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Relationships of anti-predator escape and post-escape responses with body mass and morphology: a comparative avian study

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ABSTRACT

Background: Pointed and concave wingtips and shorter hind limbs make birds more vulnerable to predation.

Question: Do behavioural anti-predator escape and post-escape responses compensate for these morphological characters that increase vulnerability to predation?

Data studied: Body mass and size, indices of wingtip shape and hind limb length, flight initiation distance (the distance at which birds escape from a threat), and landing distance (the distance at which birds land after escaping from a threat) of 83 birds, mostly from North America, Europe, and Australia. Relationship data came mostly from molecular sources.

Search method: *Phylogenetically uncorrected*: We regressed flight initiation distance and landing distance in different analyses on body mass and size, wing pointedness and convexity, femur and tarsus length. *Phylogenetically corrected*: We calculated independent contrasts with Compare 4.5 (Martins, 2004), ignoring branch lengths throughout.

Conclusions: Birds with more pointed wings fled at longer distances and landed farther away than species with rounded wings, but hind limb length was not associated with flight initiation distance and landing distance.

Keywords: flight initiation distance, hind limb morphology, landing distance, migratory species, predation, wingtip shape.

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INTRODUCTION

Animals engage in a series of sequential decisions to avoid predation (Lima and Dill, 1990; Lind and Cresswell, 2005). For instance, they allocate time to scanning to detect predators (Ferriere *et al.*, 1996; Bednekoff and Lima, 2002), leave suitable patches when the benefits of leaving after detecting a predator approaching are higher than the costs of staying (Ydenberg and Dill, 1986), modify their type of escape depending upon the distance at which the predator emerges from cover (e.g. Cresswell, 1993; Lind *et al.*, 2003), reduce the likelihood of subsequent attacks by choosing a safe refuge and remaining near it (Hamilton and Watt, 1970; Blumstein, 1998), and stay in a refuge for an optimal amount of time that is sensitive to both the costs and benefits of remaining in cover (Dill and Gillet, 1991; Martin, 2001; Hugie, 2003; Blumstein and Pelletier, 2005). Considerable research has identified social and environmental factors that influence these decisions made by individuals within a species (see reviews in Lima and Dill, 1990; Lima, 1998; Stankowich and Blumstein, 2005).

Relatively less attention has focused on the factors that have shaped the variability in anti-predator behaviour across species (Lima, 1993). Some interspecific studies have dealt with comparisons between species within certain families (Tobalske and Dial, 2000; Van Der Veen and Lindström, 2000; Burns and Ydenberg, 2002), but broader-scale comparative analyses across families are also necessary (Tobalske *et al.*, 2004; Blumstein *et al.*, 2004, 2005; Blumstein, 2006). Comparative analyses are justified for both theoretical and applied reasons. Theoretically, we must develop a better understanding of the factors that have co-evolved with anti-predator behaviour and ultimately affected patterns of habitat selection (Lima, 1993). From an applied perspective, we must predict the distribution and abundance of species influenced by anthropogenic environmental change (Blumstein and Fernández-Juricic, 2004) given that wildlife react to humans in similar ways as they do to predators (Frid and Dill, 2002).

Between species, body mass and size have been associated with some anti-predator responses. For instance, body mass is related to the distance at which birds detect potential threats: larger species tend to have higher detection distances (Blumstein *et al.*, 2005). Bird species with high detection distances usually exhibit high flight initiation distances [the distance between a predator and the prey at which the latter vacates a patch in response to the predator's approach (Fernández-Juricic *et al.*, 2002; Blumstein *et al.*, 2005; Blumstein, 2006)]. Furthermore, species with greater body mass have higher velocity at the end of take-off (Tobalske *et al.*, 2004). Lima (1993) showed that within some avian families, larger species would travel farther to reach cover after fleeing from a predator (hereafter, landing distance) to prevent further attacks. These findings indicate that there are systematic interspecific differences in the perception of predation risk, and that body mass and size may be implicated. Interestingly, Swaddle and Lockwood (1998) found that morphology (wing shape and hind limb length) also influences interspecific variation in predation rates. Studies involving comparisons between pairs of species suggest a relationship between these morphological characters and some escape response [e.g. take-off angle and speed, flight speed (Van der Veen and Lindström, 2000; Burns and Ydenberg, 2002)], but little is known about the general relationship between morphology and escape and post-escape anti-predator responses related to resource patch exploitation across many species.

Our goal was to conduct an interspecific study of the effects of body mass and size, and wing and hind limb morphology, on two stages of anti-predator decision making; we focused on escape (flight initiation distance) and post-escape (landing distance) responses.

We made the following predictions about the effects of body mass and body size:

1. We predicted that species with greater body mass would initiate flight at greater distances because they are less agile than smaller-bodied species (Marden, 1987; Witter *et al.*, 1994) and because they may benefit from flushing earlier (Blumstein, 2006).
2. We predicted that species with larger size would initiate flight at greater distances because they could be detected by predators more easily, and thus for a given distance they would be more vulnerable than small species (Blumstein, 2006).
3. We also predicted that landing distance would increase with body mass because higher wing loading may increase the time flapping (and as a result the distance to cover) to counter the increase in the rate of altitude loss (Pennycuick, 1989; Nudds and Bryant, 2002).
4. Finally, we predicted that landing distance would increase with body size because larger species may be more easily detected by predators visually and would seek cover farther away to reduce vulnerability (Lima, 1993).

Our general hypothesis about wing and hind limb morphology was that morphological features that decrease the probability of successful escapes would be associated with behavioural traits that compensate for the increased risk (Lind and Cresswell, 2005). Thus, we made the following specific predictions:

1. We predicted that flight initiation distance would be greater in species with pointed and concave wingtips because they would have reduced lift and thrust (Lockwood *et al.*, 1998) compared with species with rounded and convex wingtips.
2. We predicted that flight initiation distance would be greater in species with shorter hind limbs (femur and tarsus), because it will take longer for these species to provide the necessary acceleration to take-off (Heppner and Anderson, 1985; Bonser and Rayner, 1996).
3. We predicted that landing distance would be greater in species with low manoeuvrability at low speeds [pointed and concave wingtips (Pennycuick, 1983; Norberg, 1990)], because they would try to compensate by distancing themselves farther away from chasing predators (Lima, 1993; Lockwood *et al.*, 1998).
4. We predicted that species with shorter hind limbs would have greater landing distance because the longer time needed to take-off might increase vulnerability (Lockwood *et al.*, 1998).

Finally, we assessed the effects of landing distance, controlling for confounding factors, on two other post-escape indicators: the height of the substrate where individuals landed (hereafter, landing height) and the time to resume pre-disturbance behaviour. We expected positive associations between landing distance and these factors, because species that landed farther away would require higher perches and extra time to locate safer new resource patches (Fernández-Juricic *et al.*, 2002, 2004; Blumstein *et al.*, 2005).

MATERIALS AND METHODS

General sampling procedures

We studied 83 species (Appendix 1), living in a variety of habitat types in California, Colorado, Eastern Australia, Spain, and Tasmania. The studied species belonged to 29 families (Aegithalidae, Alcedinidae, Anatidae, Ardeidae, Certhiidae, Charadriidae, Columbidae, Corvidae, Emberizidae, Fringillidae, Laridae, Megapodiidae, Mimidae, Motacillidae, Muscicapidae, Odontophoridae, Paridae, Passeridae, Phalacrocoracidae, Picidae, Polioptilidae, Psittacidae, Recurvirostridae, Regulidae, Scolopacidae, Sturnidae, Sylviidae, Timaliidae, and Tyrannidae) and 61 different genera (see Appendix 1). For all species included in these analyses, we had at least 15 experimental observations. Mean body mass was tabulated from Dunning (1993) and, when a species was not reported there, we obtained values from species accounts published in the multi-authored series *The Birds of North America*. The latter source, together with bird guides (de Juana and Varela, 2000; Simpson and Day, 2000; Watts, 2000), was used to gather body size length estimates.

