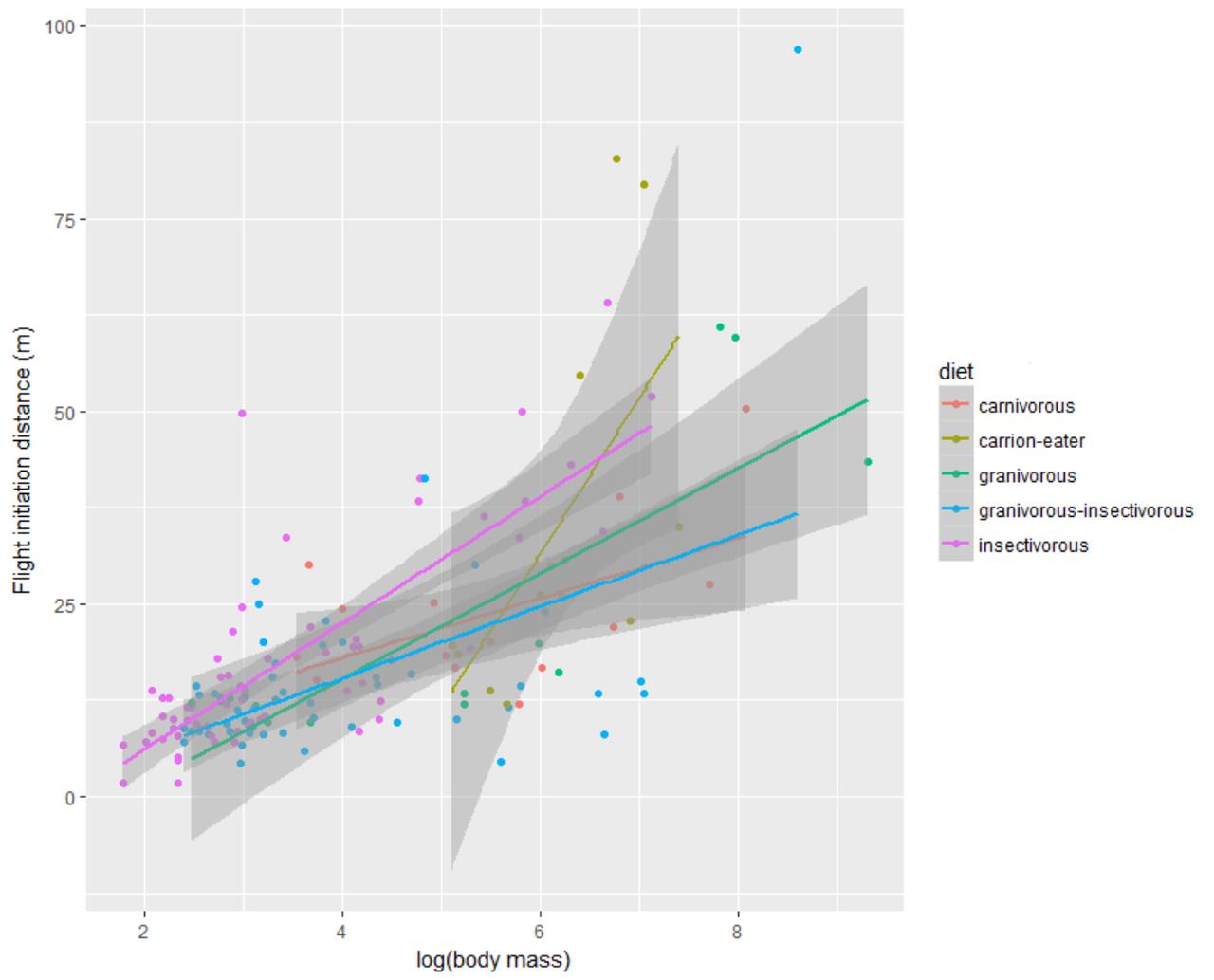


Fig. 3

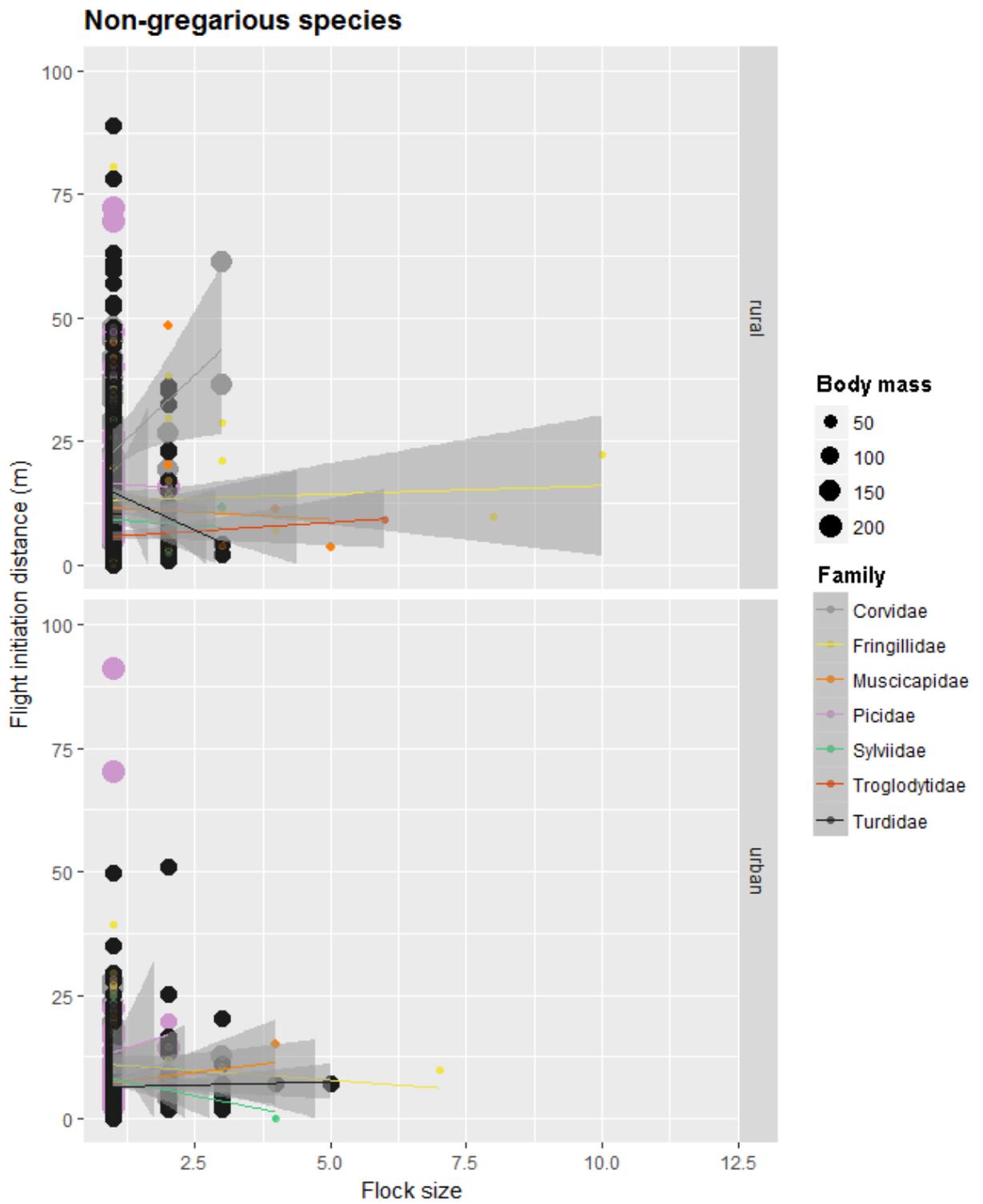
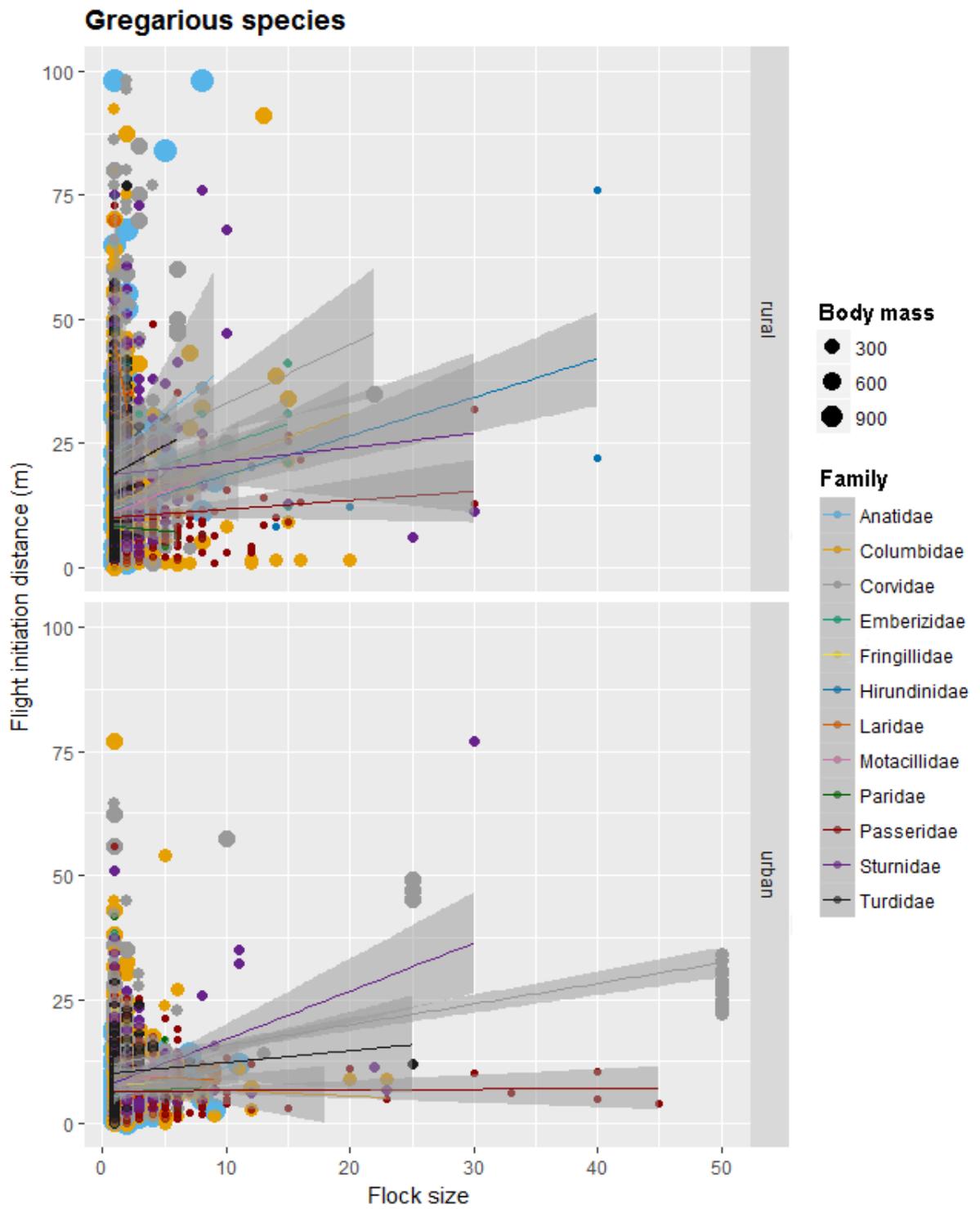


Fig. 4



Résumé en français

Cette partie est google traduit en fonction de la partie d'introduction. Pour mieux comprendre la thèse, veuillez lire la version anglaise.

