

Risk-taking and the evolution of mechanisms for rapid escape from predators

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Abstract

Flight initiation distance (FID) is the distance at which an individual animal takes flight when approached by a human. This behavioural measure of risk-taking reflects the risk of being captured by real predators, and it correlates with a range of life history traits, as expected if flight distance optimizes risk of predation. Given that FID provides information on risk of predation, we should expect that physiological and morphological mechanisms that facilitate flight and escape predict interspecific variation in flight distance. Haematocrit is a measure of packed red blood cell volume and as such indicates the oxygen transport ability and hence the flight muscle contracting reaction of an individual. Therefore, we predicted that species with short flight distances, that allow close proximity between a potential prey individual and a predator, would have high haematocrit. Furthermore, we predicted that species with large wing areas and hence relatively low costs of flight and species with large aspect ratios and hence high manoeuvrability would have evolved long flight speed. Consistent with these predictions, we found in a sample of 63 species of birds that species with long flight distances for their body size had low levels of haematocrit and large wing areas and aspect ratios. These findings provide evidence consistent with the evolution of risk-taking behaviour being underpinned by physiological and morphological mechanisms that facilitate escape from predators and add to our understanding of predator–prey coevolution.

Introduction

Animals react to predators through vigilance, assessment, being alert, flight and escape that all constitute behavioural interactions between prey and predators (Caro, 2005). Morphological adaptations of prey that prevent capture or allow escape once captured are well established both in theory and empirically (e.g. Penny-cuick, 1989; Norberg, 1990; Houston *et al.*, 1993; Witter & Cuthill, 1993). However, few studies address (i) the physiological mechanisms of escape (Møller, 2009) and (ii) the evolution of escape by integrating anti-predator behaviour, physiology and morphology that allow flight

and escape (Bauwens *et al.*, 1995). Animals face trade-offs between resource acquisition and risk of predation through vigilance and/or flight (starvation–predation dilemma; Ydenberg & Dill, 1986; Giraldeau & Caraco, 2000; reviewed by Witter & Cuthill, 1993). Such trade-offs occur perpetually thereby enforcing individuals to optimize their resource acquisition by minimizing exposure to predators. A prime example of such behavioural anti-predator behaviour is flight initiation distance (FID), which is the distance at which an individual takes flight when approached by a potential predator (Hediger, 1934; Burger & Gochfeld, 1981; Stankowich & Blumstein, 2005; Blumstein, 2006). Quantitative information on flight responses and the physiological and morphological underpinnings may help integrate the study of behavioural, physiological and morphological aspects of coevolution both at the proximate and ultimate levels.

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The scientific study of flight distance implicitly assumes that such distances reliably reflect actual risk of predation, that is, an individual indeed incurs a fitness cost by taking greater risks. Four explicit tests lend support for this assumption. First, Møller *et al.* (2008) demonstrated that the risk of being killed by a sparrowhawk *Accipiter nisus* decreased with longer FID of common passerines. Across the range of mean FID of 5–50 m for different species of prey, the risk of predation relative to the expectation based on the abundance of different prey species increased from being 100 times less frequent to almost 100 times more frequent than expected by chance (i.e. by four orders of magnitude). Likewise, Møller *et al.* (2010) showed that susceptibility to cat *Felis catus* predation was negatively related to flight distance of male birds when singing. Further, bird species with a shorter flight distance for their body size were more likely to be hit by a car than expected from their abundance (Møller *et al.*, 2011). Finally, Zanette *et al.* (2011) showed experimentally that even playback of the calls of a predator increased FID of individuals. Therefore, there is evidence suggesting that FID and flight reactions have evolved and are under current selection due to predation.