We measured escape responses by approaching individual birds that reacted towards the observer as if he or she were a potential predator (Frid and Dill, 2002; Blumstein, 2003; Blumstein *et al.*, 2004). When animals were in groups, we chose at random one individual before the approach. We focused on birds that were foraging or engaged in 'relaxed behaviours', such as preening or roosting. Highly vigilant, alarmed, and nesting birds were not approached, nor were endangered species. To our knowledge, our experimental approaches did not harm the birds.

At any given time, a single observer directly approached animals at a steady pace ($\sim 0.5\ \mathrm{m \cdot s^{-1}}$) in areas without vegetation visually blocking the pathway between the observer and the animal. We paid particular attention to ensure that all observers collected data consistently. New observers were trained until their observations were identical to those of a trained observer. Additionally, all observers were trained to discard a potential response if there was any doubt about any of the variables collected.

Subjects were not marked; however, we avoided re-sampling individuals by focusing on birds in different geographic locations and not re-sampling the same location more than once. Birds were studied in both 'pristine' environments with few if any visitors, and in areas with human activity. Analyses excluded observations on individuals in highly visited city parks, and individuals that approached humans (for handouts) rather than fleeing. To our knowledge, none of the species included in our analyses were actively hunted at the locations where we studied them.

Escape responses

We noted the distance we started walking towards birds (starting distance), because it could affect flight initiation distance (Blumstein, 2003). We recorded the distance the focal bird moved away from the patch (flight initiation distance$_{\mathbf{horizontal}}$) in response to our approach either on foot or by flight. Moving away behaviours were obvious, except for some species that actively moved while foraging (namely, shorebirds). When birds were already moving, we focused on obvious departures from their typical movement (e.g. a double-step or movement in another direction) to score flight initiation distance. This problem applied only to situations in which the bird walked away, instead of flying away, as they usually did. We measured flight initiation distance in paces and converted them to metres. We also measured the height of the bird when off the ground (if it was off the ground). Perching height was estimated by visually rotating the location of the bird in the tree/bush onto the ground, and then measuring the ground distance with a metre tape (±0.05 m). From flight initiation distance$_{\mathbf{horizontal}}$ and perching height, we used the Pythagorean theorem to calculate the 'direct' flight initiation distance [flight initiation distance$_{\mathbf{direct}} = \sqrt{}$(flight initiation distance$_{\mathbf{horizontal}}{}^2$ + perching height^2)], and considered this flight initiation distance$_{\mathbf{direct}}$ measurement in subsequent analyses (Blumstein, 2003; Fernández-Juricic *et al.*, 2004). Many of the birds we studied were perched in the outer portion of trees. However, we neither systematically recorded where in the tree the bird was located, nor did we record the type of tree or whether it had leaves or not. We acknowledge that location in canopy and leafiness could influence predation risk, visibility, and detectability (Suhonen, 1993; Krams, 2001). We think this is unlikely to confound our interpretations because of the large number of species studied. Our data included species with a range of mean flight initiation distances (15.32 ± 8.92 m; range = 3.19–39.88 m) and starting distances (29.61 ± 18.06 m; range = 8.64–77.08 m).

We used 47 species to assess the effects of wingtip morphology on flight initiation distance (Appendix 1). To characterize wing morphology, we measured feathers with digital Vernier calipers to 0.01 mm accuracy on 1–5 museum skins per species from the Vertebrate Museum at California State University Long Beach following the primary distance method (reviewed in Lockwood *et al.*, 1998). We measured total wing length as the length of the longest primary to the base of the folded wing (wrist). Primary feathers were numbered from most distal (#1) to most proximal (#8) (Lockwood *et al.*, 1998). Differences in primary lengths were obtained by subtracting the length of the subsequent feathers to the longest primary. Differences were then subtracted from the total wing length to acquire primary feather lengths. We calculated mean primary lengths values (including right and left wings per specimen) per species. Lockwood *et al.* (1998) pointed out some potential biases with this method due to the variability in the folded wings and the statistical distribution of the estimates. However, we decided to use this method over the primary length method (in which each primary feather is measured) to avoid damaging the museum specimens, many of which were very fragile. Nevertheless, individuals involved in measuring museum specimens were thoroughly trained until their measurements were highly repeatable. We also assessed the statistical distribution of our data following Lockwood and colleagues' (1998) recommendations. The primary distance method used in this study has been found to be correlated with other methods to characterize wingtip shape (Lockwood *et al.*, 1998).

We used 41 species to assess the effects of hind limb morphology on flight initiation distance (Appendix 1). We used 1–5 specimens per species from skeletons at the Vertebrate Museum, California State University Long Beach. The three principal hind limb bones (femur, tibiotarsus, and tarsometatarsus) were measured to 0.01 mm accuracy using digital Vernier calipers following Swaddle and Lockwood (1998). Specimens from both sexes were measured, with approximately 45% females and 20% males, with the remaining specimens of unknown sex. We calculated a mean value per hind limb bone (including right and left hind limbs per specimen) per species.

Post-escape responses

We recorded three variables to assess anti-predator responses after vacating the patch: landing distance, landing height, and time to resume pre-disturbance behaviour. Landing distance was defined as the distance between the point at which the bird left the patch (either by flying or walking) in response to the observer's approach to the point at which the bird landed (ground, shrub, tree). Landing distance was measured on 52 species (Appendix 1) with a Bushnell Sport Yardage Pro Sport laser rangefinder. Landing distance ranged from 0.11 to 109 m across all individuals included in the analyses (mean 11.06 ± 12.33). We excluded species where more than 10% of the landing distance measurements exceeded 125 m, because we could not obtain reliable estimates. Hence, our results are applicable only to species with the aforementioned range of landing distances.

Landing height was estimated by visually rotating the location of the bird in the tree/bush onto the ground, and then measuring the ground distance with a metre tape (±0.05 m).

Mean landing height varied from 0 to 8.57 m (2.81 ± 1.93 m). Pre-disturbance behaviour was determined before initiating the approach. When the individual detected the observer, its scanning (based on head position) and movement behaviour increased substantially before fleeing and immediately after landing. We recorded the amount of time it took the bird to resume foraging or roosting activity after vacating the original patch. Mean time to resume pre-disturbance behaviour varied from 3.88 to 130.55 s (32.58 ± 23.27 s). In each approach, we also measured potentially confounding factors around the point the bird occupied before fleeing: the number of conspecifics within 10 m, and the distances (in metres) to the nearest shrub and the nearest tree as indicators of habitat structure. A mean value for each of these variables per species was included in subsequent analyses.

We used 27 species to assess the effects of wing morphology on landing distance (Appendix 1). Wing shape was estimated following the procedures described previously. We used 14 species to analyse the effects of hind limb morphology on landing distance (Appendix 1). Femur, tibiotarsus, and tarsometatarsus lengths were measured as described previously.

Statistical analyses

Hind limb morphology and wingtip morphology were analysed following Lockwood and colleagues' (1998) method of size-constrained component analysis, which has been widely used in the literature (Pérez-Tris and Tellería, 2001; Burns and Ydenberg, 2002; Burns, 2003; Swaddle and Lockwood, 2003). Size-constrained component analysis permits separation of the effects of isometric size from other morphological traits (e.g. shape) by defining a specific size component, with subsequent components being geometrically orthogonal to it (methodological details in Lockwood *et al.*, 1998).

We ran four size-constrained component analyses for different databases to assess the effects of wing (primary feather lengths) and hind limb (femur, tibiotarsus, and tarsometatarsus lengths) morphology on flight initiation distance and landing distance (Appendices 1 and 2). For wing morphology, the first factor of the size-constrained component analyses (C1) was associated with wingtip isometric size, the second factor (C2) with wingtip pointedness (higher values indicated rounded wings), and the third factor (C3) with wingtip convexity (higher values indicated increased convexity of the outline of the wingtip). For hind limb morphology, in both the flight initiation distance and landing distance databases, C1 was associated with total hind limb length. In the flight initiation distance database, C2 was positively associated with femur length and negatively associated with tibiotarsus length, and C3 was negatively associated with tarsometatarsus length (Appendix 2). In the landing distance database, however, C2 was positively associated with femur length, and C3 was positively associated with tibiotarsus length and negatively associated with tarsometatarsus length (Appendix 2). Since we were interested in the effects of wing shape and hind limb length controlling for isometric size, and since body size was highly correlated with body mass (see Results), C1 was not included in the morphological analyses (see also Swaddle and Lockwood, 2003).