Introduction

I Stratégie anti-prédatrice et comportement d'échappement

Les animaux évaluent l'environnement environnant, y compris l'état de menace posé par cet environnement et prennent des décisions sur les réponses à ces informations par des moyens comportementaux. Les interactions entre les prédateurs et les proies représentent l'un des événements les plus importants de la nature et posent des questions importantes pour la plupart des créatures qui ont affaire à un ou plusieurs prédateurs probables. Pour faire face à la pression de la prédation et survivre, les proies ont développé de nombreuses mesures de protection séquentielles et des stratégies anti-prédatrices complexes. De nombreux paramètres comportementaux anti-prédateurs ont évolué pour réduire en partie le risque de prédation, comme le mimétisme, le regroupement en groupes, les appels d'alarme, les signaux d'alerte et les comportements d'évasion (Caro, 2005), et l'origine et le maintien de cette diversité .

i Coloration du plumage

Prey peut éviter la prédation en se dissimulant dans l'environnement afin que les prédateurs ne parviennent pas à les trouver. De nombreuses études ont abordé les avantages anti-prédateurs du plumage cryptique chez les adultes (Götmark, 1992, Götmark & Hohlfält, 1995, Slagsvold et al., 1995), et la prédation est une force sélective en raison des avantages potentiels de la coloration du plumage (p. 1986). Chez certaines espèces, les individus changent de couleur selon les saisons (Slagsvold et Lifjeld, 1985, Steen et al., 1992) et / ou reproducteurs (Slagsvold et al., 1995), ce qui fournit des preuves additionnelles, mais non concluantes, de réduction du pelage ou du plumage. risque de prédation. La ressemblance des couleurs est plus bénéfique chez certaines espèces que chez d'autres (Cott, 1940). Par exemple, les espèces nocturnes telles que les hiboux doivent être cryptiques car elles ont tendance à rester immobiles et à dormir pendant la journée, comme le suggère Cott (1940). Cependant, même après des recherches de longue durée, il existe encore peu de preuves systématiques indiquant que la coloration du

plumage a un impact évident sur l'évitement des prédateurs. Les scientifiques ont progressivement porté leur attention sur la corrélation entre la coloration du plumage et la préférence du partenaire (par exemple Bennett et al., 1997, Ballentine et Hill, 2003, Leitão et al., 2014) et l'allocation sexuelle des descendants (Sheldon et al. et al., 2003, Romano et al., 2015).

ii Flocage

De nombreuses espèces ont développé des agrégations sociales. Un troupeau a plus de chances de détecter un danger qu'un individu solitaire (Darwin, 1871) en raison de la détection collective (Pulliam, 1973). La distance individuelle de détection d'un prédateur augmente également avec la taille du troupeau, ce qui augmente la probabilité d'évasion (Kenward, 1978). Si un prédateur ne prend qu'une proie individuelle ou un nombre inférieur à la taille d'un groupe, la probabilité d'être capturé serait plus faible que pour un individu solitaire d'une proie (Hamilton, 1971). Cette dilution du risque, la probabilité réduite d'être capturée dans des groupes plus importants, a été observée à de nombreuses reprises (par exemple, Munro et Bedard, 1977, Cresswell, 1994, Beauchamp et Ruxton, 2008). Les avantages de la détection et de la dilution s'entrecroisent à un moment donné (Bednekoff & Lima, 1998): la vigilance offre relativement moins d'avantages aux groupes plus importants, mais les deux avantages peuvent atteindre des limites et la probabilité diminue légèrement lorsque la taille du groupe augmente. En plus de réduire le risque de prédation, la collecte en groupe réduit également le temps consacré à la vigilance et améliore les possibilités de recherche de proies individuelles (Morse, 1977, Fernández et al., 2003, Beauchamp, 2014, 2015).

iii Appels d'alarme

Quand une personne-proie a déjà découvert un prédateur, sa proie peut émettre des appels d'alarme ou percevoir des signaux d'avertissement d'autres individus. Les appels d'alarme transmettent des informations sur la menace, y compris le type de prédateur (Seyfarth et al., 1980), la taille d'un prédateur (Templeton et al., 2005), le comportement d'un prédateur (Griesser, 2008), l'urgence de répondre (Leavesley et Magrath, 2005) et beaucoup d'autres indices de la menace. Ainsi, les appels d'alarme protègent les individus du groupe qui parasitent le comportement anti-prédateur de l'individu qui émet l'appel d'alarme, tout en bénéficiant à l'individu alarmé lui-même. Il y a des appels de fausse alarme effectués comme un moyen d'usurpation des ressources, augmentant ainsi la propre probabilité des appelants d'accéder à la nourriture (par exemple Munn, 1986, Møller, 1988). La reconnaissance des signaux d'avertissement intraspécifiques et interspécifiques constitue

une partie importante de la stratégie anti-prédatrice des individus qui réduit les coûts de réponse aux fausses alarmes (Treisman, 1975, Koops, 2004, Magrath et al., 2007).

iv Comportement d'évasion

Si toutes ces actions précédentes échouent, les proies devront affronter directement le prédateur. Prey ne peut rien faire d'autre que de s'échapper lorsque cette rencontre est inévitable. Contrairement à d'autres comportements anti-prédateurs avec des stratégies de suivi potentielles en cas d'échec, le comportement d'évasion est la dernière ligne de défense (Cooper & Blumstein, 2015). Ainsi, le comportement d'évasion est d'une importance particulière pour la survie et constitue une partie spécifique de la stratégie anti-prédatrice. Simultanément, l'interaction prédateur-proie a été une force motrice majeure causant l'évolution changer pour réduire le risque de prédation et améliorer la condition physique.

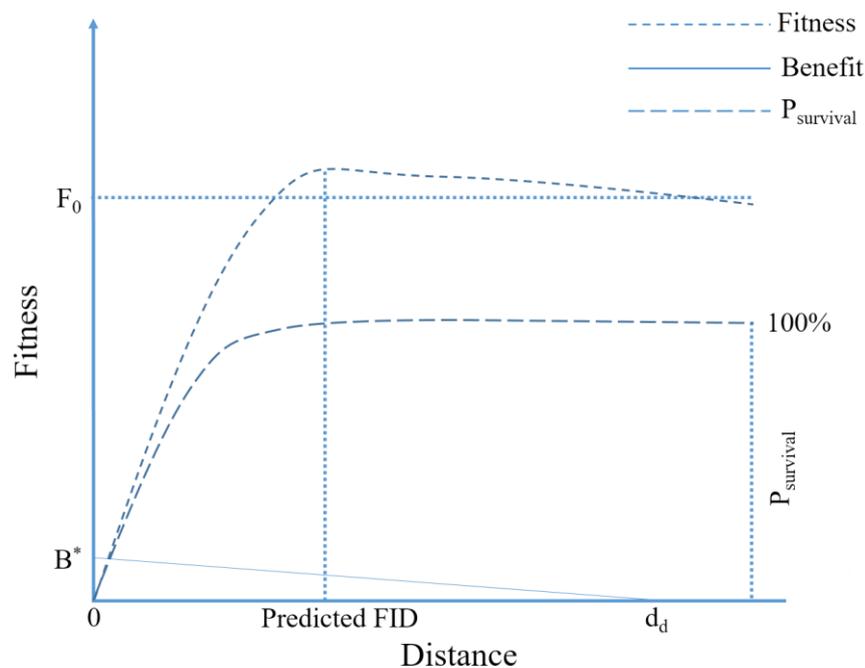


Fig. 1. Modèle d'échappement optimal. F_0 est la forme physique à l'extérieur de la rencontre; B est bénéfique lors de la rencontre représentée par une fonction linéaire passant de zéro lorsque la proie détecte le prédateur à la distance dd à B^* (le bénéfice maximum pouvant être obtenu en ne fuyant pas); le coût d'évasion est omis du graphique (y compris l'énergie dépensée sans s'engager dans des activités d'amélioration de la forme physique et pendant l'évasion) et $P_{survival}(d) = 1 - e^{-kd}$, $0 \leq d \leq dd$, est la probabilité de survie. La forme physique attendue (valeur reproductive résiduelle) dépasse la forme initiale lorsque les

bénéfices s'accroissent plus rapidement que le risque augmente. La distance d'approche optimale, prédite FID, se produit lorsque la condition physique est maximisée. Modifié par Cooper & Frederick (2007).

Plus la distance entre la proie et le prédateur est courte, plus grande est la probabilité que la proie soit tuée car l'évasion prend du temps avant de commencer alors que le prédateur se rapproche. Un individu qui n'a pas réussi à s'échapper face à un prédateur est mort. Une fuite inefficace pourrait causer des blessures à la proie, même si cela peut impliquer la survie (Dickey et McCarthy, 2002; Heithaus et al., 2002) et même les possibilités de reproduction subséquentes s'ils ont des queues ou des ailes endommagées (Fitzpatrick & Price, 1997; & Petrie, 1997). L'évasion semble être une action simple: Tant que la proie court au moment où un prédateur est détecté, la proie atteindra la probabilité maximale de survie de cette rencontre. La réponse d'un individu à un prédateur potentiel peut faire l'objet de compromis (Ydenberg et Dill, 1986, Blumstein et Bouskila, 1996, Cooper et Frederick, 2007) parce que les proies, en plus d'éviter d'être poursuivies, doivent aussi se nourrir et se reproduire. Le vol direct implique la fin / le changement de comportement en cours, ce qui signifie abandonner les avantages potentiels. Même si les individus se reposent lorsqu'ils rencontrent un prédateur, quitter immédiatement les amène à consommer plus d'énergie (Tatner et Bryant, 1986), abandonner l'habitat d'alimentation potentiel (Brown, 1999), et par la suite réduire leur forme physique. Ainsi, les animaux doivent optimiser la distance à laquelle ils commencent à s'échapper, de sorte que les avantages de rester en place sont mis en balance avec les coûts de vol (figure 1, Ydenberg et Dill, 1986). Cette distance reflète le compromis du cycle de vie entre le risque de prédation et les avantages de la recherche de nourriture.

