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Morphological adaptations to predation risk in passerines

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Avoiding predation is an important factor in avian life-history strategies and there are many examples of adaptations that appear to decrease predation risk. However, we are not aware of any studies of structural morphological adaptations to reduce predation risk in any avian species. Here, we have compared published indices of relative predation risk for passerine species with two size-constrained measures of wingtip shape and relative hind limb morphology. Our analyses indicate that species with rounded wingtips and those with relatively short femora compared with tarsi are at a lower relative predation risk than those with more pointed wingtips and relatively longer femora. These relations are discussed in terms of the functional morphology of wingtip shape and hind limb morphology and suggestions for further experimental investigations are made.

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Predator avoidance is an important factor in avian life-history strategies (Lima and Dill 1990) and many examples of adaptations to minimise predation risk have been reported. These examples include both behavioural (e.g. Page and Whitacre 1975, Kenward 1978, Elgar 1989, Cresswell 1993, 1994, Lima 1993, Witter et al. 1994, Metcalfe and Ure 1995, Götmark and Post 1996) and morphological (e.g. Witter et al. 1994, Götmark 1997) adaptations. Although there is some evidence to indicate that factors such as body mass (Witter et al. 1994, Kullberg et al. 1996) and coloration (e.g. Hasson 1991, Götmark and Hohlfält 1995, Götmark 1997) may influence predation risk in some bird species, there is still relatively little known about structural morphological changes that minimise the risk of being preyed upon. Pennycuick et al. (1994) have noted that morphological differences can occur between predator (Gyrfalcon *Falco rusticolus*) and prey species (Sage grouse *Centrocercus urophasianus*) that may favour predatory escape by the prey. Also, Andersson and Norberg (1981) have presented an aerodynamic-based model which suggests that predatory performance of raptors may increase with decreasing body size; hence there is selection for smaller male body size in a number of species. In this study we investigated wingtip shape and hind limb adaptations to predation risk in a variety of common passerine species.

Recently, Götmark and Post (1996) examined and quantified the relative predation risk of passerine species preyed on by Sparrowhawks *Accipiter nisus* during the breeding season near Göteborg, Sweden. Relative predation risk was assessed by the over- and under-representation of species in Sparrowhawk diets compared with the number of each species in local populations. Götmark and Post revealed that several factors (foraging sites, prey density, singing, body mass) appear to influence predation risk among the species that they studied. Here, we have compared the relative predation risk indices calculated by Götmark and Post (1996) with two measures of size-constrained wingtip shape (wingtip roundedness and convexity; Lockwood et al. 1998) and hind limb morphology (relative proportions of the length of femur and length of tarsus). Such an analysis is important in determining avian anti-predatory adaptations to maximise the probability of survival and also indicates a further component of the suite of interacting factors that influence avian morphology.

Methods

Wingtip shape

Two size-constrained (derived from Burnaby 1966) indices of wingtip shape, roundedness and convexity, were derived for 26 passerine species by applying the formulas presented by Lockwood et al. (1998) to the lengths of the eight distal-most primary feathers. Primary length measurements were obtained either from the literature (Brown et al. 1987) (N = 11) or from preserved skins at the British Museum, Tring (to 0.1 mm accuracy with Vernier callipers; N = 15; sample sizes ranged from 1 to 5, median = 3). These two wingtip shape indices accurately capture morphological variability in wing design among flighted species more comprehensively than previously published measures (details in Lockwood et al. 1998).

Hind limb morphology

Two size-constrained indices of hind limb morphology were constructed using the same mathematical procedure as employed for the wing feathers. Hind limb bones were measured to 0.01cm accuracy using Vernier callipers; sample sizes ranged from 1 to 5, median = 3 on museum specimens for 160 species as part of a larger study of avian morphology (R. Lockwood unpubl. data) in which the lengths of the three principal hind limb bones: femur, tibiotarsus and tarsometatarsus were entered into a size-constrained components analysis (Lockwood et al. 1998) to generate three significant components (Table 1). Measurements were log-transformed, which increased normality, and were standardised to equal unit variances for each bone length. The first index was interpreted as isometric size variation and hence was not used in further analyses. The two remaining indices explained a further 3.85% and 0.57% of variation in the data and represented size-independent allometric shape variation. Component 2 (femur) was interpreted as increasing proximal leg length (femur/tarsometatarsus); whereas component 3 (tibia) was interpreted as increased relative tibia length (tibiotarsus/femur and tarsometatarsus) (see Table 1). Of the species studied by Lockwood (unpubl. data), 15 satisfied the criteria detailed below, hence hind limb morphology indices were used for these 15 species in subsequent analyses.