For flight initiation distance and landing distance, we first analysed the effects of body mass and size (including group size, distance to the nearest shrub and tree as covariates) to assess their relative importance. Second, we analysed the effects of wing and hind limb morphology including the covariates that were significant in the previous analysis. We analysed wing and hind limb morphology effects independently to maximize the sample size in relation to the availability of preserved specimens and field data.

Since starting distance explains a significant variation in escape responses (Blumstein, 2003), we included it in our flight initiation distance analysis. This relationship logically should be forced through the origin, because a person beginning to approach a bird at 0 m could only elicit a 0 m detection distance.

Our results showed that wingtip pointedness was associated with flight initiation distance (see below), so we conducted another test to assess whether wingtip pointedness would vary with migratory status (resident, short-term migrant, long-term migrant), as has been suggested in the literature (Mönkkönen, 1995; Lockwood *et al.*, 1998; Copete *et al.*, 1999; Pérez-Tris and Telleria, 2001; Peiro, 2003; but see Keast, 1996; Burns, 2003).

We also analysed the effects of landing distance on landing height and time to resume pre-disturbance behaviour, controlling for group size, distance to the nearest shrub and tree. In the analysis of time to resume pre-disturbance behaviour, we also incorporated landing height as a potential confounding factor.

We present both results of single species analyses and analyses calculated from phylogenetically independent contrasts (Felsenstein, 2004), since trait values from related species are not phylogenetically independent (i.e. species may resemble each other because of shared ancestry). We used Sibley and Ahlquist's (1990) phylogeny and Sibley and Monroe's (1990) taxonomy to generate our phylogeny. Unresolved congeners not specifically included in Sibley and Ahlquist's phylogeny were left as polytomies. Polytomies were later resolved randomly using MacClade 4.03 (Maddison and Maddison, 2001). We assumed a punctuational model of evolution, calculated contrasts using Compare 4.5 (Martins, 2004), and, as required by the method, forced the regression through the origin (Felsenstein, 2004).

Analyses were conducted using SPSS 13.1. Variables that were not normally distributed were log-transformed before non-phylogenetic and phylogenetic analyses (see Results). We interpreted all two-tailed P-values < 0.05 as significant. Residuals from general linear models were visually scrutinized and did not deviate substantially from normality.

RESULTS

Escape responses

In the analysis of species values, flight initiation distance was positively associated with body mass and body size, after controlling for the significant variation in starting distance (adjusted $R^2 = 0.96$; Table 1a). However, body mass explained five times more variability in flight initiation distance than body size (Table 1a). The other confounding factors did not have a significant influence on flight initiation distance (Table 1a). In the analysis of independent contrasts, we also found that body mass was positively related to flight initiation distance, after controlling for the significant variation in starting distance (adjusted $R^2 = 0.44$; Table 1a). Given the high correlation between body mass and body size (Pearson correlation, single species, $r = 0.91$, $P < 0.001$; independent contrasts, $r = 0.75$, $P < 0.001$), and the greater effect of body mass on flight initiation distance, we elected to focus on the effects of body mass in the subsequent analyses.

Species with pointed wings tended to flee at longer distances than species with rounded wings, but these results were not consistent across analyses. In an analysis of species values, flight initiation distance was positively associated with body mass, after controlling for the

Table 1. Effects of (a) body mass and size, (b) wing shape, and (c) hind limb length on flight initiation distance

	Coefficient	*F*	d.f.	*P*	Partial η^2
(a) Body mass and size effects on flight initiation distance					
(*log*) *Flight initiation distance* (*species values*)					
(log) Body mass	0.443	77.46	1, 55	**<0.001**	0.585
(log) Body size	0.016	7.44	1, 55	**0.009**	0.119
Starting distance	0.028	25.25	1, 55	**<0.001**	0.315
Group size	0.065	2.65	1, 55	0.109	0.046
(log) DNShrub	−0.004	0.55	1, 55	0.462	0.010
(log) DNTree	0.001	0.13	1, 55	0.718	0.002
Flight initiation distance (*independent contrasts*)					
(log) Body mass	0.010	4.81	1, 54	**0.033**	0.082
(log) Body size	−0.088	1.92	1, 54	0.171	0.034
Starting distance	0.021	26.03	1, 54	**<0.001**	0.325
Group size	−0.001	0.00	1, 54	0.980	0.000
(log) DNTree	0.006	3.57	1, 54	0.064	0.062
(log) DNShrub	−0.002	1.40	1, 54	0.241	0.025
(b) Wing shape effects on flight initiation distance					
Flight initiation distance (*species values*)					
(log) Body mass	0.390	63.36	1, 43	**<0.001**	0.596
Starting distance	0.020	7.91	1, 43	**0.007**	0.155
C2 (wingtip pointedness)	0.031	0.13	1, 43	0.719	0.003
C3 (wingtip convexity)	−0.224	3.95	1, 43	0.053	0.084
Flight initiation distance (*independent contrasts*)					
(log) Body mass	0.089	3.09	1, 42	0.086	0.069
Starting distance	0.018	19.28	1, 42	**<0.001**	0.315
C2 (wingtip pointedness)	−0.175	8.04	1, 42	**0.007**	0.161
C3 (wingtip convexity)	−0.126	1.97	1, 42	0.168	0.045
(c) Hind limb length effects on flight initiation distance					
Flight initiation distance (*species values*)					
(log) Body size	0.461	68.82	1, 37	**<0.001**	0.650
Starting distance	0.009	1.43	1, 37	0.240	0.037
C2 (femur/tibiotarsus length)	−0.644	7.28	1, 37	**0.010**	0.164
C3 (tarsometatarsus length)	−0.326	1.46	1, 37	0.234	0.038
Flight initiation distance (*independent contrasts*)					
(log) Body size	0.062	3.94	1, 36	0.055	0.098
Starting distance	0.025	48.81	1, 36	**<0.001**	0.576
C2 (femur/tibiotarsus length)	−0.018	0.02	1, 36	0.880	0.001
C3 (tarsometatarsus length)	0.153	1.77	1, 36	0.192	0.047

Note: In part (a), we considered the effects of covariates (starting distance; group size; distance to the nearest tree, DNTree; distance to the nearest shrub, DNShrub), from which the significant ones were included in parts (b) and (c). We conducted analyses using species values and independent contrasts. Significant ($P < 0.05$) results are printed in **bold**. Partial eta-squared values indicate effect size.

significant variation in starting distance (adjusted $R^2 = 0.95$; Table 1b). No measure of wing shape (C2 – wingtip pointedness, or C3 – wingtip convexity) explained significant variation in flight initiation distance (Table 1b). However, in the analysis of independent contrasts, flight initiation distance was negatively associated with C2 (wingtip pointedness), after controlling for the significant variation in starting distance (adjusted $R^2 = 0.43$; Table 1b, Fig. 1).

In the analysis of species values, we found that C2 (wingtip pointedness) was significantly affected by migratory status ($F_{3,42} = 5.34$, $P = 0.003$), after controlling for body mass ($F_{1,42} = 0.21$, $P = 0.652$) and starting distance ($F_{2,42} = 10.90$, $P = 0.002$): long-distance migrants (−0.688 ± 0.241) tended to have more pointed wings than resident species (1.027 ± 0.229), with short-distance migrants having intermediate values (0.060 ± 0.317). A similar significant difference in C2 (wingtip pointedness) was found in an analysis of independent contrasts (migratory status, $F_{1,43} = 8.98$, $P = 0.005$; body mass, $F_{1,43} = 0.04$, $P = 0.838$; starting distance, $F_{1,43} = 1.71$, $P = 0.198$).

In the analysis of species values, flight initiation distance was negatively associated with C2 (femur/tibiotarsus length), after controlling for significant variation in body mass (adjusted $R^2 = 0.97$; Table 1c). However, in the analysis based on independent contrasts, neither C2 (femur/tibiotarsus length) nor C3 (tarsometatarsus length) was significantly associated with flight initiation distance, after controlling for the significant variation in starting distance (adjusted $R^2 = 0.65$; Table 1c).