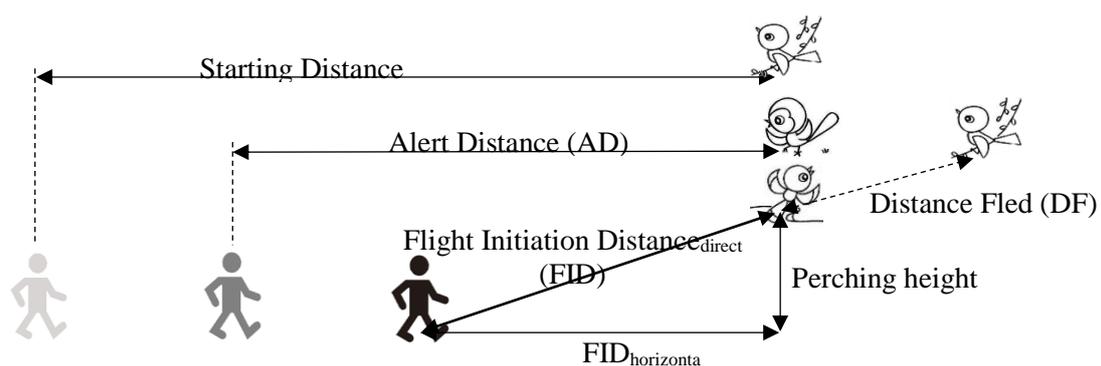


Fig. 2. Représentation schématique de plusieurs distances liées au comportement d'échappement et du calcul de la distance d'amarçage du vol.

II Distance d'initiation au vol

Tous les animaux fuient les prédateurs et les humains potentiels, et la faune réagit aux humains de la même manière qu'aux prédateurs (Frid et Dill, 2002). Les événements de prédation suivent généralement une séquence: rencontre, détection, identification, approche, assujettissement et consommation du point de vue des prédateurs (Endler, 1991). Pour cette étude de la distance de fuite, les humains sont les prédateurs présumés de la rencontre. Quand un oiseau individuel est initialement vu, il est identifié aux espèces. La distance de départ (SD) est la distance à laquelle un humain commence à s'approcher de l'individu cible, et la distance d'alerte (AD) est la distance à laquelle l'individu cible montre un comportement d'alerte clair (figure 2). La distance d'initiation de vol (FID) est la distance à laquelle un animal prend son envol lorsqu'il est approché par un humain. La rencontre est interrompue à ce moment et la distance parcourue (DF) enregistre ce qui se passe après. La SD est positivement corrélée avec le FID (par exemple Blumstein et al., 2004, Cooper, 2005, 2008). Cette relation est d'abord contrôlée mathématiquement (la FID ne peut être égale ou inférieure à SD), mais elle a aussi une composante biologique (Dumont et al., 2012). Les animaux ont un coût attentionnel pour la surveillance continue d'un prédateur qui s'approche (Blumstein, 2003, Samia et Blumstein, 2015).



Fig. 3. Photo montrant une situation similaire à celle du FID. La personne qui s'approchait s'arrêtait lorsque la personne ciblée volait ou s'éloignait, puis enregistrait la distance en mètres.

Dans cette thèse, je cible un individu avec un binoculaire et approche la cible de 100m pour les espèces de grande taille (plus de 150g) ou 30m pour les plus petites espèces (Møller & Erritzøe, 2014) pour éliminer ce problème potentiel . J'ai utilisé le théorème de Pythagore pour calculer le FID direct:

$$FID_{\text{direct}} = \sqrt{FID_{\text{horizon}}^2 + \text{Perching height}^2}$$

montré à la Fig. 2. Le vol est défini comme lorsqu'un individu focal s'éloigne à pied ou en vol en réponse à l'approche. Enfin, j'enregistre la hauteur à laquelle l'individu se perchait du sol (s'il était hors du sol, sinon cette valeur était de 0m). Les distances ont été mesurées en pas et converties en mètres ou en utilisant un télémètre laser tenu à la main. La hauteur a été estimée en tournant visuellement l'emplacement de l'individu en comparant la position avec la taille de la personne qui s'approchait (Møller, 2008a).

Il existe une abondante littérature sur la méthodologie des études de FID, et ils ont trouvé une forte relation positive entre FID enregistrée par différents observateurs, cohérence temporelle de FID dans les estimations de différentes années et FID cohérente entre différents sites (par exemple Blumstein, 2003; ., 2003, Møller et al., 2008, Møller & Erritzøe, 2014). Dans les études qui ont suivi des individus marqués, on a vérifié que le FID avait une répétabilité élevée (Carrete et Tella, 2010, 2013), ce qui est une mesure de la cohérence intra-individuelle. Ainsi, le FID est une mesure fiable du risque réel de prédation. La littérature sur le FID, mettant l'accent sur les oiseaux (Møller, 2015), les mammifères (Stankowich & Reimers, 2015) et les lézards (Cooper, 2015), ont identifié une variété de facteurs corrélés avec le FID (Cooper & Blumstein, 2015). dans le tableau 1. Le FID, en tant qu'indicateur du comportement anti-prédateur, est également connu pour être héritable et faire l'objet d'une sélection directionnelle (Dall et al., 2004; Blumstein et al., 2010; Møller & Nielsen, 2010; Bize et al. ., 2012).

III L'héritabilité du comportement d'évasion

Le comportement d'échappement est la dernière étape du comportement anti-prédation avant la capture. L'individu est susceptible de faire face à la mort une fois que sa fuite échoue. Par conséquent, un comportement d'évasion efficace devrait avoir une forte composante héréditaire, car son lien fort et direct avec la survie offre des possibilités limitées de «pratique». La plupart des caractères ont une base génétique quantitative avec la progéniture ressemblant à leurs parents dans le phénotype. La répétabilité est une limite supérieure de

l'héritabilité, et le produit de l'héritabilité et de l'intensité de la sélection est égal à la réponse à la sélection (Falconer et Mackay, 1996). Ainsi, des estimations d'héritabilité sans biais et des estimations de sélection peuvent être utilisées pour prédire la réponse micro-évolutive. Ainsi, si par exemple l'intensité de la sélection augmente, nous devrions être en mesure de prédire l'augmentation du phénotype en raison de la réponse à la sélection. Généralement, le comportement d'échappement est une réponse à l'environnement et est sujet à la sélection naturelle. Moins d'études ont étudié l'héritabilité du comportement. Le comportement lui-même est le résultat d'une performance globale en réponse à divers facteurs (Sih et al., 2004, Bonduriansky et Day, 2009), incluant la régulation physiologique (Ricklefs & Wikelski, 2002), la capacité cognitive (Griffin et al. Cole et al., 2012) et les contraintes morphologiques (Foster et al., 2015). Pour de nombreuses espèces, les parents et leur progéniture vivent dans des territoires géographiquement adjacents (si ce n'est les mêmes) et ils sont susceptibles de se comporter de la même façon (Wilson, 1998). Les effets sur la maternité peuvent également jouer un rôle important en affectant les réactions comportementales de la progéniture à l'environnement, y compris l'environnement maternel (Eising et al., 2006). En outre, l'apprentissage et l'imitation peuvent être d'autres explications des similitudes de comportement entre les générations, qui peuvent provenir des soins parentaux aussi bien que des pairs (Koolhaas et al., 1999, Hamm, 2000).

Il y a peu d'études qui démontrent que le comportement d'évasion est héritable, car il est difficile d'étudier l'héritabilité du comportement d'évasion dans des conditions de terrain. Les pétoncles juvéniles, *Argopecten purpuratus*, présentaient une héritabilité significative et une corrélation génétique significative entre plusieurs caractères de réponse à l'échappée en utilisant le modèle de fraie complète / demi-fratrie (Brokordt et al., 2012). Les couleuvres rayées *Thamnophis ordinoides* ont montré des héritabilités et des corrélations génétiques significatives parmi les caractères d'échappement en utilisant une analyse génétique quantitative basée sur le pedigree (Brodie, 1989), et sa distance d'initiation en vol a montré un effet familial significatif (King, 2002). Le comportement antiprédateur des martinets alpins adultes *Apus melba* était significativement reproductible et héritable sur la base des observations comportementales à long terme des parents et de la progéniture croisée (Bize et al., 2012). Des données à long terme sur la FID dans une population d'hirondelles rustiques *Hirundo rustica* ont rapporté une héritabilité significative du FID avec un effet de taille de la couvée maternelle et des héritabilités similaires basées sur la ressemblance père-enfant et la ressemblance mère-progéniture (Møller, 2014). Ce dernier peut suggérer que les effets maternels ne sont pas des déterminants majeurs de la FID chez cette espèce.

IV Risque de prédation et FID

i Risque de prédation et FID

Le risque de prédation est susceptible d'avoir une relation concave à la hausse avec la distance par rapport aux prédateurs potentiels, et il augmente fortement à de courtes distances (figure 1, Cooper et Frederick, 2007). Cette hypothèse inhérente à la prise de risque et au FID a été confirmée par des preuves empiriques basées sur des différences intra et inter-espèces. Une étude portant sur 30 agames *Agama planiceps* mâles de Namibie a révélé que les mâles audacieux ayant une FID relativement courte subissaient des niveaux plus élevés de perte de queue, probablement en raison de la prédation (Carter et al., 2010). Møller (2014) a analysé des données à long terme sur le FID dans une population d'hirondelles rustiques *Hirundo rustica* au cours de la période 1984-2013 avec 2196 enregistrements pour 1789 individus. Parmi ces oiseaux, un total de 13 adultes tués par des chats *Felis catus domesticus* et 5 adultes chassés par des éperviers ont été identifiés à partir des restes, y compris des bagues. Ces 18 individus qui sont morts de la prédation avaient significativement moins de FID que les survivants. Des preuves plus indirectes d'espèces d'oiseaux tropicaux jumelés et d'espèces d'oiseaux tempérés proches ont montré que les espèces tropicales avaient une FID relativement plus courte, comme le prédit la grande différence d'abondance ou de diversité de la communauté de prédateurs par rapport à la latitude (Møller & Liang, 2013).

La différence entre les espèces dans le FID moyen reflète également la différence de risque de prédation entre les espèces. Par exemple, dans une analyse comparative de 40 espèces d'oiseaux, les espèces particulièrement sensibles à la prédation par les éperviers ont pris leur envol à des distances plus courtes (figure 4, Møller et al., 2008). Le risque de prédation par les chats domestiques (Møller et al., 2010) et le risque de collision avec les véhicules (Møller et al., 2011) étaient également négativement liés au FID parmi les espèces, et ces relations restaient robustes même après contrôle des facteurs associés au risque de prédation tels que la masse corporelle et le dichromatisme sexuel. Ainsi, des FID plus longs sont associés à un risque réel de prédation plus faible et à des niveaux plus faibles de prise de risque en présence d'un véritable prédateur.