Table 1. Loading factors of hind limb size-constrained components in relation to hind limbs. The first component accounted for isometric size. The second and third components described elements of allometric shape variation. Component 2 was interpreted as increased relative femur length and decreased tarsus length; component 3 was interpreted as increased relative tibia length.

Component	Femur	Tibiotarsus	Tarsometatarsus
1	0.551	0.567	0.612
2	0.711	0.017	−0.700
3	−0.437	0.821	−0.367

Predation risk and morphology

The two wingtip shape and hind limb parameters were compared with the published estimates of relative predation risk for passerine species from habitats (mostly forest areas) near to Sparrowhawk nests (Götmark and Post 1996; Table 2). This particular index of relative predation risk was used in an effort to minimise among-species morphological adaptations to different habitats (reviews in James 1982, Leisler and Winkler 1991). To minimise the influence of species size on relative predation risk we have performed analyses only on the smaller species (≤ 31 g) reported by Götmark and Post (1996). Additionally, to account for morphological adaptations to migratory behaviour (e.g. Winkler and Leisler 1992, Mönkkönen 1995, Lockwood et al. 1998), we performed correlation analyses between relative predation risk and the residuals of morphological indices and migratory categories from a linear regression. Migratory categories (1 – *Migratory*, all or most individuals make regular seasonal movements between breeding and wintering ranges; 2 – *Partially Migratory*, populations contain substantial migratory and non-migratory elements; 3 – *Dispersive*, population can undergo infrequent, random movements over a long distance; 4 – *Non-migratory*, either resident or sedentary species) were obtained from the literature (Harrison 1982, Cramp 1985, 1988, 1992, Cramp and Perrins 1993). All analyses were performed using Minitab for Windows 10.2 (Minitab Inc. 1994) employing two-tailed tests of probability throughout.

Results and discussion

Wingtip shape

Species with rounded wingtips had a lower relative predation risk than those with more pointed wings ($r = -0.433$, $N = 26$, $P = 0.021$, Fig. 1). There was no significant relation between wingtip convexity and relative predation risk ($r = 0.363$, $N = 26$, $P = 0.058$). It has been hypothesised that a wing with a more rounded tip can maximise thrust from flapping, while a more pointed wingtip minimises wing weight and wing inertia (Rayner 1986, 1993). Additionally, rounded wings will produce relatively more lift toward the wingtip, where the wing is moving faster, but also more drag. These factors are likely to enhance flight performance at slow speeds, particularly in terms of take-off from the

Table 2. Wingtip shape and relative predation risk for passerine species. RPR denotes mean relative predation rates for bird species in habitats near to Sparrowhawk nests (see Götmark and Post 1996 for further details). Wingtip roundedness and convexity were calculated using formulas presented by Lockwood et al. (1998). Refer to text for details of how femur and tibia indices were calculated.