Responses after vacating the patch

In the analysis of species values, landing distance was positively associated with body mass; however, there was no significant relationship between body size and landing distance (adjusted $R^2 = 0.25$; Table 2a). Of all the covariates, only the distance to the nearest shrub was positively related to landing distance: the farther away the nearest cover, the greater the landing distance. In the analysis of independent contrasts, we found that body mass was significantly associated with landing distance: larger species tended to land farther away after fleeing from a threat (adjusted $R^2 = 0.21$; Table 2a, Fig. 2a). Furthermore, distance to the nearest shrub also had a positive effect on landing distance (Table 2a).

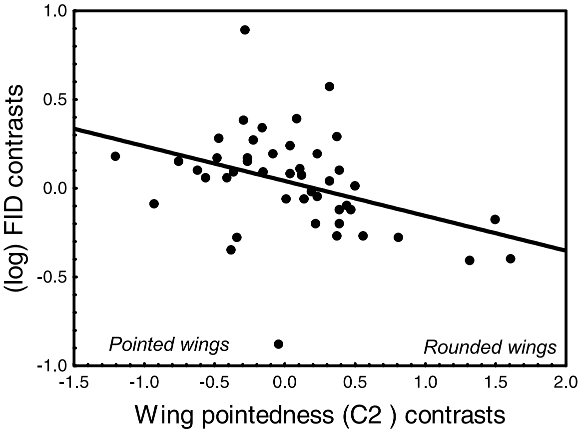

Fig. 1. Relationships between independent contrasts of C2 (wingtip pointedness) and independent contrasts of flight initiation distance (FID).

Table 2. Effects of (a) body mass and size, (b) wing shape, and (c) hind limb length on landing distance

	Coefficient	F	d.f.	P	Partial η^2
(a) Body mass and size effects on landing distance					
Landing distance (*species values*)					
Intercept	5.676	4.40	1, 46	0.483	0.011
(log) Body mass	2.873	0.50	1, 46	**0.043**	0.086
(log) Body size	−2.908	4.34	1, 46	0.495	0.010
Group size	0.067	0.47	1, 46	0.898	0.000
(log) DNTree	0.842	0.02	1, 46	0.458	0.012
DNShrub	0.171	0.56	1, 46	**0.019**	0.114
Landing distance (*independent contrasts*)					
(log) Body mass	3.832	2.76	1, 46	**0.013**	0.126
(log) Body size	−5.653	6.65	1, 46	0.249	0.029
Group size	−0.443	1.36	1, 46	0.409	0.015
(log) DNTree	0.742	0.70	1, 46	0.520	0.009
DNShrub	0.153	0.42	1, 46	**0.029**	0.100
(b) Wing shape effects on landing distance					
Landing distance (*species values*)					
Intercept	4.646	1.62	1, 22	0.216	0.069
(log) Body mass	1.545	4.92	1, 22	**0.037**	0.183
C2 (wingtip pointedness)	−1.820	3.19	1, 22	0.088	0.127
C3 (wingtip convexity)	2.417	4.12	1, 22	0.055	0.158
DNShrub	0.056	0.17	1, 22	0.682	0.008
Landing distance (*independent contrasts*)					
(log) Body mass	2.635	7.97	1, 22	**0.010**	0.266
C2 (wingtip pointedness)	−2.660	7.57	1, 22	**0.012**	0.256
C3 (wingtip convexity)	1.716	0.86	1, 22	0.364	0.038
DNShrub	0.043	0.14	1, 22	0.716	0.006
(c) Hind limb length effects on landing distance					
Landing distance (*species values*)					
Intercept	−2.402	0.82	1, 9	0.389	0.084
(log) Body size	3.742	23.55	1, 9	**0.001**	0.724
C2 (femur length)	−7.554	6.21	1, 9	**0.034**	0.408
C3 (tibiotarsus/tarsometatarsus length)	−4.350	0.04	1, 9	0.843	0.005
DNShrub	−0.570	1.10	1, 9	0.322	0.109
Landing distance (*independent contrasts*)					
(log) Body size	3.610	5.77	1, 9	**0.005**	0.719
C2 (femur length)	−7.721	13.54	1, 9	0.092	0.601
C3 (tibiotarsus/tarsometatarsus length)	−14.647	3.57	1, 9	0.579	0.284
DNShrub	−0.742	0.33	1, 9	0.316	0.036

Note: In part (a), we considered the effects of covariates (group size; distance to the nearest tree, DNTree; distance to the nearest shrub, DNShrub), from which the significant ones were included in parts (b) and (c). We conducted analyses using species values and independent contrasts. Significant ($P < 0.05$) results are printed in **bold**. Partial eta-squared values indicate effect size.

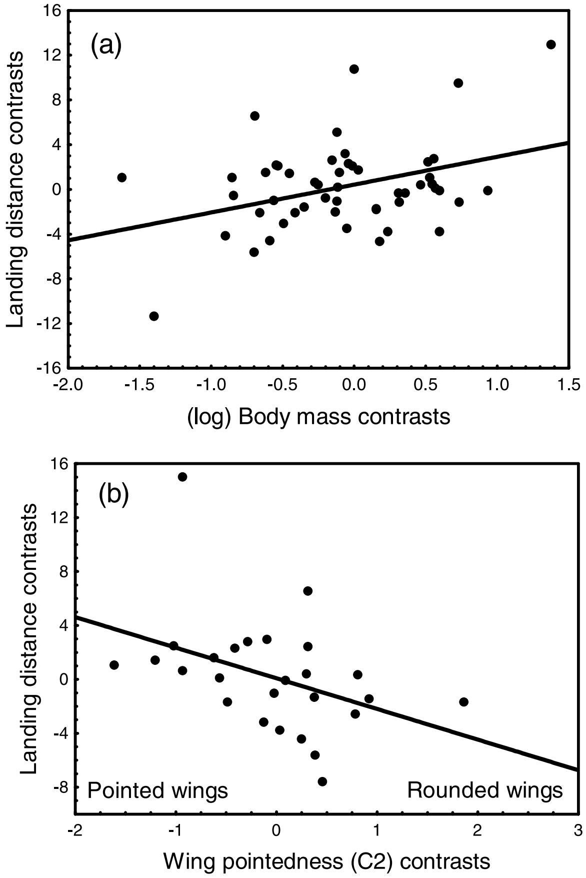

Fig. 2. Relationships between (a) independent contrasts of body mass and independent contrasts of landing distance, and (b) independent contrasts of C2 (wingtip pointedness) and independent contrasts of landing distance.

There was no relationship between body size and landing distance in either analysis; hence, due to its high correlation with body mass (single species, $r = 0.93$, $P < 0.001$; independent contrasts, $r = 0.82$, $P < 0.001$), we decided not to include body size in the following analyses.

In the analysis of species values, we found that body mass was significantly associated with landing distance, whereas wingtip morphology was not (adjusted $R^2 = 0.33$; Table 2b). However, in the analysis of independent contrasts, wingtip pointedness was associated with landing distance, when controlling for significant body mass effects: species with more pointed wings showed larger landing distances (adjusted $R^2 = 0.33$; Table 2b, Fig. 2b).

In the analysis of species values, we found that C2 (wingtip pointedness) was significantly affected by migratory status ($F_{1,23} = 4.04$, $P = 0.031$), when controlling for body mass ($F_{1,23} = 0.01$, $P = 0.977$): long-distance migrants (−0.211 ± 0.096) tended to have more pointed wings than short-distance migrants (0.212 ± 0.123) and resident species (0.173 ± 0.132). However, in the analysis of independent contrasts, there was no relationship between C2 (wingtip pointedness) and migratory status (migratory status, $F_{1,24} = 0.61$, $P = 0.443$; body mass, $F_{1,24} = 2.02$, $P = 0.167$).