Certaines études ont montré un effet du risque perçu de prédation sur la FID des oiseaux. La visibilité artificiellement modifiée n'a pas affecté la décision de vol des rosellums cramois *Platycercus elegans* lorsque leur perception globale du risque est restée la même (Boyer et al., 2006). Le pluvier à double baguette *Charadrius bicinctus* a réagi à la présence de chats et d'autres prédateurs de mammifères en augmentant le FID en réponse à l'approche

des humains (St. Clair et al., 2010). Une étude intraspécifique a montré que le FID chez *Melospiza melodia* était plus long suite à la reproduction expérimentale des appels de prédateurs que les vocalisations de non-prédateurs (Zanette et al., 2011).

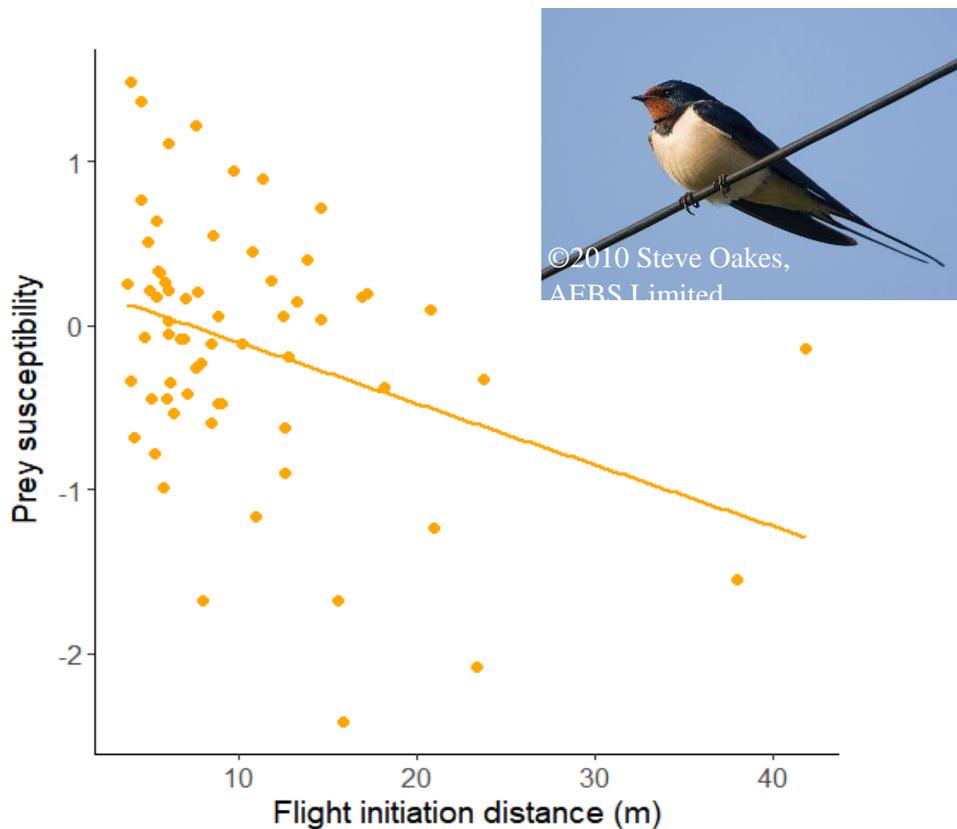


Fig. 4. Vulnérabilité à la prédation par l'épervier par rapport à la distance d'initiation en vol (m) par différentes espèces d'oiseaux. La susceptibilité aux proies est calculée comme étant le nombre de proies transformées log₁₀ observées moins le nombre attendu de proies transformées log₁₀. La ligne est la ligne de régression linéaire. Modifié à partir de Møller et al. (2008).

ii Trois variables potentielles prédisant la variation interspécifique dans le FID

a masse corporelle

La performance au décollage diminue avec l'augmentation de la masse corporelle (Metcalf et Ure, 1995, Warrick et Dial, 1998). Un organisme volant relativement grand prend plus de temps avant le décollage, car avec l'augmentation de la taille du corps, les besoins en puissance du vol augmentent plus vite que la capacité du muscle à fournir de l'énergie (Tobalske & Dial, 2000). Outre la relation directe entre la masse corporelle et la performance

en vol, la masse corporelle est également le meilleur prédicteur de l'histoire de la vie, du comportement, de la physiologie et du risque d'extinction (Bennett et Owens, 2002). Il y a des raisons de croire que la FID et la masse corporelle sont significativement associées. Les scientifiques ont remarqué que les oiseaux plus petits étaient plus accessibles que les espèces plus grosses (Hemmingsen, 1951, Cooke, 1980). L'un des meilleurs prédicteurs de la réponse des oiseaux aux perturbations humaines est la masse corporelle (Samia et al., 2015b). De nombreuses études ont rapporté des corrélations positives constantes entre la FID et la masse corporelle. Blumstein (2006) a rapporté une taille d'effet en termes de coefficient de corrélation produit-moment de Pearson de 0,044 pour 150 espèces d'oiseaux. Fernández-Juricic et al. (2006) ont analysé spécifiquement la masse corporelle et la FID de 83 espèces de 29 familles et trouvé une taille d'effet de 0,585, tandis que Weston et al. (2012) ont rapporté des FID et des informations sur la masse corporelle de 250 oiseaux australiens et ont trouvé une taille d'effet de 0,48. Møller (2008a) a étudié des populations urbaines de 40 espèces d'oiseaux et signalé une taille d'effet de 0,78. Une méta-analyse portant sur le DIF chez les oiseaux a rapporté la deuxième plus grande taille de l'effet (0,39) de la masse corporelle (après l'urbanisation) parmi les différentes catégories de traits phénotypiques (Møller, 2015). Ainsi, les grandes espèces ont un FID relativement long (figure 5).

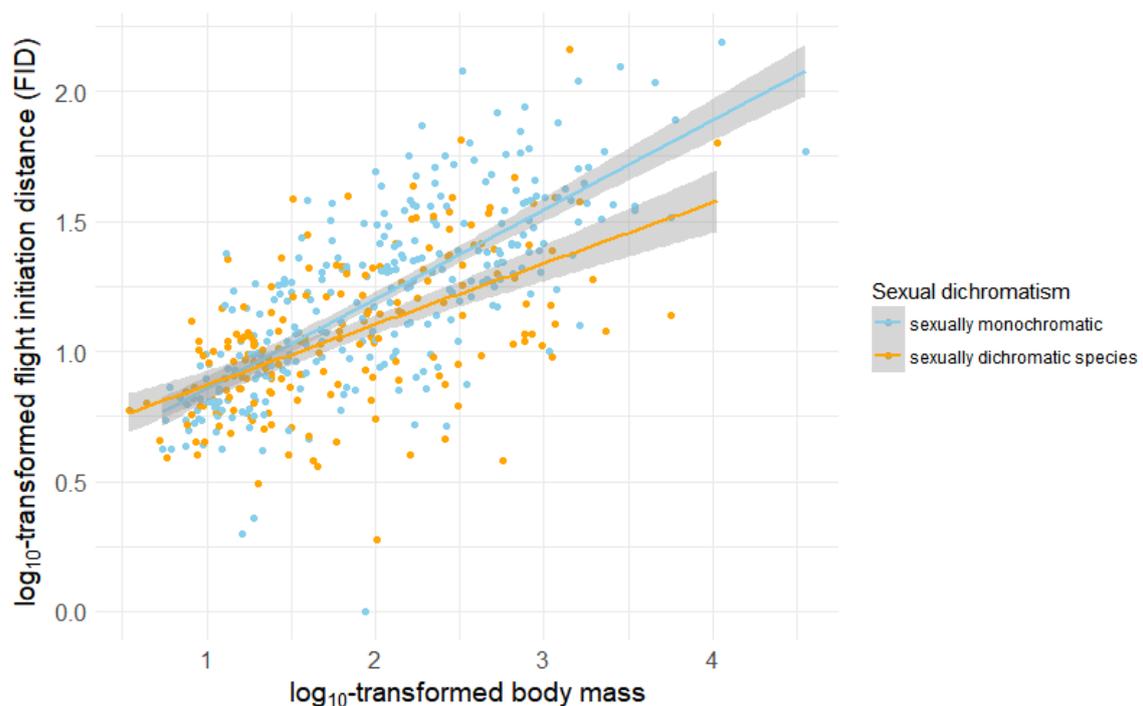


Fig. 5. Distance d'initiation du vol par rapport à la masse corporelle et au dichromatisme sexuel. Les deux droites sont les droites de régression linéaire pour les espèces sexuellement monochromatiques (points bleus et ligne bleue) et sexuellement dichromatiques (points

orange et ligne orange). Les zones grises sont les intervalles de confiance de 95% pour chaque régression linéaire. Modifié à partir de Møller et al. (2016).

Alors que les études ont souvent montré des distances de vol moyennes pour les espèces augmentant de manière significative avec la masse corporelle, la pente de cette relation est toujours inférieure à un. Par exemple, dans une étude portant sur 250 espèces d'oiseaux australiens, $R^2 = 0,480$, pente = 0,293 (0,046, Weston et al., 2012). Møller (2008c) a trouvé que cette relation était beaucoup plus faible dans une régression phylogénétique basée sur des observations de 100 espèces d'oiseaux européennes avec une pente (SE) = 0,20 (0,10), beaucoup plus petite qu'une. Ainsi, le FID augmente plus lentement que la masse corporelle et les grandes espèces ont une FID relativement plus courte pour leur masse corporelle.

b Morphologie

Les caractéristiques morphologiques et comportementales influencent la variation interspécifique du comportement d'échappement. Bauwens et al. (1995) ont trouvé que l'évolution du comportement d'échappement (capacités maximales de sprint maximales) était mécaniquement liée à l'évolution de la morphologie (membres postérieurs plus longs par rapport à la longueur du corps) chez 13 espèces de lézards. La morphologie des oiseaux a été fermée en relation avec les performances de vol et le coût de l'énergie tel que prédit par la théorie de la dynamique de vol (Rayner, 1988). Les oiseaux migrateurs ont montré une vitesse de fuite réduite avec l'augmentation de la charge alaire (masse / aile) (Burns & Ydenberg, 2002). La morphologie de la forme des ailes et de la morphologie des membres postérieurs influence également la variation interspécifique des taux de prédation chez les passereaux (Swaddle et Lockwood, 1998). Ainsi, le DIF chez les oiseaux pourrait varier avec la morphologie des ailes et des membres postérieurs. Par exemple, une étude comparative sur 83 espèces d'oiseaux a montré que les oiseaux ayant des ailes plus pointues fuyaient sur de plus longues distances et se posaient plus loin que les espèces aux ailes arrondies (Fernández-Juricic et al., 2006). De même, les espèces ayant une FID longue pour leur taille corporelle avaient également de grandes surfaces alaires et des rapports d'aspect (figure 6, Møller et al., 2013b). La relation entre la morphologie des espèces et le DIF pourrait également être expliquée d'un point de vue physiologique puisque le FID est négativement relié à l'hématocrite, une mesure du volume des globules rouges tassés et indique ainsi la capacité de transport de l'oxygène et donc la réaction de contraction des muscles. Møller et al., 2013b). Le taux métabolique de base (BMR), représentant le niveau

minimum de métabolisme qui permet le fonctionnement normal d'un individu dans son environnement, était également positivement lié au FID (Møller, 2009). Ainsi, le comportement d'échappement a coopéré avec un certain nombre d'adaptations et de contraintes différentes en termes de morphologie.