	RPR	Roundedness	Convexity	Femur	Tibia
Barn Swallow *Hirundo rustica*	4.2	−1.6438	0.143	0.565	0.864
White Wagtail *Motacilla alba*	6.1	0.0151	−0.884	−0.766	0.442
Meadow Pipit *Anthus pratensis*	−3.4	−0.3766	−0.421	−0.663	0.286
Wren *Troglodytes troglodytes*	−9.4	1.3766	−2.21	−0.416	0.085
Dunnock *Prunella modularis*	−2.8	1.4698	−0.838	−0.050	−0.182
Robin *Erithacus rubecula*	0.1	1.6344	0.396	−0.836	0.192
Blackcap *Sylvia atricapilla*	−0.7	0.7544	−0.612		
Lesser Whitethroat *S. curruca*	1.4	1.2772	−0.975	−0.751	−0.375
Willow Warbler *Phylloscopus trochilus*	−9.7	0.9162	−1.397		
Goldcrest *Regulus regulus*	−12.2	0.5126	−1.098	−1.416	0.196
Pied Flycatcher *Fidecula hypoleuca*	3.0	−0.3032	0.561		
Spotted Flycatcher *Muscicapa striata*	3.3	−0.2847	−0.075	−0.028	0.166
Coal Tit *Parus ater*	−8.4	1.3506	−0.272		
Blue Tit *P. caeruleus*	0.2	0.8416	−1.057		
Great Tit *P. major*	3.4	1.3616	0.0004		
March Tit *P. palustris*	0.8	1.092	−0.85	−0.255	0.611
Nuthatch *Sitta europaea*	2.4	0.4096	−7.54		
Treecreeper *Certhia familiaris*	−4.6	0.7683	−0.171	−0.466	−1.029
Yellowhammer *Emberiza citrinella*	4.6	0.1435	−0.664	0.373	−0.143
Reed Bunting *E. schoeniclus*	8.6	1.1014	−0.997		
Chaffinch *Fringilla coelebs*	−4.4	0.3031	−0.443	0.231	0.407
Greenfinch *Carduelis chloris*	3.4	0.0671	−1.301	0.441	0.136
Siskin *C. spinus*	−0.4	−0.4288	−0.465		
Redpoll *C. flammea*	6.2	−0.2807	−0.793		
Bullfinch *Pyrrhula pyrrhula*	0.3	0.9377	−0.806		
House Sparrow *Passer domesticus*	17.2	−0.0856	−0.401	0.537	−0.018

ground and aerial manoeuvrability (see Pennycuick 1971, 1983, Norberg 1990, Thollesson and Norberg 1991). Direct observations of flight performance in European Starlings *Sturnus vulgaris* has indicated that wingtip shape does influence take-off behaviour; individuals with more rounded wingtips take-off from the ground faster and at a steeper angle of ascent (J. P. Swaddle, J. M. V. Rayner and R. Lockwood unpubl. data). The ability to take off quickly from the ground and perform aerial manoeuvres has been associated with lower predation risk in a range of species (Rudebeck 1950, Page and Whitacre 1975, Kenward 1978, Bijlsma 1990, Cresswell 1993, Witter et al. 1994, Metcalfe and Ure 1995, Kullberg et al. 1996).

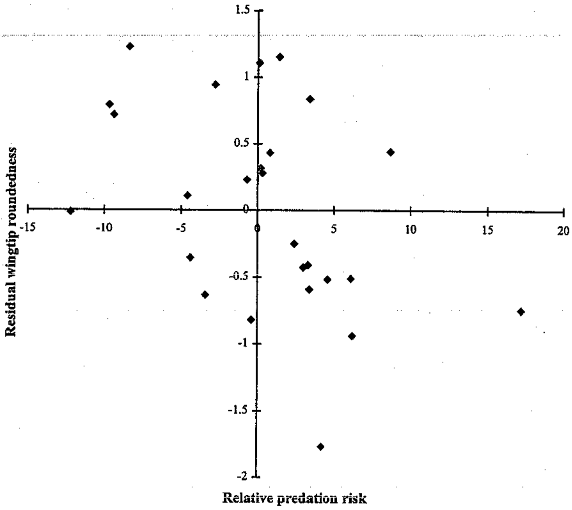

Fig. 1. Residual wingtip roundedness (controlling for migratory behaviour, see text) versus relative predation risk. Each data point represents a separate species.

Previous examination of the morphology of insectivorous neotropical birds has revealed that birds which catch flies by manoeuvrable flight tend to have wings of lower aspect ratio (i.e. shorter, broader wings) than birds that catch their prey by prolonged aerial pursuit (D. F. Sherry unpubl. data, reported in Leisler and Winkler 1985). Our data are in general agreement with these findings; birds with more rounded wingtips have lower predation risk as they are, presumably, more manoeuvrable.

Hind limb morphology

Bird species with relatively long femora and short tarsi were at a higher predation risk than those with relatively short femora ($r = 0.589$, $N = 15$, $P = 0.028$, Fig. 2). There was no relation between hind limb component 3 (increased relative tibia length) and relative predation risk ($r = 0.118$, $N = 15$, $P = 0.652$).