Controlling for significant body mass effects, C2 (femur length) was negatively associated with landing distance (adjusted $R^2 = 0.69$; Table 2c) in the single species analysis. However, in the independent contrasts analysis, we found no significant relationship between C2 (femur length) and landing distance after controlling for the significant effects of body mass (adjusted $R^2 = 0.59$; Table 2c)

Landing height was positively associated with landing distance and negatively associated with distance to the nearest tree in the analysis of species values (adjusted $R^2 = 0.37$; Table 3). In the analysis of independent contrasts, we found that only landing distance was significant (Table 3): species that landed farther away also landed higher in the substrate (Fig. 3a), after controlling for body mass, group size, and habitat structure (adjusted $R^2 = 0.20$; Table 3).

Table 3. Effects of body mass and covariates (group size; distance to the nearest tree, DNTree; distance to the nearest shrub, DNShrub) on landing height, and time to resume pre-disturbance behaviour (Time resume PDB) in analyses of species values and independent contrasts

	Coefficient	F	d.f.	P	Partial η^2
Landing height (*single species*)					
Intercept	2.526	6.40	1, 46	0.015	0.122
(log) Body mass	−0.221	0.93	1, 46	0.340	0.020
Landing distance	0.157	10.01	1, 46	**0.003**	0.179
Group size	0.780	2.76	1, 46	0.103	0.057
(log) DNTree	−0.970	7.61	1, 46	**0.008**	0.142
DNShrub	0.004	0.02	1, 46	0.881	0.000
Landing height (*independent contrasts*)					
(log) Body mass	−0.083	0.06	1, 46	0.807	0.000
Landing distance	0.139	7.91	1, 46	**0.007**	0.145
Group size	0.880	3.02	1, 46	0.088	0.058
(log) DNTree	−0.212	0.32	1, 46	0.574	0.013
DNShrub	0.001	0.04	1, 46	0.842	0.000
Time resume PDB (*single species*)					
Intercept	2.161	0.04	1, 46	0.852	0.036
(log) Body mass	0.437	0.02	1, 46	0.879	0.011
Landing distance	1.639	7.07	1, 46	**0.011**	0.117
Landing height	−0.731	0.23	1, 46	0.630	0.049
(log) DNTree	1.152	0.07	1, 46	0.789	0.029
DNShrub	0.402	1.77	1, 46	0.190	0.039
Time resume PDB (*independent contrasts*)					
(log) Body mass	−0.528	0.02	1, 46	0.888	0.002
Landing distance	1.477	6.58	1, 46	**0.013**	0.133
Landing height	3.125	3.92	1, 46	0.054	0.077
(log) DNTree	5.173	1.58	1, 46	0.215	0.048
DNShrub	0.002	0.10	1, 46	0.753	0.004

Note: Significant ($P < 0.05$) results are printed in **bold**. Partial eta-squared values indicate effect size.

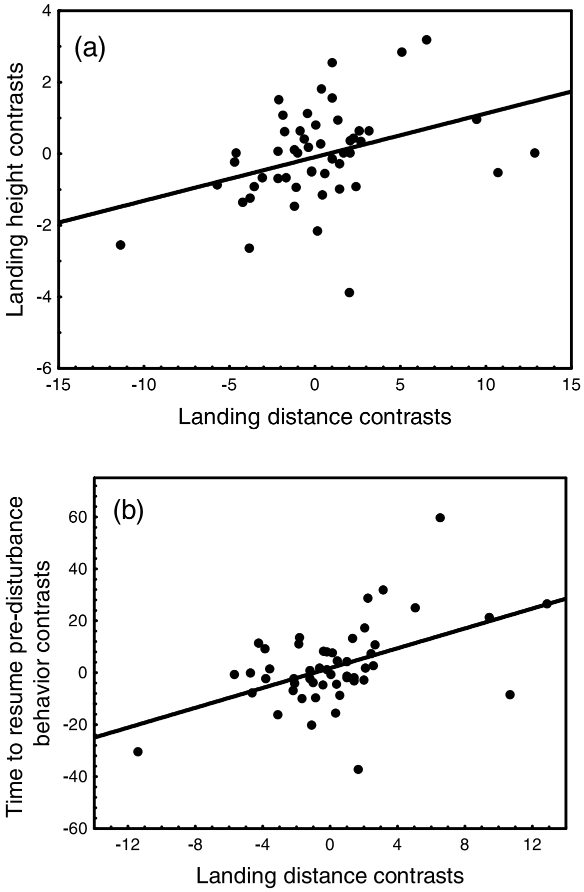

Fig. 3. Relationships between (a) independent contrasts of landing distance and independent contrasts of landing height, and (b) independent contrasts of landing distance and independent contrasts of time to resume pre-disturbance behaviour.

The time to resume pre-disturbance behaviour was positively associated with landing distance, but the other factors were not significant in an analysis of species values (adjusted $R^2 = 0.34$; Table 3). In the analysis of independent contrasts, landing distance was associated with time to resume pre-disturbance behaviour: species that landed farther away took longer to resume the behaviour prior to disturbance (adjusted $R^2 = 0.33$; Table 3, Fig. 3b). Landing height was positively associated with time to resume pre-disturbance behaviour, but this effect was only marginally significant (Table 3).

DISCUSSION

We found that body mass and wingtip pointedness were associated with both escape and post-escape responses in a variety of avian species, and that these effects appear to be related to compensatory behavioural mechanisms that reduce the chances of being caught by predators. However, we note that these are not causal relationships. Thus, we discuss potential mechanisms involved in leaving a resource patch in time and finding a safe refuge to prevent further attacks that could be tested in future studies.

Body mass explained more of the variability in flight initiation distance and landing distance than did body size. Although we cannot conclude that size-dependent changes in vulnerability to predation are unimportant, because body size was highly correlated with body mass, we restrict our discussion to body mass effects.

Previous intra- and interspecific studies have suggested that increases in body mass are associated with reduced escape abilities (e.g. Witter *et al.*, 1994; Metcalfe and Ure, 1995; Kullberg *et al.*, 1996; Lind *et al.*, 1999; Nudds and Bryant, 2000; Tobalske and Dial, 2000; but see Kullberg, 1998; Kullberg *et al.*, 1998; Van der Veen and Lindström, 2000; Nudds and Bryant, 2002). Our results corroborate those of Blumstein (2006): larger species initiate flight at greater distances from an approaching threat than do smaller species. Different factors may explain this pattern. If body mass is negatively associated with take-off ability (see references above), then the benefits of an early escape will be comparatively higher for larger than for smaller species provided there is similar predation risk. Furthermore, if larger species have relatively lower energy requirements than small species (Bennett and Harvey, 1987), then it is expected that they would tolerate less risk than small species in a given foraging situation (Blumstein, 2006).

In a seminal study, Lima (1993) proposed that within some avian families, landing distance would be affected by habitat structure and species size. We found that as the distance to the nearest shrub increased, so did landing distance, which suggests the value of refuge availability to minimize predation risk. This interpretation assumes that shrub acts as a protective cover, but previous research on the factors that affect escape responses has shown that cover may well increase risk if predators hide there and that different species may perceive cover differently (e.g. Lima, 1987; Blumstein and Daniel, 2002). Thus, our result is applicable only to post-escape responses in species that seek some type of cover after leaving a patch due to a potential predator attack.

In phylogenetically based analyses that controlled for variation in habitat structure, we found that body mass is positively associated with landing distance. Because we found a high correlation between body size and mass, we cannot rule out Lima's (1993) mechanism that larger species were more visible and thus more vulnerable. However, we only recorded relatively short flights, which are more likely to be affected by variation in mass loading than steady-state flights (Norberg, 1990). Species with higher body masses are expected to have higher wing loadings, which could increase the rate of loss in altitude and lead to longer flapping flights (Pennycuick, 1989; but see Nudds and Bryant, 2002), resulting in a greater distance between the escape site and the refuge. For instance, there is a positive relationship between body mass and percent time spent flapping across flap-bounding woodpeckers, although the relationship was negative in relation to wing-beat frequency and flapping phase (Tobalske, 1996). Despite species-specific differences in escape tactics (Lima, 1993), many of our model species used flapping flight in their anti-predator responses. Alternatively, the fact that larger species have larger home range sizes and respond to larger elements in the landscape [large grain size (Hostetler and Holling, 2000; Holling, 1992)] may explain the greater landing distances in search for cover. Future research to identify the mechanism behind the body mass–landing distance relationship needs to account for variations in flight type and neuromuscular activity with body mass (e.g. Tobalske, 2001).