Flight initiation distance (FID) can be considered a behavioural response to life history trade-offs (Ghalambor & Martin, 2001; Møller & Garamszegi, 2012; Møller & Liang, 2013). If FID reliably reflects the behavioural risk that individuals take when confronted with potential predators, we can expect evolution of underlying physiological and morphological mechanisms underpinning such anti-predator behaviour. For example, bird species with high basal metabolic rates for their body size have relatively longer FID indicating that an elevated level of BMR is a cost of wariness towards predators (Møller, 2009). Haematocrit, which is the fraction of blood volume that consists of s (RBCs), constitutes a physiological adaptation to energy use and oxygen consumption that is a prime candidate as a variable that affects FID (Sturkie, 1986; Fair *et al.*, 2007). Haematocrit changes in response to exercise and parasitism, but it is also known to have a quantitative genetic basis (Fair *et al.*, 2007). Despite showing phenotypic plasticity, estimates of haematocrit are consistent among populations of the same species (this study). Haematocrit reflects an optimal balance between the benefits and costs of a large fraction of RBCs. Because RBCs play a crucial role in transport of oxygen (Sturkie, 1986), we should expect that individuals with higher haematocrit would be able to sustain higher levels of work. Migratory birds have high haematocrit during migration but reduce haematocrit soon after arrival to the breeding grounds, suggesting that there are costs associated with the maintenance of high haematocrit (Saino *et al.*, 1997a,b). Haematocrit scales inversely with body mass and high haematocrit in small species may be an adaptation to their relatively higher metabolic rate (Sturkie,

1986). Because small-sized species have relatively high BMR for their body mass and because small-sized species have high haematocrit, we would expect a negative relationship between FID and haematocrit once we have accounted for the effects of body size.

We could also expect morphological traits to correlate with FID. Flying species have streamlined bodies, and the size and shape of their wings allow them to use flight as a means of efficient locomotion at a relatively low energetic cost (Rayner, 1988; Pennycuik, 1989; Norberg, 1990). Theoretical considerations have suggested that birds with a high aspect ratio (i.e. long and narrow wings) can afford to spend more time flying (Norberg, 1990). Large wing areas, streamlined body shapes and narrow and long wings all contribute to a reduction of the costs of flight (Norberg, 1985, 1990; Rayner, 1988). Insects provide a striking example of convergence concerning intraspecific and interspecific variation in wing loading (Starmer & Wolf, 1989; Moreteau *et al.*, 1997; Morin *et al.*, 1999). During predation and escape from predators, both flight speed and manoeuvrability should be important. Flight speed and manoeuvrability are determined by wing area and aspect ratio. For example, large wing areas may result from long or broad wings. Long wings with high aspect ratio may increase speed while reducing manoeuvrability. In contrast, broad wings may confer lower flight speed but higher manoeuvrability (Thollessen & Norberg, 1991).

We predicted that species with long FIDs have lower haematocrit, large wing areas that would facilitate manoeuvring and higher aspect ratios that would favour rapid and energetically cheap escape. We tested these predictions in a sample of 63 species of birds with information on behaviour, physiology and morphology.

Materials and methods

Study areas

Flight distances of birds were recorded during February–September 2006–2012 by APM in Ile-de-France, France and Northern Jutland, Denmark.

We captured adult birds for haematocrit and wing morphology measurements in Ukraine and Romania during the breeding season 2009–2011.

Flight initiation distance

When an individual bird had been located with a pair of binoculars, APM moved at a normal walking speed towards the individual, while recording the number of steps between where the observer was at the moment of birds' take-off and the position of the bird. Number of steps approximately equals the distance in metres (Møller, 2008a). The distance at which the individual took flight was recorded as the FID, while the starting

distance was defined as the distance from where the observer started walking towards the bird to the position of the bird. If the individual was positioned in the vegetation, the height above ground was recorded to the nearest metre. While recording these FIDs, we also recorded date, time of day and sex if possible. FID was estimated as the Euclidean distance, which equals the square-root of (squared horizontal distance + squared height above ground level) (Blumstein, 2006).

Møller (2008c) has shown that flight distance does not depend on season. Indeed, 2018 observations assessed during winter (December 2006 to February 2007) and summer revealed a strong positive relationship between estimates (weighted regression: $F_{1,23} = 41.50$, $r^2 = 0.64$, $P < 0.0001$, slope (SE) = 0.98 (0.15). The intercept did not differ significantly from zero (0.02 (SE = 0.12), $t_{23} = 0.15$, $P = 0.88$), and the slope did not differ from one ($t_{23} = 0.10$, $P = 0.92$), implying that estimates were very similar and proportional during the two seasons.