Birds that hop (as opposed to walk) tend to have relatively longer tarsi (Leisler 1977). It is possible that hopping is a more effective anti-predatory tactic than

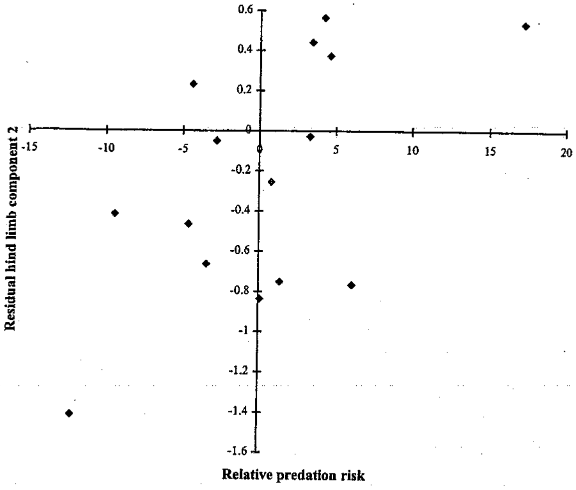

Fig. 2. Residual hind limb component 2, femur (controlling for migratory behaviour, see text) versus relative predation risk. Each data point represents a separate species.

walking as it could aid take-off leap; additionally walking may expose individuals to more open habitats and hence higher relative predation risk. Our data appear to indicate that birds with longer tarsi do have lower relative predation risk.

Similarly, it has previously been indicated that *Sylvia* warblers with shorter hind limbs may be capable of taking off more quickly than those with relatively long hind limbs (Leisler and Winkler 1991). As hind limb lever-length (as related to take-off) is largely influenced by femur length (and muscle insertion along the length of the femur), this previous study could imply that birds with long femora take off more slowly and hence suffer increased predation risk. On the other hand, it could be argued that longer legs would permit a longer acceleration phase when flexing before a take-off leap. Our data appear to support the former hypothesis, as species with relatively long femora appear to experience increased predation risk. Leisler and Winkler (1991) have also reported a general tendency for hind limbs to be smaller when flight muscles are well-developed; this relationship may also help to explain the correlation between relative femoral length and relative predation risk.

General

The relationships between morphology and relative predation risk that our data have revealed may be, in part, a reflection of adaptations to the habitats which these passerine species normally occupy. Species occupying cluttered arboreal habitats may have evolved relatively rounded wingtips and shorter femora, and cluttered habitats may have an inherently lower predation risk. Similar arguments could be made for the relations between morphology and locomotion, i.e., birds with more rounded wings are more agile fliers. Hence, it is not possible to demonstrate a direct causal relationship between morphology and predation risk in this preliminary study. However, we have attempted to minimise specific affects by (1) controlling for migratory categories; (2) using only data collected from a narrow range of habitats; and (3) restricting analyses to smaller species to reduce size-specific effects (cf. Götmark and Post 1996). These precautions will at least reduce the influence of such correlated non-random elements. Therefore, we hope that this study will generate interest in the morphological adaptations to predation risk and lead to detailed experimental field studies of factors that directly affect the probability of individuals avoiding predation. In further studies it may also be important to control for phylogenetic relatedness in comparisons of morphology. In this present study, it was not possible to perform pairwise comparisons of closely related species due to small sample sizes; however, it could be possible to generate mathematical models which take into account relatedness in subsequent investigations (cf. Brandl et al. 1994).

Previously, structural morphological adaptations in response to predatory stimuli have been demonstrated in a number of taxa, most notably aquatic species (review in Harvell 1990). For example, Smith and Van Buskirk (1995) reported that tail shape of two frog tadpole species differs between habitats of high and low predation. Similarly, McCollum and Leimberger (1997) demonstrated that predatory stimuli can induce body shape differences in treefrog tadpoles which act to aid swimming behaviour and, hence, increase the likelihood of avoiding predation. In bird species, there is some evidence to indicate that body size may be related to predatory performance in raptors (Andersson and Norberg 1981). However, we are not aware of any studies that relate predation risk to morphology in avian taxa. Hence, this study is a valuable first step in indicating anti-predatory structural adaptations in birds; passerine species with rounded wingtips and relatively longer tarsi experience lower relative predation risk.

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