Different wingtip designs have been associated with differential vulnerability to predation (e.g. Swaddle and Lockwood, 1998; Pérez-Tris and Telleria, 2001; Burns and Ydenberg, 2002). The fact that species with pointed wingtips have lower lift and thrust when taking off from a resource patch may increase their vulnerability to a predator attack (Rayner, 1993; Van der Veen and Lindström, 2000; Swaddle and Lockwood, 2003). A recent study showed that species with more pointed wings experienced a higher predation rate by Eurasian Sparrowhawks (Swaddle and Lockwood, 1998). Other comparative studies found that species with pointed wingtips tended to adjust their take-off behaviour by increasing flapping (Raikow, 1973) and take-off speed (Burns and Ydenberg, 2002), probably to compensate for the increased risk.

We found that species with more pointed wings escape at greater distances from a threat, after controlling for confounding effects. This means that after detecting a threat, species with pointed wingtips might spend less time on a given resource patch than species with more rounded wings. It can be argued that this trend in flight initiation distance could be a function of a specific flight mode. For instance, increased thrust in species with rounded wings generally applies to birds with rapid wing beats that take-off at steep angles. However, our data set included species with a diversity of flight modes (Rayner *et al.*, 2001), such as bounding flight (many Passeriformes), flap-gliding flight (*Sturnus* sp.), alternating flapping (*Pica pica*), undulating flight (some Charadriiformes), and flight with brief intermittent glides (some Psitaciiformes and Piciformes).

This relationship between wing morphology and flight initiation distance was associated with migratory behaviour. Previous studies also found that migratory species tend to have greater flight initiation distances (Burger and Gochfeld, 1991), but our results suggest a mechanism based on wingtip morphology that had not been reported previously to explain such a response. Alternatively, this compensatory behavioural mechanism could be the result of less behavioural flexibility of migratory species (Sol *et al.*, 2005).

Wingtip pointedness was also associated with landing distance, but this relationship was not influenced by migratory behaviour. Low-speed flights require high lateral manoeuvrability to escape a chasing predator, for which rounded wingtips are more suitable (Pennycuick, 1983, Norberg, 1990). It is likely that species with pointed wingtips may compensate for reduced flight performance at low speeds by flying farther away, because this wingtip design favours sustained flight (Lockwood *et al.*, 1998).

The lack of an effect of wingtip convexity has previously been reported. Swaddle and Lockwood (1998) argued that this relationship could be intrinsic to the index of wingtip convexity, because it usually explains much less of the variability in wingtip shape (< 10% in our case; Appendix 2). Previous evidence linked hind limb morphology to mortality risk (Swaddle and Lockwood, 1998) and flight speed while taking off (Burns and Ydenberg, 2002). In the single species analysis, we found that short femurs were associated with higher flight initiation distance and landing distance as expected, maybe as a result of compensatory effects to reduce the chances of predation. However, such effects vanished after controlling for phylogenetic effects, which suggests an effect in species sharing similar ancestry rather than a widespread trend across families.

Our results, in combination with previous findings (Blumstein *et al.*, 2005), have important implications for birds living in human-disturbed habitats. For instance, the same amount of human visitation could differentially influence species of different body sizes. Thus, we predict that large species would have higher detection abilities (Blumstein *et al.*, 2005), greater flight initiation distances (Blumstein, 2006; present study), and move farther away and perch higher following flight (this study). Moreover, the association we found between landing distance and time to resume pre-disturbance behaviour indicates that larger species affected by disturbance may have larger reductions in the amount of time allocated to foraging, breeding, and roosting behaviour. Therefore, human disturbance would increase the spatial and temporal limitations on accessing suitable habitat relatively more for large species than for small species, which could lead to reductions in carrying capacity and temporal persistence (Fernández-Juricic, 2002). Developing management strategies that consider these interspecific variations in habitat selection could certainly enhance co-existence between humans and wildlife.

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REFERENCES

Bednekoff, P.A. and Lima, S.L. 2002. Why are scanning patterns so variable? An overlooked question in the study of anti-predator vigilance. *J. Avian Biol.*, **33**: 143–149.

Bennett, P.M. and Harvey, P.M. 1987. Active and resting metabolism in birds: allometry, phylogeny and ecology. *J. Zool.*, **213**: 327–363.

Blumstein, D.T. 1998. Quantifying predation risk for refuging animals: a case study with golden marmots. *Ethology*, **104**: 501–516.

Blumstein, D.T. 2003. Flight initiation distance in birds is dependent on intruder starting distance. *J. Wildl. Manage.*, **67**: 852–857.

Blumstein, D.T. 2006. Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Anim. Behav.*, **71**: 389–399.

Blumstein, D.T. and Daniel, J.C. 2002. Isolation from mammalian predators differentially affects two congeners. *Behav. Ecol.*, **13**: 657–663.

Blumstein, D.T. and Fernández-Juricic, E. 2004. The emergence of conservation behavior. *Conserv. Biol.*, **18**: 1175–1177.

Blumstein, D.T. and Pelletier, D. 2005. Yellow-bellied marmot hiding time is sensitive to variation in costs. *Can. J. Zool.*, **83**: 363–367.

Blumstein, D.T., Fernández-Juricic, E., LeDee, O., Larsen, E., Rodriguez-Prieto, I. and Zugmeyer, C. 2004. Avian risk assessment: effects of perching height and detectability. *Ethology*, **110**: 273–285.

Blumstein, D.T., Fernández-Juricic, E., Zollner, P.A. and Garity, S.C. 2005. Interspecific variation in anti-predator behaviour and human–wildlife coexistence. *J.Appl. Ecol.*, **42**: 943–953.

Bonser, R.H.C. and Rayner, J.V.M. 1996. Measuring leg thrust forces in the common starling. *J. Exp. Biol.*, **199**: 435–439.

Burger, J. and Gochfeld, M. 1991. Human distance and birds: tolerance and response distances of resident and migrant species in India. *Environ. Conserv.*, **18**: 158–165.

Burns, J.G. 2003. Relationship of *Calidris* sandpiper wing shape with relative fuel load and total migration distance. *Auk*, **120**: 827–835.

Burns, J.G. and Ydenberg, R.C. 2002. The effects of wing loading and gender on the escape flights of least sandpipers (*Calidris minutilla*) and western sandpipers (*Calidris mauri*). *Behav. Ecol. Sociobiol.*, **52**: 128–136.

Copete, J.L., Mariné, R., Bigas, D. and Martínez-Vilalta, A. 1999. Differences in wing shape between sedentary and migratory Reed Bungings *Emberiza schoeniclus*. *Bird Study*, **46**: 100–103.

Cresswell, W. 1993. Escape responses by redshanks, *Tringa totanus*, on attack by avian predators. *Anim. Behav.*, **46**: 609–611.

de Juana, E. and Varela, J.M. 2000. *Guía de las aves de España: Península, Baleares y Canarias*. Barcelona: Lynx.

Dill, L.M. and Gillett, J.F. 1991. The economic logic of barnacle *Balanus glandula* (Darwin) hiding behavior. *J. Exp. Mar. Biol. Ecol.*, **153**: 115–127.

Dunning, J.B. 1993. *CRC Handbook of Avian Body Masses*. Boca Raton, FL: CRC Press.

Felsenstein, J. 2004. *Inferring Phylogenies*. Sunderland, MA: Sinauer Associates.

Fernández-Juricic, E. 2002. Can human disturbance promote nestedness? A case study with birds in an urban fragmented landscape. *Oecologia*, **131**: 269–278.

Fernández-Juricic, E., Jimenez, M.D. and Lucas, E. 2002. Factors affecting intra- and inter-specific variations in the difference between alert and flight distances in forested habitats. *Can. J. Zool.*, **80**: 1212–1220.

Fernández-Juricic, E., Vaca, R. and Schroeder, N. 2004. Spatial and temporal responses of forest birds to human approaches in a protected area and implications for two management strategies. *Biol. Conserv.*, **117**: 407–416.

Ferriere, R., Cazalles, B., Cezilly, F. and Desportes, J.-P. 1996. Predictability and chaos in vigilant behaviour. *Anim. Behav.*, **52**: 457–472.