We avoided pseudoreplication by only recording individuals of a given sex, age and species at a given site. Thus, if a male and a female were recorded at a given site, both were included in the data set, while one male recorded at a given site on two different days was recorded as a single observation. For the present study, we recorded a total of 4190 FIDs for 63 species.

Flight initiation distance (FID) was consistent for the same species in different studies, as shown by a comparison of data from previous studies (data and analyses reported in Møller (2008a,b,c)) and those of Blumstein (2006). Furthermore, FIDs estimated by an independent observer (E. Flensted-Jensen) were also very similar to the estimates of APM (data and analyses reported in Møller (2008a,b,c)). In addition, FIDs estimated in Denmark were similar to distances in France (data and analyses reported in Møller (2008c)).

Previous studies have shown that starting distance is strongly positively correlated with FID (e.g. Blumstein, 2003, 2006), thereby causing a problem of collinearity when entering both starting distance and flight initiation distance into the same model. We eliminated this problem by searching habitats for birds with a pair of binoculars. In this way, we assured that almost all individuals were approached from a distance of at least 30 m, thereby keeping starting distances constant across species. FID was positively related to starting distance in a model that included species, age, habitat (urban or rural) and country as factors ($F_{1,4188} = 37.97$, $P < 0.0001$), but only explained 1% of the variance in FID. None of the results presented in this paper changed statistically when including starting distance as an additional variable (not shown), and we thus excluded this variable from all subsequent analyses for simplicity.

Estimating haematocrit

We collected 50–250 μL blood using 75 μL heparinized capillary tubes by venipuncture of the brachial vein directly after capture. Total amount collected was related to the body size of the bird. Blood was stored in a cooling bag before being centrifuged in the field or in the laboratory for 10 min at 16 000 g (Ukraine) or 5 min at 6200 g (Romania) using professional haematocrit centrifuges. Haematocrit was estimated as the length of the capillary filled with red blood cells divided by the total length of the capillary filled with blood.

We recorded repeatability of haematocrit estimates among duplicate samples from the same individual for a subsample of individuals with repeatability exceeding 95%, and multiple samples from the same individual were therefore averaged before statistical analyses. Haematocrit was significantly repeatable among individuals within species among all samples, albeit at a very low level ($R = 0.25$, $\text{SE} = 0.04$, $F_{112,1366} = 5.26$, $P < 0.0001$, 1479 samples for 113 species, i.e. on average 13.09 samples per species). Mean haematocrit was significantly repeatable between Romania and Ukraine ($R = 0.72$, $\text{SE} = 0.11$, $F_{36,35} = 6.20$, $P < 0.0001$, 37 species), with a significant correlation between mean estimates from the two countries ($F_{1,35} = 10.39$, $P = 0.0027$, 37 species). Likewise, standard deviation in haematocrit was significantly repeatable between Romania and Ukraine ($R = 0.47$, $\text{SE} = 0.22$, $F_{26,25} = 2.78$, $P = 0.0057$, 27 species). There was a highly significant difference in haematocrit between Romania and Ukraine, with the latter being 9% lower than the former ($F_{1,1363} = 131.29$, $P < 0.0001$, 1479 samples for 115 species; mean (SE) Romania: 53.72% (0.28), Ukraine: 49.03% (0.37)). Therefore, we extracted least squares mean estimates for the remainder of the analysis to control for this variation between locations.

Aspect ratio and wing area

Wingspan was measured to the nearest mm with a ruler by stretching the wings to their maximum possible length positioned at an angle of 90° to the body axis (as recommended by Norberg (1990) and Pennycuik (1989)). We photographed the extended wing with a ruler included in the field and later based on these pictures estimated length, width and area. Total wing area was calculated as twice the area of the right wing (Pennycuik, 1989). Aspect ratio was calculated as wingspan squared divided by wing area (Pennycuik, 1989). In the following, we use wing area rather than wing loading (body mass per unit wing area) in the analyses because short-term fluctuations in body mass can dramatically affect wing loading estimates. All morphological characters were measured with a high precision as shown by high repeatabilities during recaptures (Møller *et al.*, 1995a).