c Capacité cognitive et taille du cerveau

Les informations sur le risque de prédation potentiel sont collectées par les organes sensoriels et ensuite traitées par le cerveau. La capacité cognitive fausse le comportement des animaux et influence la façon dont les animaux interagissent avec les habitats naturels (Dukas et Ratcliffe, 2009). Un certain nombre d'études ont montré que les animaux utilisent des capacités cognitives pour accéder au comportement des prédateurs qui se manifestent par une distance de vol modifiée. Par exemple, les oiseaux ont des FID plus courts s'ils sont approchés tangentiellement plutôt que directement (Fernández-Juricic et al., 2005; Geist et al., 2005; Møller & Tryjanowski, 2014), ou s'ils sont abordés avec des yeux humains plutôt ailleurs, que de les regarder directement (Bateman & Fleming, 2011). Dans une étude comparative de 107 espèces, Møller & Erritzøe (2014) ont constaté que les oiseaux ayant un cerveau relativement gros pour leur taille corporelle évitaient la ruée vers l'approche d'un prédateur. La corrélation négative pourrait être causée par des espèces avec des cerveaux relativement grands connaissant plus de coûts d'opportunité contrôlant l'intention du prédateur (par exemple, grâce à une meilleure évaluation de la distance et de la vitesse du prédateur) (Cooper & Blumstein, 2014). Ils prennent la décision d'évasion la moins chère après l'évaluation et la surveillance de la menace de prédation, réduisant ainsi les coûts énergétiques du vol (Samia et al., 2015b). La taille relative du cerveau a également influencé indirectement l'invasion des habitats urbains par son effet positif sur la variabilité interindividuelle de la FID (Carrete et Tella, 2011).

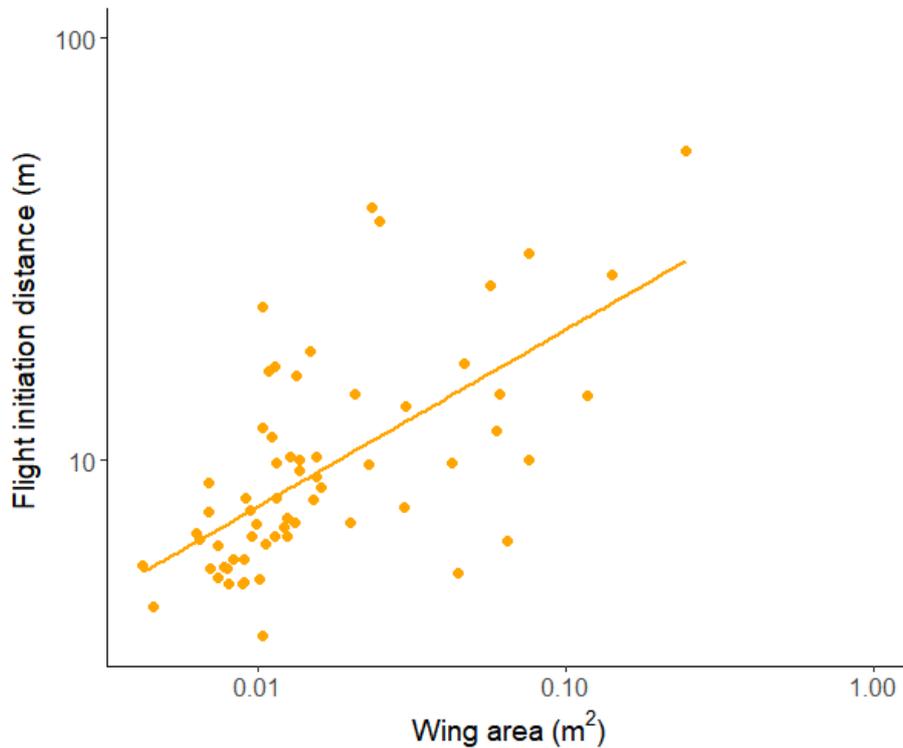


Fig.6. Distance d'initiation de vol (m) par rapport à la surface de l'aile (m²) dans 63 espèces différentes d'oiseaux. Les axes x et y sont mis à l'échelle logarithmique. L'ajustement est la ligne de régression linéaire. Modifié à partir de Møller et al. (2013b).

V Conséquences du FID

Manuscrit n° 1 p. 55-64 (Évasion des prédateurs et variance génétique chez les oiseaux)

Manuscrit n° 3 p. 72-99 (Les covariations de la spécificité évolutionnaire avec un comportement anti-prédateur dans les communautés d'oiseaux)

Manuscrit n° 4 p. 100-126 (La distance d'initiation du vol est corrélée au stress oxydatif chez les oiseaux)

i Conséquences sur la population

Les distances d'initiation au vol fournissent des informations sur le risque que les individus sont prêts à assumer compte tenu de leur état et de l'environnement, et les espèces avec des FID relativement longues devraient plus souvent souffrir de perturbations de leurs activités par les prédateurs potentiels. Sur la base d'un ensemble de données de plus de 4000 FID pour 133 espèces en Europe, la taille des populations reproductrices dans le Paléarctique

occidental était plus petite dans les espèces avec des FID moyennes longues et de faibles variations dans le FID (Møller & Garamszegi, 2012). Dans une étude comparative de 56 espèces en Europe, les espèces à FID longues ont également montré une fréquence plus élevée de populations en déclin que les espèces à FID court (Møller, 2008c). Ces résultats suggèrent que la FID moyenne pour différentes espèces fournit des informations fiables sur les conséquences sur la population du comportement à risque des individus et de la sensibilité des différentes espèces aux perturbations.

Néanmoins, l'association entre la FID et la tendance de la population est plus complexe qu'il n'y paraît. Dans une étude intercontinentale portant sur 193 espèces d'oiseaux de trois continents, l'Amérique du Nord, l'Australie et l'Europe, continent et FID ont montré une interaction significative entre toutes les variables expliquant les changements de population des oiseaux. Alors que les populations d'oiseaux diminuaient avec l'augmentation de la FID en Australie et en Europe, la tendance inverse a été observée en Amérique du Nord (Møller et al., 2014). Une autre étude sur 46 espèces d'oiseaux en Angleterre a également échoué à trouver une relation significative entre le changement de la population d'espèces et le FID (Thaxter et al., 2010). Ces cas ont déclenché des études sur la structure géographique du comportement des oiseaux, et une étude de suivi a montré des effets interactifs du comportement d'échappement des espèces et de la localisation géographique sur les tendances des populations d'oiseaux européens (Díaz et al., 2015). La susceptibilité à la prédation par les éperviers (Møller, 2014) et le taux de survie des adultes (Møller et Garamszegi, 2012) étaient significativement liés positivement à la FID moyenne. Cependant, la taille de la population et les tendances de la population tendent à être le résultat net d'interactions complexes entre l'altération de l'habitat, les changements climatiques et les stratégies migratoires (Cuervo et Møller, 2013; Reif, 2013) combinées avec un comportement d'évasion (Díaz et al. 2015).

ii Urbanisation

Les scientifiques ont remarqué que les espèces urbaines ont généralement une FID relativement courte par rapport à leurs homologues ruraux (Figure 7, Cooke, 1980, Sol et al., 2013, Møller, 2015, Samia et al., 2017). L'ampleur de la différence est directement liée au temps écoulé depuis l'urbanisation (Møller, 2008a). La variation de la FID relative (contrôlée par la masse corporelle) des populations urbaines est positivement liée à la densité de la population urbaine des différentes espèces (Lin et al., 2012). L'ampleur de la variance pourrait également être prédite par le nombre de générations depuis l'urbanisation (Møller,

2008a), comme prévu par une sélection progressive de la vie urbaine. Six composantes différentes du comportement d'évasion étaient liées à l'urbanisation, suggérant que le comportement anti-prédateur a divergé entre les populations rurales ancestrales et les populations urbaines récemment établies (Møller & Ibáñez-Álamo, 2012). Ainsi, la différence de FID entre les habitats ruraux et urbains est probablement liée aux changements récents dans la communauté des prédateurs suite à l'urbanisation. En effet, cette différence de FID est parallèle aux tendances de l'abondance des rapaces, car elle diminue avec l'augmentation de la latitude (Díaz et al., 2013). Outre les différences dans la communauté des prédateurs, d'autres impacts potentiels de l'urbanisation qui augmentent l'état corporel des individus (Geue & Partecke, 2008, Delgado-V et French, 2012), la disponibilité et la fiabilité des aliments (Jokimäki et al., 1996; Galbraith et al., 2015) réduisent également le coût relatif du vol. Par exemple, la présence de mangeoires dans les habitats urbains a également contribué de manière indépendante à une réduction de la FID, comme le montre une étude des populations hivernales en Pologne et des différences de prédateurs entre milieux urbains et ruraux (Møller et al., 2015).

Cependant, toutes les espèces ne sont pas également adaptées à l'urbanisation (McKinney, 2002, 2006, Morelli et al., 2016). Par exemple, la présence omniprésente des humains et les perturbations constantes des véhicules pourraient empêcher la plupart des espèces d'envahir avec succès les villes. Une étude menée en Europe a montré que les espèces qui réussissent à coloniser les zones urbaines présentaient des écarts plus importants dans les FID de leurs populations rurales que les colonisateurs non réussis (Møller, 2010). Ceci conforte l'hypothèse que l'urbanisation résulte d'une colonisation différentielle des zones urbaines par des espèces aux niveaux de peur hétérogènes dans les populations rurales ancestrales. Une étude sur 42 espèces d'oiseaux dans une ville sud-américaine récemment établie a également montré que la variabilité interindividuelle dans la peur des humains était positivement liée à l'invasion urbaine contemporaine des oiseaux, positivement augmentée par la taille relative du cerveau des espèces (Carrete & Tella, 2011). Ainsi, le FID peut jouer un rôle crucial dans l'urbanisation des oiseaux et des espèces avec une variance relativement importante du comportement d'évasion, au lieu que les animaux domestiques soient mieux adaptés à l'environnement urbain. En outre, les environnements urbains sont susceptibles de créer un refuge sûr pour les proies, car les prédateurs montrent une plus grande peur de la proximité des humains que leurs proies (Møller, 2012). La moyenne spécifique à l'espèce et la variance de la FID conduisent à des tendances distinctes de la population pour différentes espèces et contribuent à l'homogénéisation biotique en milieu urbain.