Frid, A. and Dill, L.M. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.*, **6** (11) [available online at: http://www.consecol.org/vol6/iss1/art11].

Hamilton, W.J., III and Watt, K.E.F. 1970. Refuging. *Annu. Rev. Ecol. Syst.*, **1**: 263–286.

Heppner, F.H. and Anderson, J.G.T. 1985. Leg thrust important in flight take-off in the pigeon. *J. Exp. Biol.*, **114**: 285–288.

Holling, C.S. 1992. Cross-scale morphology, geometry and dynamics of ecosystems. *Ecol. Monogr.*, **62**: 447–502.

Hostetler, M.E. and Holling, C.S. 2000. Detecting the scales at which birds respond to structure in urban landscapes. *Urban Ecosyst.*, **4**: 25–54.

Hugie, D.M. 2003. The waiting game: a 'battle of waits' between predator and prey. *Behav. Ecol.*, **14**: 807–817.

Keast, A. 1996. Wing shape in insectivorous passerines inhabiting New Guinea and Australian rain forests and eucalypt forest/eucalypt woodlands. *Auk*, **113**: 94–104.

Krams, I. 2001. Patch selection by singing chaffinches: a better view of surroundings and the risk of predation. *Behav. Ecol.*, **12**: 295–300.

Kullberg, C. 1998. Does diurnal variation in body mass affect take-off ability in wintering willow tits? *Anim. Behav.*, **56**: 227–233.

Kullberg, C., Fransson, T. and Jacobsson, S. 1996. Impaired predator evasion in fat blackcaps (*Sylvia atricapilla*). *Proc. R. Soc. Lond. B*, **263**: 1671–1675.

Kullberg, C., Jacobsson, S. and Fransson, T. 1998. Predator-induced take-off strategy in great tits (*Parus major*). *Proc. R. Soc. Lond. B*, **265**: 1659–1664.

Lima, S. 1987. Distance to cover, visual obstructions, and vigilance in house sparrows. *Behaviour*, **102**: 231–238.

Lima, S.L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Adv. Stud. Behav.*, **27**: 215–290.

Lima, S.L. 1993. Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. *Wilson Bull.*, **105**: 1–47.

Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, **68**: 619–640.

Lind, J. and Cresswell, W. 2005. Determining the fitness consequences of antipredator behavior. *Behav. Ecol.*, **16**: 945–956.

Lind, J., Fransson, T., Jacobsson, S. and Kullberg, C. 1999. Reduced take-off ability in robins due to migratory fuel load. *Behav. Ecol. Sociobiol.*, **46**: 65–70.

Lind, J., Hollén, L., Smedberg, E., Svensson, U., Vallin, A. and Jakobsson, S. 2003. Detection distance influences escape behaviour in two parids, *Parus major* and *P. caeruleus*. *J. Avian Biol.*, **34**: 233–236.

Lockwood, R., Swaddle, J.P. and Rayner, J.M.V. 1998. Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. *J. Avian Biol.*, **29**: 273–292.

Maddison, W.P. and Maddison, D.R. 2001. *MacClade: Analysis of Phylogeny and Character Evolution*, Version 4.03. Sunderland, MA: Sinauer Associates.

Marden, J.H. 1987. Maximum lift production during take-off in flying animals. *J. Exp. Biol.*, **130**: 235–258.

Martin, J. 2001. When hiding from predators is costly: optimization of refuge use in lizards. *Ethologia*, **9**: 9–13.

Martins, E.P. 2004. *COMPARE*, Version 4.6. Computer programs for the statistical analysis of comparative data (available at: http://compare.bio.indiana.edu/). Bloomington, IN: Department of Biology, Indiana University.

Metcalfe, N.B. and Ure, S.E. 1995. Diurnal variation in flight performance and hence potential predation risk in small birds. *Proc. R. Soc. Lond. B*, **261**: 395–400.

Mönkkönen, M. 1995. Do migratory birds have more pointed wings? A comparative study. *Evol. Ecol.*, **9**: 520–528.

Norberg, U.M. 1990. *Vertebrate Flight: Mechanics, Physiology, Morphology, Ecology and Evolution*. Berlin: Springer.

Nudds, R.L. and Bryant, D.M. 2000. The energetic cost of short flights in birds. *J. Exp. Biol.*, **203**: 1561–1572.

Nudds, R.L. and Bryant, D.M. 2002. Consequences of load carrying by birds during short flights are found to be behavioral and not energetic. *Am. J. Physiol.: Regul. Integr. Comp. Physiol.*, **283**: 249–256.

Peiro, I.G. 2003. Intraspecific variation in the wing shape of the long-distance migrant Reed Warbler *Acrocephalus scirpaceus*: effects of age and distance of migration. *Ardeola*, **50**: 31–37.

Pennycuick, C.J. 1983. Thermal soaring compared in three dissimilar tropical bird species, *Fregata magnificiens, Pelecanus occidentalis* and *Coragyps atratus*. *J. Exp. Biol.*, **102**: 307–325.

Pennycuick, C.J. 1989. *Bird Flight Performance: A Practical Calculator Manual*. Oxford: Oxford University Press.

Pérez-Tris, J. and Tellería, J.L. 2001. Age-related variation in wing shape of migratory and sedentary Blackcaps *Sylvia atricapilla*. *J. Avian Biol.*, **32**: 207–213.

Raikow, R.J. 1973. Locomotor mechanisms in North American ducks. *Willson Bull.*, **85**: 295–307.

Rayner, J.M.V. 1993. On aerodynamics and the energetics of vertebrate flapping flight. In *Fluid Dynamics in Biology* (A.Y. Cheer and C.P. van Dam, eds.), pp. 351–400. Contemporary Mathematics #141. Providence, RI: American Mathematical Society.

Rayner, J.M.V., Viscardi, P.W., Ward, S. and Speakman, J.R. 2001. Aerodynamics and energetics of intermittent flight in birds. *Am. Zool.*, **41**: 188–204.

Sibley, C.G. and Ahlquist, J.E. 1990. *Phylogeny and Classification of Birds: A Study in Molecular Evolution*. New Haven, CT: Yale University Press.

Sibley, C.G. and Monroe, B.L., Jr. 1990. *Distribution and Taxonomy of Birds of the World*. New Haven, CT: Yale University Press.

Simpson, K. and Day, N. 2000. *Birds of Australia*. Princeton, NJ: Princeton University Press.

Sol, D., Lefebvre, L. and Rodríguez-Teijeiro, J.D. 2005. Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. *Proc. R. Soc. Lond. B*, **272**: 1433–1442.

Stankowich, T. and Blumstein, D.T. 2005. Fear in animals: a meta-analysis and review of risk assessment. *Proc. R. Soc. Lond. B*, **272**: 2627–2634.

Suhonen, J. 1993. Predation risk influences the use of foraging sites by tits. *Ecology*, **74**: 1197–1203.

Swaddle, J.P. and Lockwood, R. 1998. Morphological adaptations to predation risk in passerines. *J. Avian Biol.*, **29**: 172–176.

Swaddle, J.P. and Lockwood, R. 2003. Wingtip shape and flight performance in the European Starling (*Sturnus vulgaris*). *Ibis*, **145**: 457–464.

Tobalske, B.W. 1996. Scaling of muscle composition, wing morphology and intermittent flight behavior in woodpeckers. *Auk*, **113**: 151–177.

Tobalske, B.W. 2001. Morphology, velocity, and intermittent flight in birds. *Am. Zool.*, **41**: 177–187.

Tobalske, B.W. and Dial, K.P. 2000. Effects of body size on take-off flight performance in the Phasianidae (Aves). *J. Exp. Biol.*, **203**: 3319–3332.

Tobalske, B.W., Altshuler, D.L. and Powers, D.R. 2004. Take-off mechanics in hummingbirds (Trochilidae). *J. Exp. Biol.*, **207**: 1345–1352.

Van der Veen, I.T. and Lindström, K.M. 2000. Escape flights of yellowhammers and greenfinches: more than just physics. *Anim. Behav.*, **59**: 593–601.