Body mass

We extracted information on mean body mass of adult birds from Cramp & Perrins (1977–1994). The data are reported in Appendix S1 in the Supporting Information.

Statistical analyses

We $\log_{10}$ -transformed mean FID (response variable) and wing area, aspect ratio and body mass (explanatory variables) to normalize their distribution.

Phylogenetic comparative analyses allow for control of similarity in phenotype among species due to common phylogenetic descent (Harvey & Pagel, 1991). We applied the general method of comparative analysis for continuous variables based on generalized least squares models (Pagel, 1997, 1999). First, we investigated the role of phylogenetic inertia by estimating the phylogenetic scaling parameter λ that varies between zero (phylogenetic independence) and one (traits covary in direct proportion to their shared evolutionary history) (Freckleton *et al.*, 2002). We permitted λ to take its maximum likelihood value that best fits the data and tested whether there was any evidence for $\lambda = 0$, which indicates that trait variation is independent of phylogeny, and $\lambda = 1$, which is basically identical to the trait following a Brownian motion model of evolution.

We used a composite phylogeny modified from Davis (2008) (Appendix S2). Because information for the composite phylogeny came from sources using different methods based on different molecular markers, consistent estimates of branch lengths were unavailable. Therefore, branch lengths were assumed to be constant (as in a punctuated model of evolution). Finally, we also used a standard bird taxonomy (Howard & Moore, 1991) to test for consistency in findings independent of phylogenetic hypothesis. Nowhere were results qualitatively different (results not shown).

We developed a Generalized Linear Model in which we related FID to haematocrit, aspect ratio and wing area, respectively, in a model that also included body mass to account for allometric effects. The justification for inclusion of these predictors is provided in the Introduction.

Sample sizes differed among species, and such differences in sampling effort may be the cause of bias because different estimates are not estimated with similar precision (Garamszegi & Møller, 2010, 2011). We used *ape* (Paradis *et al.*, 2004) and *nlme* (Pinheiro *et al.*, 2012) in R-2.15.1 (R Core Team, 2012) to analyse the data taking both phylogenetic similarity and heterogeneity in sampling effort into account. The results presented in Table 1 were qualitatively similar to the model weighted by sample size.

We estimated effect sizes as Pearson's product-moment correlation coefficients using Cohen's (1988)

Table 1 Multivariate phylogenetic models (A) not weighted or (B) weighted by sample size of flight initiation distance in relation to haematocrit, wing area, aspect ratio and body mass in birds. λ was 0.527 (SE = 0.194), differing significantly from zero and one in the first model and λ was 0.465 (SE = 0.185), differing significantly from zero and one in the second model. Effect size is Pearson's product-moment correlation coefficient.

Variable	<i>t</i>	<i>P</i>	Estimate (SE)	Effect size
(A) Unweighted model				
Haematocrit	-3.31	0.0016	-0.020 (0.006)	0.40
Wing area	2.77	0.0075	0.480 (0.173)	0.34
Aspect ratio	3.93	0.0002	1.411 (0.359)	0.46
Body mass	-1.52	0.13	-0.210 (0.138)	0.20
(B) Weighted model				
Haematocrit	-3.37	0.0013	-0.020 (0.006)	0.41
Wing area	2.65	0.010	0.455 (0.172)	0.33
Aspect ratio	4.33	0.0001	1.553 (0.359)	0.50
Body mass	-1.48	0.14	-0.201 (0.135)	0.19

criteria for small (Pearson's $r = 0.10$, explaining 1% of the variance), intermediate (Pearson's $r = 0.30$, 9% of the variance) and large effects (Pearson's $r = 0.50$, 25% of the variance). Pearson's r was computed as $F/(F + \text{denominator df})$ (Rosenthal, 1994).