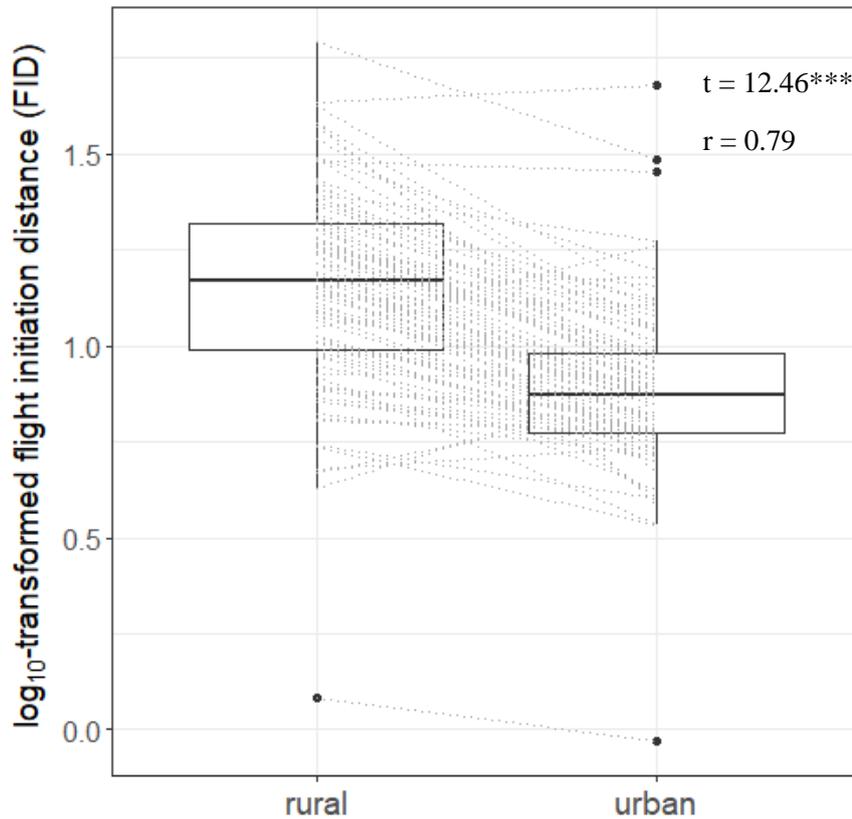


Fig. 7. Différences entre les zones rurales et les zones urbaines en matière de FID pour 92 populations d'oiseaux étudiées en Europe. Les boîtes à moustaches montrent la médiane, les quartiles, les percentiles 5 et 95 et les valeurs extrêmes. La trajectoire de chaque population est illustrée par une ligne pointillée grise. Les valeurs t et les tailles d'effet calculées comme des coefficients de corrélation partiels sont montrées. Les valeurs t étaient hautement significatives ($*** P < 0,001$). Modifié à partir de Samia et al. (2017).

iii Effets non létaux

Comme la FID est déterminée par les avantages contradictoires du gain énergétique et du risque de mortalité due à la prédation ou à d'autres causes, une FID relativement plus longue implique un abandon précoce des ressources locales et une consommation d'énergie plus importante. Le coût immédiat d'une disponibilité réduite des ressources peut alors se traduire par une réduction du rendement reproductif ou de la survie à long terme (Lima, 1998). Outre le coût énergétique du vol, le coût attentionnel de la surveillance des prédateurs pour évaluer le risque de prédation nécessite également une consommation d'énergie, ce qui explique pourquoi la FID augmente (AD) ou sa distance de départ (SD) augmente (Cooper & Blumstein, 2014). Les effets non létaux du FID, associés à la consommation directe de

prédateurs et à d'autres effets non létaux qui réduisent ou limitent l'apport énergétique, peuvent tous réduire la densité de la population (Abrams, 1984).

En tant que mesure quantitative de la tolérance des oiseaux aux perturbations, la variance de la FID devrait prédire la diversité des réponses comportementales à l'environnement. Les espèces présentant une plus grande diversité de comportements d'évasion exploitent des habitats plus différents en s'adaptant avec succès à différentes conditions environnementales imprévisibles. Compte tenu de la forte homogénéité individuelle du FID, la répartition des individus entre les habitats dépend en grande partie de leur susceptibilité aux perturbations humaines, comme le montrent les chouettes des terriers *Athene cunicularia* (Carrete et Tella, 2010). Des preuves provenant de 133 espèces d'oiseaux en Europe soutiennent que les espèces avec une plus grande variance dans le FID exploitent une plus grande diversité d'habitats que celles avec une variance relativement plus faible (Møller & Garamszegi, 2012). La variation de la variance de la volaille dans la FID était significative pour la diversité des habitats des espèces (Garamszegi & Møller, 2017). Le choix du microhabitat et l'exposition post-chant du moucherolle à collier mâle *Ficedula albicollis* au cours de la signalisation sexuelle sont étroitement liés à la FID, selon le tempérament individuel intrinsèque (Garamszegi et al., 2008). L'effet de la variance de la FID sur la sélection de l'habitat peut également se refléter dans les différences d'invasions de l'habitat urbain, comme mentionné dans la section précédente.

VI Conséquences pour la conservation et la gestion

Manuscrit n° 2 p. 65-71 (distances de fuite anti-prédateur des oiseaux communs et menacés)

Les humains influencent largement d'autres créatures vivant sur la planète et, par conséquent, nous subissons peut-être une perte de diversité biologique (McNeely, 1992, Andrén, 1994, Vitousek et al., 1997, Parmesan et Yohe, 2003). Étonnamment, la perturbation due à l'activité humaine a été le principal facteur de richesse, supplantant même la perte et la fragmentation de l'habitat dans une étude de sélection sur des communautés d'oiseaux terrestres dans un environnement urbanisé (Schlesinger et al., 2008). Ceci est plausible parce que les stimuli d'origine humaine pourraient être considérés comme une forme de risque de prédation, compte tenu de sa similitude avec le risque de prédation. Il affecte indirectement les composantes de la condition physique et la dynamique de la population par l'énergie et les coûts d'opportunité perdus de l'évitement des risques (Frid et Dill, 2002). Bien que les populations perturbées soient plus tolérantes aux perturbations humaines que les populations

moins perturbées (Samia et al., 2015b), une situation problématique apparaît lorsque les humains sont considérés comme des prédateurs potentiels, et une tolérance croissante aux proies pourrait accroître leur vulnérabilité aux prédateurs (Geffroy et al. ., 2015). Avec l'expansion continue de l'impact humain, la protection des espèces sauvages devient de plus en plus importante. Le comportement d'évasion fournit des moyens importants pour résoudre les problèmes de conservation dans la recherche de moyens de conservation plus efficaces.

De nos jours, l'application la plus courante de FID sur la conservation est de définir la «distance tampon» ou les «zones tampons» (par exemple Rodgers & Smith, 1995, Rodgers & Schwikert, 2002). De même, le FID est également utilisé comme référence pour l'aménagement paysager dans les réserves naturelles ou les parcs (Fernández-Juricic et al., 2001a, b, Blackwell et al., 2009) afin de réduire les impacts humains sur la faune. Certaines de ces études ont porté sur des espèces menacées (par exemple González et al., 2006, Zuberogitia et al., 2014), tandis que d'autres ont tenté d'inclure autant d'espèces que possible pour établir une norme uniforme pour la conservation des espèces locales. (2012) ont suggéré de gérer la perturbation des oiseaux australiens.

Questions de recherche

I Le comportement d'échappement interfère-t-il avec la variance génétique?

Alors que les scientifiques ont trouvé une relation significative mais complexe entre la taille de la population, la tendance de la population et la FID, il existe peu de connaissances sur la relation entre la taille effective de la population et la FID. Les populations consanguines sont menacées parce qu'elles ont peu de possibilités de réactions micro-évolutives aux changements environnementaux, et la fécondité et la viabilité des individus consanguins sont souvent réduites par rapport aux individus non consanguins. Le comportement d'évasion fournit le mécanisme comportemental sous-jacent qui explique la réaction des individus à des conditions environnementales défavorables. Je prédis que les espèces à FID relativement longues sont aussi celles qui ont une grande variabilité génétique. Une FID courte indiquant un risque de prédation supérieur favorise une taille de population plus petite avec une variabilité génétique ou pourrait être le résultat d'une faible variabilité génétique chez ces espèces. En établissant une corrélation entre les distances d'échappement des antiprédateurs et la variabilité génétique, nous pouvons mieux comprendre les mécanismes

responsables de la réduction de la taille de la population, mais aussi adopter un meilleur choix de projets de rétablissement compte tenu du grand nombre de prédateurs dans la nature.

II Le FID pourrait-il servir d'indicateur du statut de menace des espèces?

L'état de menace des espèces est évalué en fonction de l'étendue de leur habitat, de la taille de la population, du développement de la population au cours des dernières années et de nombreux autres facteurs. Pendant ce temps, la distance d'initiation de vol reflète le compromis de cycle de vie entre le risque de prédation et les avantages de la recherche de nourriture à court et à long terme. Les espèces ayant une FID relativement courte sont mieux à même de faire face à la proximité des humains et peuvent avoir plus de temps et d'opportunités pour obtenir de la nourriture et des perspectives de reproduction et de survie supérieures dans l'environnement avec une interférence humaine élevée. Ainsi, le FID peut être un prédicteur pratique de l'état de menace de différentes espèces. Je m'attends à ce que les espèces relativement menacées aient une FID plus longue que les espèces étroitement apparentées, étant donné le taux croissant de perturbation humaine et les normes d'état de menace. J'ai vérifié la relation entre la FID moyenne des espèces et le statut de la menace chez les espèces étroitement apparentées.

III Le FID pourrait-il contribuer au caractère distinctif évolutif du trait à long terme?

La coévolution prédateur-proie peut entraîner une divergence rapide à la fois des prédateurs et des proies et un comportement de fuite, car la dernière ligne d'évasion des prédateurs devrait jouer un rôle crucial dans la survie des individus. Le caractère distinctif de l'évolution (ED) reflète l'isolement phylogénétique des taxons avec des valeurs élevées caractérisant les espèces avec des phénotypes uniques qui dévient le plus des autres taxons. Alors que la plus grande préoccupation en matière de conservation concerne les espèces les plus distinctes du point de vue de l'évolution mondiale, le caractère distinctif phylogénétique global des zones urbaines diminue à travers le monde. Des décisions d'évasion appropriées devraient équilibrer les coûts de la perte de nourriture ou des possibilités d'accouplement, et les avantages de s'échapper du risque de prédation réduit. Un tel comportement anti-prédateur devrait affecter la capacité à éviter la prédation et devrait donc contribuer à des valeurs élevées de DE chez certaines espèces. Je m'attends à ce que la dysfonction érectile soit

positivement liée à la FID, car les espèces qui prennent le moins de risques lorsqu'elles rencontrent des prédateurs sont moins sensibles à la prédation. Le test de cette corrélation entre les caractères ED et comportementaux en cas de sélection forte peut nous aider à comprendre l'évolution de l'ED et donc à permettre une meilleure protection de ces espèces.