Watts, D. 2000. *Field Guide to Tasmanian Birds*. London: New Holland Publishers.

Witter, M.S., Cuthill, I.C. and Bonser, R.H.C. 1994. Experimental investigation of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. *Anim. Behav.*, **48**: 201–222.

Ydenberg, R.C. and Dill, L.M. 1986. The economics of fleeing from predators. *Adv. Stud. Behav.*, **16**: 229–249.

APPENDIX 1

Scientific and common names of the species used in this study. Database indicates the type of analysis a given species was included in: I, body mass and size, and flight initiation distance; II, wing morphology vs. flight initiation distance; III, hind limb morphology vs. flight initiation distance; IV, body mass and size, and landing distance; V, wing morphology vs. landing distance; VI, hind limb morphology vs. landing distance. Database IV was used to assess the effects of landing distance on landing height and time to resume pre-disturbance behaviour.

Scientific name	Common name	Database
Acridotheres tristis	Common Myna	IV
Agelaius phoeniceus	Red Winged Blackbird	I, II, IV, V
Alectura lathami	Brush Turkey	I, III
Anthus novaeseelandiae	Australasian Pipit	I, III
Aphelocoma californica	Western Scrub Jay	I, II, III, IV, V, VI
Ardea alba	Great Egret	I, II, III
Ardea herodias	Great Blue Heron	I, II, III, IV, V, VI
Arenaria interpres	Ruddy Turnstone	I, III, II
Bubulcus ibis	Cattle Egret	I, II, IV, V
Cacatua galerita	Sulfur-crested Cockatoo	I, II, III
Cacatua roseicapilla	Galah	I, III

APPENDIX 1—*continued*

Scientific name	Common name	Database
Calidris mauri	Western Sandpiper	I, II, III
Calidris minutilla	Least Sandpiper	I, II, III
Callipepla californica	California Quail	I, II, IV, V
Callipepla gambelii	Gambels Quail	I, II, IV, V
Cardinalis cardinalis	Northern Cardinal	I, II, IV, V
Carduelis carduelis	Gold Finch	I, II, IV, V
Carduelis chloris	Green Finch	IV
Carpodacus mexicanus	House Finch	I, II, IV, V
Carpodacus purpureus	Purple Finch	IV
Catoptrophorus semipalmatus	Willet	I, II, III
Certhia brachydactyla	Short-toed Treecreeper	IV
Chamaea fasciata	Wrentit	I, II, III, IV, V, VI
Chenonetta jubata	Maned Duck	I, III
Corvus brachyrhynchos	American Crow	I, II, IV, V
Corvus corax	Common Raven	I, II, IV, V
Corvus monedula	Jackdaw	IV
Dacelo novaeguineae	Laughing Kookaburra	I, III
Dendroica coronata	Yellow-rumped Warbler	I, II, III, IV, V, VI
Egretta thula	Snowy Egret	I, II, III, IV, V, VI
Empidonax oberholseri	Dusky Flycatcher	IV
Empidonax wrightii	Gray Flycathcer	IV
Erithacus rubecula	Robin	IV
Euphagus cyanocephalus	Brewer's Blackbird	I, II, IV, V
Fringilla coelebs	Chaffinch	IV
Guiraca caerulea	Blue Grosbeak	IV
Himantopus mexicanus	Black Necked Stilt	I, II, III, IV, V, VI
Junco hyemalis	Dark-eyed Junco	I, II, III, IV, V, VI
Larus delawarensis	Ring-billed Gull	I, II, III
Larus occidentalis	Western Gull	I, II, III
Limnodromus griseus	Short-billed Dowitcher	I, III
Limosa fedoa	Marbled Godwit	I, II, III
Melanerpes formicivorus	Acorn Woodpecker	I, II, IV, V
Melospiza melodia	Song Sparrow	I, II, III, IV, V, VI
Mimus polyglottos	Northern Mockingbird	I, II, IV, V
Motacilla alba	Pied Wagtail	IV
Myiarchus cinerascens	Ash-throated Flycatcher	I, II, IV, V
Numenius americanus	Long-billed Curlew	I, II, III
Numenius phaeopus	Whimbrel	I, II, III
Parus ater	Coal Tit	IV
Parus caeruleus	Blue Tit	IV
Parus major	Great Tit	IV
Passer domesticus	House Sparrow	I, III, IV, VI
Passer montanus	Tree Sparrow	IV
Phalacrocorax carbo	Great Cormorant	I, III
Phalacrocorax melanoleucos	Little Pied Cormorant	I, III
Phalacrocorax sulcirostris	Little Black Cormorant	I, III
Phylloscopus collybita	Chiffchaff	IV

Scientific name	Common name	Database
Pica pica	Magpie	I, II
Picoides nuttallii	Nutall's Woodpecker	IV
Picus viridis	Green Woodpecker	IV
Pipilo maculatus	Spotted Towhee	I, II
Pipilo crissalis	California Towee	I, III, IV, VI
Pipilo fuscus	Canyon Towhee	I, II
Pipilo maculates	Spotted Towhee	IV
Piranga ludoviciana	Western Tanager	I, II, IV, V
Pluvialis squatarola	Black-billed Plover	I, II, III
Polioptila californica	California Gnatcatcher	IV
Psaltriparus minimus	Bushtit	I, II, III
Quiscalus mexicanus	Great-tailed Grackle	I, II, IV, V
Regulus calendula	Ruby-crowned Kinglet	I, II, III
Sayornis nigricans	Black Phoebe	IV
Sterna albifrons	Little Tern	I, III
Sterna antillarum	Least Tern	I, II
Sterna caspia	Caspian Tern	I, II, III
Streptopelia chinensis	Spotted Turtledove	I, II, III
Sturnus unicolor	Spotless Starling	IV
Sturnus vulgaris	European Starling	I, III, IV, VI
Toxostoma redivivum	California Thrasher	I, II, IV, V
Trichoglossus haematodus	Rainbow Lorikeet	I, III
Turdus migratorius	American Robin	I, II, III, IV, V, VI
Zenaida macroura	Mourning Dove	I, II, III, IV, V, VI
Zonotrichia leucophrys	White crowned Sparrow	I, II, III, IV, V, VI

APPENDIX 2

Size-constrained component analysis (following Lockwood *et al.*, 1998) on wing and hind limb morphology.

(a) Factor loadings of size-constrained component analysis of wing morphology in the flight initiation distance database:

	C1	C2	C3
Primary 1	0.9908	−0.2471	−0.0523
Primary 2	0.9908	−0.1310	0.0152
Primary 3	0.9908	−0.0533	0.0411
Primary 4	0.9908	0.0009	0.0353
Primary 5	0.9908	0.0523	0.0301
Primary 6	0.9908	0.0965	0.0053
Primary 7	0.9908	0.1252	−0.0267
Primary 8	0.9908	0.1564	−0.0482
Percent of total variance explained	98.182	1.666	0.123

(b) Factor loadings of size-constrained component analysis of hind limb morphology in the flight initiation distance database:

	C1	C2	C3
Femur	0.9581	0.2467	0.1459
Tarsometatarsus	0.9581	0.0357	−0.2843
Tibiotarsus	0.9581	−0.2702	0.0956
Percent of total variance explained	91.784	4.505	3.709

(c) Factor loadings of size-constrained component analysis of wing morphology in the landing distance database:

	C1	C2	C3
Primary 1	0.9906	−0.2760	−0.0490
Primary 2	0.9906	−0.1208	0.0266
Primary 3	0.9906	−0.0237	0.0505
Primary 4	0.9906	0.0173	0.0430
Primary 5	0.9906	0.0649	0.0318
Primary 6	0.9906	0.1060	−0.0103
Primary 7	0.9906	0.1131	−0.0399
Primary 8	0.9906	0.1190	−0.0529
Percent of total variance explained	98.131	1.676	0.163

(d) Factor loadings of size-constrained component analysis of hind limb morphology in the landing distance database:

	C1	C2	C3
Femur	0.9836	0.2443	0.0099
Tarsometatarsus	0.9836	−0.0680	−0.0388
Tibiotarsus	0.9836	−0.1762	0.0288
Percent of total variance explained	96.739	3.179	0.081