Results

Relative haematocrit, after inclusion of body mass ($t_{60} = 3.56$, $P = 0.0007$, estimate (SE) = 0.251 (0.071); effect size = 0.42), was inversely related to FID in a phylogenetic analysis (Fig. 1). λ was estimated to 0.53. There was a small to intermediate effect of the relationship between haematocrit and FID ($t_{60} = -1.97$, $P = 0.053$, estimate (SE) = -0.014 (0.007); effect size = 0.25). In a model weighted by sample size, $\lambda = 0.59$, with a non-significant relationship between haematocrit and FID ($t_{59} = -1.80$, $P = 0.077$, estimate (SE) = -4.085 (2.267); effect size = 0.23).

Wing area, after accounting for body mass ($t_{60} = -1.08$, $P = 0.28$, effect size = 0.14), increased

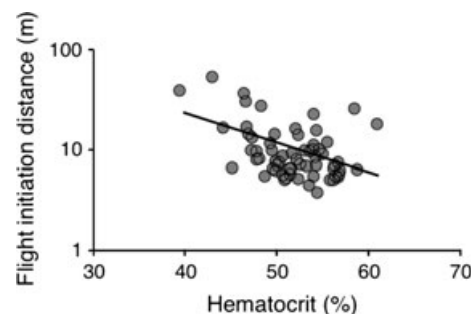


Fig. 1 Flight initiation distance (m) in relation to haematocrit (%) in different species of birds. The fit is the regression line.

with increasing FID (Fig. 2). $\lambda = 0.66$. There was a large effect size for the relationship between wing area and FID ($t_{60} = 3.78$, $P = 0.002$, estimate (SE) = 1.235 (0.383); effect size = 0.44). In a model weighted by sample size, $\lambda = 0.10$, with a significant relationship between wing area and FID ($t_{59} = 10.81$, $P = 0.002$, estimate (SE) = 0.131 (0.032); effect size = 0.82).

Aspect ratio, after accounting for the allometric effects of body mass ($t_{60} = 2.50$, $P = 0.015$, effect size = 0.31), increased with increasing FID (Fig. 3). λ was estimated to 0.75. There was an overall strong positive effect size for the relationship between aspect ratio and FID ($t_{60} = 3.25$, $P = 0.002$, estimate (SE) = 0.616 (0.189); effect size = 0.39). In a model weighted by sample size, λ was estimated to 0.94, with a significant relationship between aspect ratio and FID ($t_{59} = 4.06$, $P = 0.0001$, estimate (SE) = 0.131 (0.032); effect size = 0.46).

Because the different variables were correlated, we estimated the partial effects of the four predictors. The overall phylogenetic model showed significant effects of all predictors, except body mass, with intermediate to large effect sizes (Table 1). FID decreased with increasing haematocrit, but increased with aspect ratio and wing area. After controlling for haematocrit, aspect ratio and wing area, the effect of body mass was small and negative albeit not significant (Table 1). In a second phylogenetic analysis that weighted observations by sample size, we found $\lambda = 0.47$ with significant effects of haematocrit, aspect ratio and wing area as in the unweighted model (Table 1).

Discussion

The main findings of this study of risk-taking behaviour and physiological and morphological adaptations to escape from predators by birds were that FID, as an estimate of the risk that individuals take when approached by a putative predator, decreased with increasing haematocrit, but increased with wing area and aspect ratio. These variables accounted for a large fraction of the variance, implying that there was

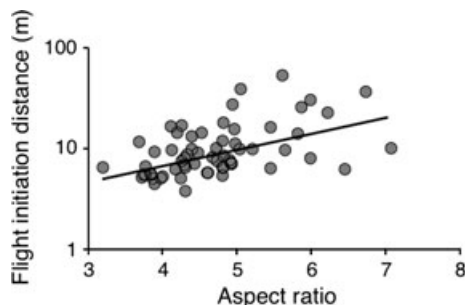


Fig. 2 Flight initiation distance (m) in relation to aspect ratio in different species of birds. The fit is the regression line.