IV Y a-t-il un «effet secondaire» d'une évasion précoce?

Bien que les individus qui prennent un vol rapide à l'approche des prédateurs prennent de petits risques lors des rencontres, ils doivent également décoller plus fréquemment à la même fréquence d'interférence. Un battement aérien court et bref est métaboliquement coûteux, ce qui peut entraîner un taux métabolique basal de 23 fois (Tatner et Bryant, 1986). Les vols d'évasion fréquents en présence de prédateurs potentiels sont énergétiquement coûteux et stressants, contribuant potentiellement à la production de radicaux libres et donc au stress oxydatif, résultat du métabolisme. Le stress oxydatif joue un rôle clé dans l'évolution des modèles d'investissement optimaux entre la reproduction et la survie et d'autres composantes de la condition physique. L'activité physique est une cause potentielle importante de stress oxydatif mais, étonnamment, aucune étude n'a examiné comment le stress oxydatif est lié au comportement d'évasion qui reflète le compromis de vie entre le risque de prédation et les avantages du butinage. Je prédis que les espèces ayant une FID relativement courte pour leur masse corporelle connaîtraient plus de stress oxydatif, car les vols fréquents entraînent une consommation d'énergie et un stress élevés. J'ai testé cette relation causale possible dans des analyses comparatives avec trois indicateurs différents pour le stress oxydatif et considéré la masse corporelle et la taille du cerveau comme des facteurs de confusion.

V Le comportement social affecte-t-il le comportement d'évasion?

La sociabilité (directement liée à la taille du groupe) a une taille d'effet moyenne intermédiaire de 0,26 sur FID dans une méta-analyse de facteurs coopératifs chez les oiseaux (Møller, 2015). La taille du groupe a également été suggérée comme un trait de proie important qui influence les décisions d'évasion (Samia et al., 2017). La détection collective (probabilité accrue de détection d'un prédateur dans des groupes plus importants, Pulliam, 1973) et la dilution du risque (probabilité réduite d'être capturée dans des groupes plus importants, Hamilton, 1971) pourraient affecter le comportement d'échappement des

individus. Des études antérieures avaient démontré que le FID était positivement lié à la taille du troupeau (Laursen et al., 2005, Tätté et al., 2018). Cependant, la grégarité (la tendance à vivre en groupes) pourrait potentiellement affecter la capacité de l'individu à communiquer avec les autres et ensuite affecter le comportement d'évasion de l'individu. En conséquence, le but de cette étude était de tester si la FID chez les oiseaux augmentait avec la taille du troupeau, en mettant l'accent sur les différences entre les espèces grégaires et non grégaires.

Résumé

I S'échapper des prédateurs et de la variance génétique chez les oiseaux

Cette étude a utilisé des analyses phylogénétiques généralisées des moindres carrés pondérées avec la taille de l'échantillon dans 128 espèces d'oiseaux. Les résultats ont révélé que trois variables représentatives de la variabilité génétique (1) partage des bandes minisatellites (figure 8), (2) hétérozygotie et (3) coefficient de consanguinité étaient toutes liées à la forte approximation du risque de prédation réel (FID). Ainsi, des niveaux plus élevés de variabilité génétique étaient systématiquement associés à une FID plus longue. Ces résultats étaient robustes aux effets potentiellement confondants de variables telles que l'aire de reproduction, la taille de la population et la masse corporelle.

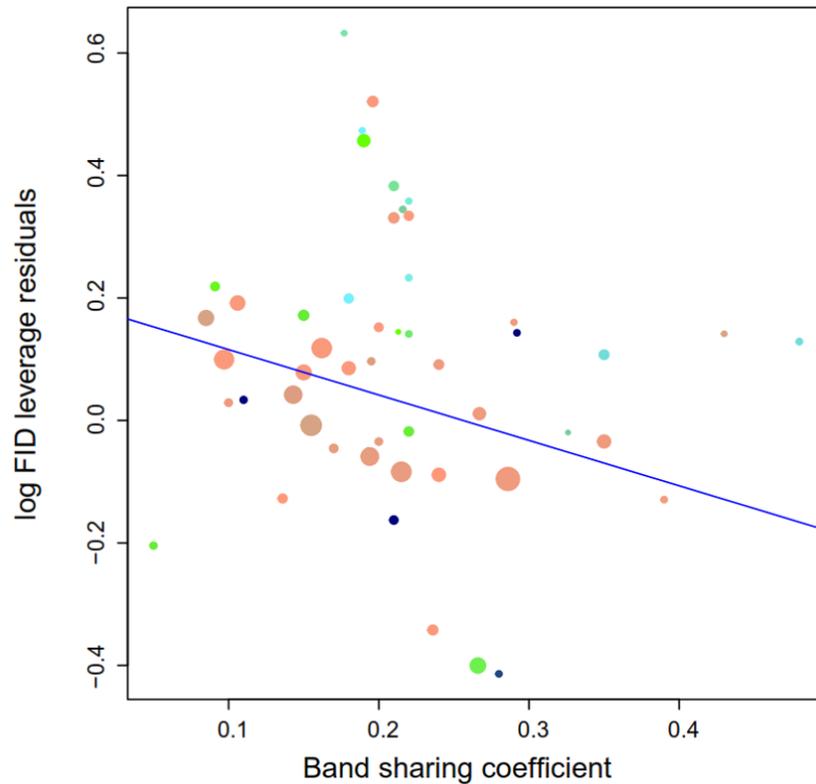


Fig. 8. La distance d'amorçage du vol transformé en log10 (FID (m)) a diminué avec l'augmentation du coefficient de partage de la bande sur 52 espèces d'oiseaux. La taille des symboles est proportionnelle à la taille de l'échantillon transformé par la racine carrée. Les couleurs représentent différentes espèces avec des espèces plus proches ayant des couleurs plus similaires. La ligne est la ligne de régression linéaire.

II Distances de fuite anti-prédateur des oiseaux communs et menacés

Cette étude a associé le risque d'extinction à la distance d'évasion chez les oiseaux européens. En analysant le DIF de 48 paires d'espèces d'oiseaux étroitement liées différant dans leur statut de menace, j'ai conclu que les oiseaux menacés ont généralement un FID plus élevé que les espèces proches non menacées. Cette différence de FID entre les espèces communes et menacées était presque double et était cohérente dans les tests paramétriques et non paramétriques.

III Les covariances évolutionnistes de la spécificité avec un comportement anti-prédateur dans les communautés d'oiseaux

Ce chapitre a porté sur le rôle possible du comportement d'échappement (FID) dans un contexte évolutif chez les oiseaux d'eau. Au total, 48 oiseaux aquatiques migrateurs et 30 oiseaux résidents ont été étudiés. Les résultats du modèle linéaire généralisé phylogénétique ont montré une corrélation positive significative entre le score ED et le FID relatif (contrôlé par la masse corporelle) (figure 9). Ce résultat était robuste aux différences d'effort d'échantillonnage et aux effets potentiellement confondants de la masse corporelle, de l'état migratoire, de l'étendue des aires de reproduction et de la similitude entre les taxons en raison de la descendance phylogénétique commune.

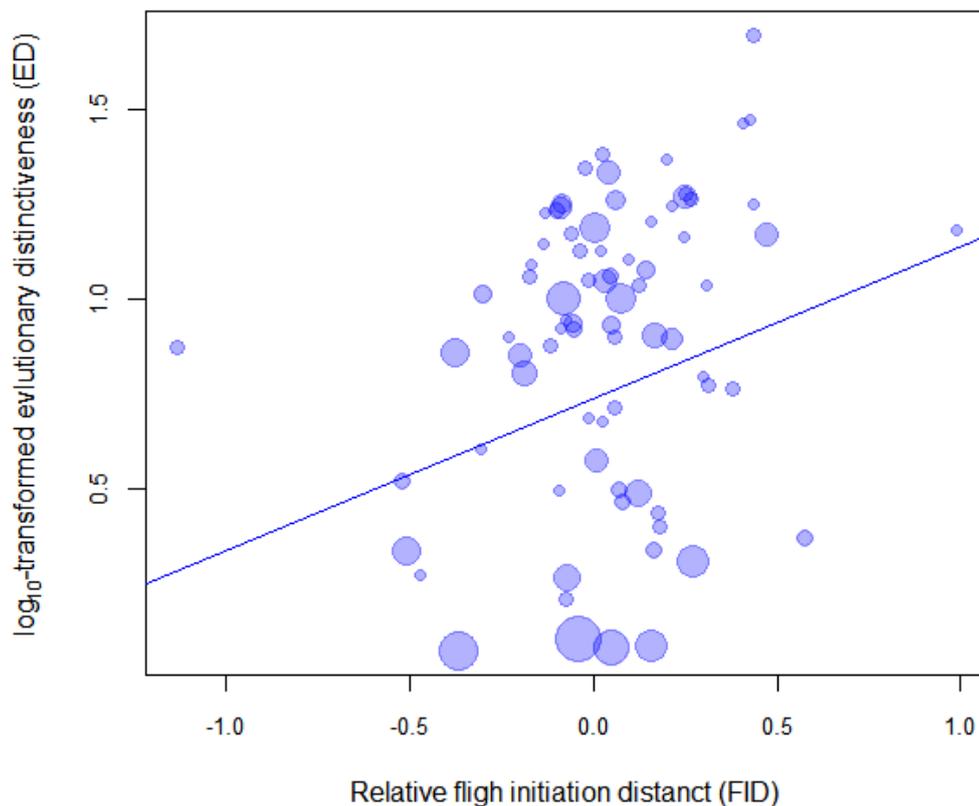


Fig. 9. La spécificité évolutive (ED) a augmenté avec l'augmentation de la distance d'initiation relative du vol (FID (m)) à travers 78 espèces d'oiseaux d'eau européens. Chaque point représente une espèce. La taille des symboles est proportionnelle à la taille de l'échantillon transformé par la racine carrée. La ligne est la ligne de régression linéaire.

IV La distance d'initiation du vol est corrélée avec le stress oxydatif chez les oiseaux

Cette étude a testé la relation entre le FID et trois marqueurs de stress oxydatif (malondialdéhyde, MDA, statut antioxydant total, TAS et acide urique, UA) sur 72 espèces

d'oiseaux. Pour modéliser la relation, j'ai utilisé des modèles de régression phylogénétique des moindres carrés généralisés (PGLS), suivis d'une analyse de trajectoire phylogénétique pour examiner les relations causales potentielles entre plusieurs caractères. La principale conclusion de cette étude était que la FID moyenne de différentes espèces d'oiseaux était positivement corrélée avec les niveaux de MDA et d'UA spécifiques à l'espèce et médiée par leur relation avec la masse corporelle. Ce résultat était robuste aux différences dans la taille de l'échantillon et la similitude en raison de la descendance phylogénétique commune.