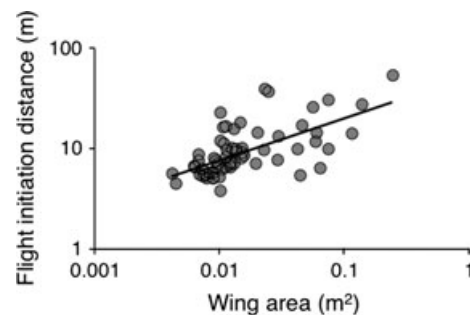


Fig. 3 Flight initiation distance (m) in relation to wing area (m²) in different species of birds. The fit is the regression line.

current selection on flight distance through the indirect effects of physiology and morphology.

We have analysed data on flight initiation distance, haematocrit and flight morphology of birds, partly relying on estimates from different countries. Although there are differences in flight initiation distance among countries (Møller & Liang, 2013), differences in haematocrit among countries (this study) and differences in morphology among populations (Norberg, 1990), there is still highly significant consistency in these variables among populations of the same species (e.g. Møller & Liang, 2013; this study). Here, we adjusted statistically for differences in haematocrit between areas (neighbouring countries) by using least square means after adjustment for the effect of area. If there are differences in phenotypic traits among populations, this would only make comparative tests for covariation among traits conservative.

Prey initially interact with predators by behavioural means such as vigilance and assessment of the risk of attack (Ydenberg & Dill, 1986; Frid & Dill, 2002; Caro, 2005), eventually followed by flight or escape that both rely on physiological and morphological adaptations such as running ability, muscle mass, ability to withstand attack and ability to escape once captured (Vermeij, 1987). Thus, we can expect significant correlations between behaviour and the phenotypic traits that at a later stage of the interaction prevent capture and allow escape. Here, we provide such a test relying on a behavioural fear response to a potential predator (i.e. FID) and physiological (i.e. haematocrit) and morphological means (i.e. wing area and aspect ratio) of rapid and efficient flight or escape. Haematocrit scales inversely with body mass (Sturkie, 1986), apparently as a consequence of relatively higher metabolic rates and hence greater rate of oxygen use in small-sized species. Here, we have shown that bird species with long FIDs have low haematocrit for their body size. This implies that species with long FID have a relatively low ability of oxygen transport, and hence, the escape ability of such species with long flight distances is limited, thus explaining their early initiation of escape. In contrast,

species with short flight distances are able to escape rapidly through their high haematocrit that may help sustain the high metabolic cost of short flights. For example, Tatner & Bryant (1986) estimated the metabolic costs of such short flights at 23 times basal metabolic rate in the robin *Erithacus rubecula*. Because birds maintain high haematocrit levels at a cost, high levels of haematocrit in species with short flight distances may suggest that such species retain high haematocrit despite its costs. We suggest that the high haematocrit in birds is an adaptation to escape from predators that due to the short flight distances approach such species closely.

Flight initiation distance (FID) implies the maintenance of a minimum distance to a predator, but such flight that can be straight escape or involve manoeuvrability or agility to outpace a potential predator (Domenici *et al.*, 2011a,b). Here, we have shown that wing area and aspect ratio, two important components of flight ability of birds (Rayner, 1988; Norberg, 1990), are strongly and independently related to FID. These results for FID differ from selection on morphology that directly relates to escape from predators (McPeck, 1997; Calsbeek & Irschick, 2007; Møller *et al.*, 2009) because flight distance is the distance at which an individual initiates its flight thus including aspects of risk assessment and life history trade-offs. Wing area is a measure of the lift of the wing during flight (Hedenström & Møller, 1992), implying that bird species with large wing areas have greater ability to escape a potential predator. Aspect ratio is an important component of flight speed (Hedenström & Møller, 1992) and as such may reflect the ability of birds to evade an approaching predator. Indeed, while most flights are directional away from a potential predator, a significant number are complex and not unidirectional (Domenici *et al.*, 2011a,b). Such deviations from the behavioural norm by prey may constitute unpredictable responses for a predator. Larger wing areas and aspect ratios may allow birds to show flexible flight responses that will further reduce the risk that an encounter with a predator results in successful predation. A number of studies of birds have suggested that male sexual display is associated with large wing areas and aspect ratios (e.g. Møller, 1991; Hedenström & Møller, 1992; Møller *et al.*, 1995a,b) and convergent adaptations have been reported for fruit flies and butterflies (Starmer & Wolf, 1989; Wickman, 1992). Given the short mating season, we should expect even greater selection pressures arising from the risk of predation that is bound to be important throughout the annual cycle. This study is consistent with such an interpretation.

Flight distance is strongly positively correlated with body mass across species (Blumstein, 2006; Møller, 2008a). One interpretation of this positive relationship is that it takes longer distances and longer time for large species to get airborne (Blumstein, 2006; Møller,

2008a). Therefore, large species must initiate escape flights earlier than small species simply to get airborne at the same distance as small species. We have shown here that this positive relationship between FID and body mass was present in the analyses of haematocrit and aspect ratio, but not in the analysis of wing area. Likewise, the relationship between flight distance and body mass was negative in the multivariate analysis. Although the negative relationship for body mass was not statistically significant, it did differ significantly from the estimate reported by Møller (2008b) (phylogenetic estimate = 0.270; estimate for analysis of wing area in the present study: -0.169 (SE = 0.156), $t_{60} = 2.81$, $P = 0.007$; estimate in multivariate analysis: -0.210 (0.138), $t_{60} = 3.48$, $P = 0.0001$). The fact that the body mass effect disappears after inclusion of wing area as a predictor implies that this positive allometric relationship between FID and body mass is caused by wing area and its effects on aerodynamics. These findings provide support for the hypothesis that longer flight distances in larger species are due to the aerodynamic costs of large body size (Blumstein, 2006; Møller, 2008a).

There are several implications of our study. First, we should expect intraspecific variation in FID to be predicted by individual differences in haematocrit, wing area and aspect ratio and associated directional predation selection on these traits. Second, the link between behavioural response as reflected by flight distance and the physiological and morphological means of escape imply that several variables are optimized simultaneously. While flight distance and haematocrit can change on short time scales (Fair *et al.*, 2007) that is not the case for wing area and aspect ratio that are fixed during the annual moult. Thus, flight distance and haematocrit are likely to reliably reflect the current state of an individual to a greater extent than morphology, and the relationship between FID and haematocrit, wing area and aspect ratio, respectively, allows for some flexibility through short-term changes in haematocrit. Third, predator-prey signalling that relies on information exchange between a predator and a prey individual (Caro, 2005) may depend on whether this information has a behavioural, physiological or morphological basis. Would an individual in temporarily poor condition adjust its flight distance to an approaching predator to take this reduction in condition into account? Given that birds infected with blood parasites seem to take greater risks as reflected by shorter flight distances (Møller, 2008c), this suggests that flight distance is adjusted to residual reproductive value. Finally, the study of the integration of anti-predator behaviour with physiology and morphology may also be of importance in conservation biology where the objective is often to assess the impact of humans on animal populations as viewed from the perspective of the animal. A comparative study has

shown that FID is negatively related to population trends of European birds such that birds with longer FID have declining populations (Møller, 2008b). This raises questions about the extent to which this relationship between behaviour and population dynamics is underpinned by physiological adaptations such as haematocrit and/or morphological adaptations such as wing area and aspect ratio.

In conclusion, we have shown that FID as a behavioural measure of risk-taking behaviour is mediated by physiological (haematocrit) and morphological adaptations (wing area and aspect ratio). Bird species with short flight distances have high levels of haematocrit and large wing areas and aspect ratios, providing such species with physiological and morphological mechanisms that allow for safe escape from predation.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Summary information on mean flight initiation distance (FID)(m), body mass (g), hematocrit (%), wing area (cm²), aspect ratio and sample sizes.

Appendix S2 Coordinates for study sites in Romania.

Appendix S3 Coordinates for study sites in Ukraine.

Figure S1 Phylogenetic hypothesis used in the comparative analyses.

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