V Peur contagieuse: La distance d'initiation du vol augmente avec la taille du troupeau chez les oiseaux grégaires

Au total, 7 768 observations de 35 espèces d'oiseaux provenant de huit pays européens différents ont été recueillies. Différentes espèces ont été classées en fonction de trois variables écologiques: la guildes trophique, la masse corporelle et la grégarité. Deux séries de modèles ont été exécutées: Premièrement, contrôler le signal phylogénétique entre espèces et ensuite les modèles non phylogénétiques en utilisant la taille du troupeau comme facteur fixe et d'autres variables comme facteurs aléatoires. La principale conclusion de cette étude était que les oiseaux sociaux réagissaient rapidement à un prédateur potentiel (représenté par un FID relativement long) lorsqu'ils étaient regroupés en grands troupeaux (figure 10), alors que ce n'était pas le cas chez les espèces non grégaires. Ces effets étaient indépendants de la masse corporelle et de la zone géographique où les données ont été recueillies, ainsi que du signal phylogénétique entre les espèces.

Points de vue

Au moins trois mécanismes ont été proposés pour tenir compte des différences de FID entre les populations d'animaux vivant dans les habitats urbains et ruraux (Møller et al., 2015, Samia et al., 2015b, Miranda, 2017). Premièrement, la tolérance accrue pourrait résulter de l'accoutumance. Les processus de type habituel se produisent lorsque les individus sont particulièrement sensibles aux comportements inattendus des humains et des prédateurs potentiels, mais pas aux comportements attendus. Les changements dans la population signifient que la FID pourrait être due au fait que les activités humaines sont inoffensives et régulières la plupart du temps. Deuxièmement, la sélection différentielle parmi les syndromes comportementaux pourrait expliquer la variation du recrutement dans les

habitats urbains menant à un tri phénotypique sous différentes pressions d'interférence entre les habitats urbains et ruraux. Troisièmement, l'adaptation locale aux habitats urbains implique que les génotypes spécifiques ont augmenté en fréquence ou ont été favorisés parmi les individus urbains et devraient généralement aboutir à une différenciation génétique (Atwell et al., 2012, Miranda et al., 2013). Afin de comprendre le mécanisme sous-jacent de ces différences, nous avons besoin d'expériences bien conçues.

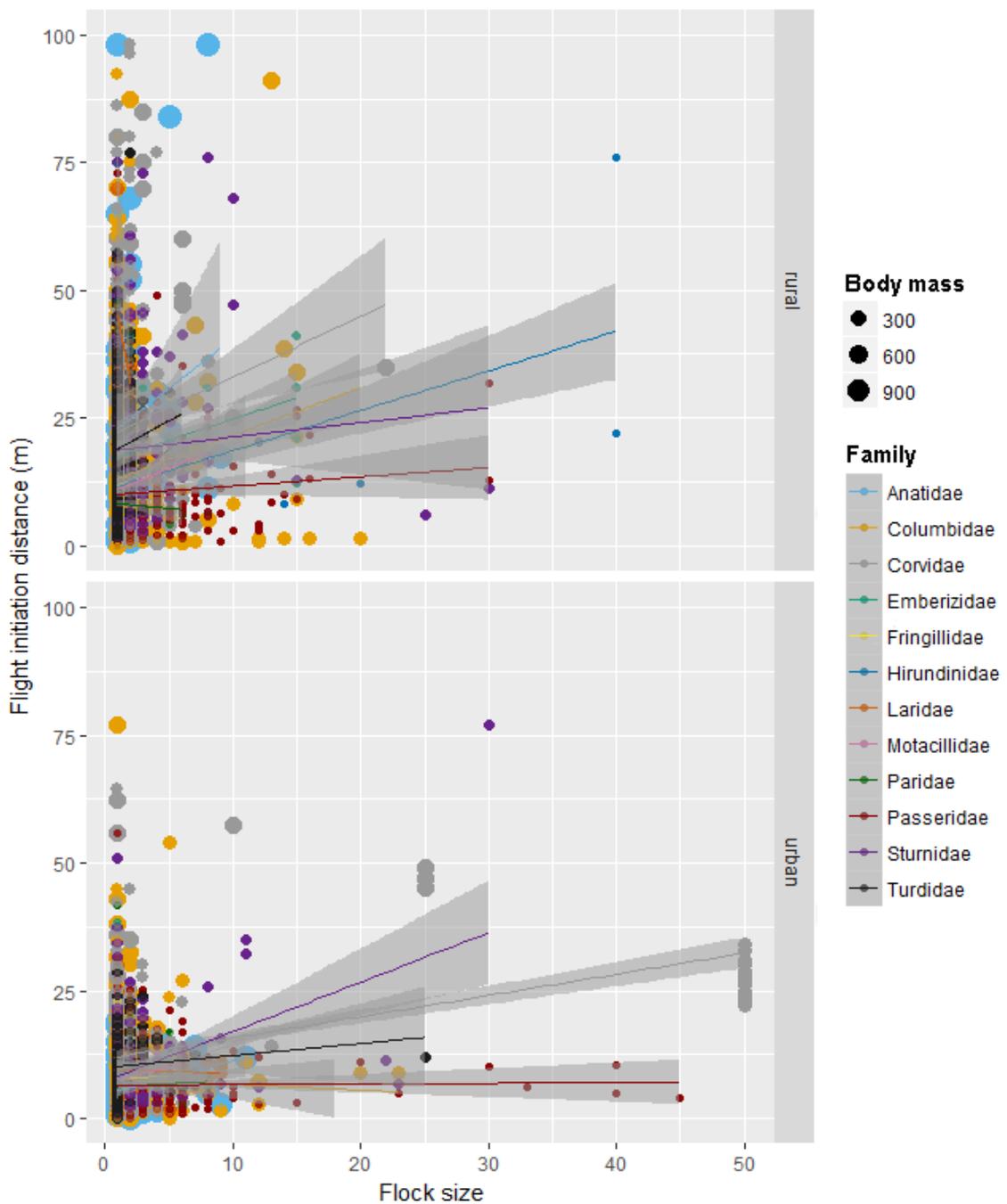


Fig. 10. Lignes de régression linéaires entre la distance d'initiation du vol (FID, m) et la taille du troupeau dans les espèces d'oiseaux grégaires provenant d'environnements ruraux

et urbains dans huit pays européens. Les couleurs indiquent la famille d'oiseaux, et la taille du cercle est proportionnelle à la masse corporelle des oiseaux (g). Les enveloppes autour des lignes sont des intervalles de confiance à 95%.

Le comportement d'évasion est souvent fortement intégré avec d'autres aspects de la biologie d'un organisme, par ex. stratégies d'accouplement et de reproduction (Møller, 2014), systèmes génétiques (Storfer & Sih, 1998) et morphologie (Losos et al., 2002). Ces corrélations suggèrent que le comportement d'évasion peut être utilisé comme un indicateur relativement facilement accessible de l'état général d'un organisme dans son environnement. La FID moyenne relative et la variance de la FID des espèces devraient être davantage considérées comme un prédicteur des espèces identifiées qui sont potentiellement plus vulnérables à l'augmentation des perturbations humaines plutôt que de simples mesures de la «distance tampon». En faisant intervenir les distances d'évacuation des antiprédateurs dans les plans de conservation et les projets de rétablissement, il peut être possible d'évaluer pourquoi certaines espèces deviennent menacées alors que d'autres ne le sont pas. Il pourrait aussi être possible d'identifier au préalable les espèces prédisposées au déclin de la population en s'appuyant sur le FID comme outil prédictif. Ces différences de comportement peuvent fournir des moyens de récupération de ces espèces menacées contre les menaces causées par la présence de prédateurs, y compris les humains.

Néanmoins, des expériences bien conçues peuvent permettre d'analyser la direction de la causalité et de mieux comprendre les FID, les syndromes comportementaux et leur signification écologique.

Titre: Comportement anti-prédateur des oiseaux et conservation.

Mots clés: masse corporelle, taille du cerveau, taille effective de la population, modèle linéaire phylogénétique, stress oxydatif, comportement social

Résumé: Prey s'appuie sur les décisions d'évasion lorsqu'il est confronté à des prédateurs pour maximiser les avantages de rester en place tout en réduisant les coûts de la prédation. Ce compromis de l'histoire de vie peut être reflété par la distance d'initiation de vol (FID), la distance à laquelle un individu prend son envol lorsqu'il est approché par un humain. J'ai abordé les facteurs potentiels expliquant la variation FID avec des données d'espèces d'oiseaux en Europe. La variabilité génétique était liée au risque de prédation FID; les espèces d'oiseaux menacées avaient généralement une FID plus longue que les espèces proches non menacées; le caractère distinctif de l'évolution (ED), un indicateur reflétant l'isolement phylogénétique des taxons, était positivement lié à la FID chez les oiseaux d'eau; La FID moyenne de différentes espèces d'oiseaux était positivement corrélée avec les niveaux spécifiques de MDA (malondialdéhyde qui est un indice de stress oxydatif) et UA (acide urique, qui est une mesure de la capacité antioxydante) et FID augmentée avec la taille du troupeau chez les espèces grégaires mais pas chez les espèces non grégaires. Ces résultats peuvent contribuer à la compréhension des causes et des conséquences des différences interspécifiques dans le comportement de fuite des prédateurs contre les prédateurs, et, plus important encore, ils peuvent fournir des moyens de résoudre les problèmes de conservation.

Title: Anti-predator Behavior of Birds and Conservation

Keywords: body mass, brain size, effective population size, phylogenetic linear model, oxidative stress, social behavior

Abstract: Prey rely on escape decisions when confronted with predators to maximize the benefits of staying put while reducing the costs of predation. This life history compromise can be reflected by flight initiation distance (FID), the distance at which an individual takes flight when approached by a human. I addressed potential factors explaining variation FID with data from bird species in Europe. Genetic variability was related to predation risk FID; threatened bird species generally had a longer FID than non-threatened closely related species; evolutionary distinctiveness (ED), an indicator reflecting the phylogenetic isolation of taxa, was positively related to FID in waterbirds; mean FID of different species of birds was positively correlated with species-specific levels of MDA (malondialdehyde which is an index of oxidative stress) and UA (uric acid, which is a metric of antioxidant capacity) and FID increased with flock size in gregarious species but not in non-gregarious species. These findings may contribute to the understanding of the causes and consequences of interspecific differences in anti-predator escape behavior of birds, and, more importantly they may provide means for resolving conservation problems.

