



Flight initiation distances in relation to sexual dichromatism and body size in birds from three continents

ANDERS P. MØLLER^{1*}, DIOGO S. M. SAMIA², MICHAEL A. WESTON³, PATRICK-JEAN GUAY⁴ and DANIEL T. BLUMSTEIN⁵

¹*Laboratoire d'Ecologie, Systématique et Evolution, Centre National de la Recherche Scientifique Unité Mixte de Recherche 8079, Université Paris-Sud, Bâtiment 362, F-91405, Orsay Cedex, France*

²*Ecology and Evolution, Laboratory of Theoretical Ecology and Synthesis, Federal University of Goiás, Caixa Postal 131, 74001-970, Goiânia, Brazil*

³*Centre for Integrative Ecology, School of Life and Environmental Sciences, Faculty of Science, Engineering and the Built Environment, Deakin University, Burwood, Vic., 3125, Australia*

⁴*Institute for Sustainability and Innovation, College of Engineering and Science, Victoria University, Footscray Park Campus, PO Box 14428, Melbourne MC, Vic., 8001, Australia*

⁵*Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA, 90095-1606, USA*

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Predators exert strong selection pressures on their prey. Prey would therefore benefit by adjusting their behaviour to the risk of predation, while predators conversely would benefit from adjusting their behaviour to that of their prey. Extravagant ornamentation has evolved to attract mates and/or successfully compete with conspecifics of the same sex to secure high mating success, even if that occurs at a cost of increased risk of predation. Thus, sexually dichromatic species may be more susceptible to predation than sexually monochromatic species, and the presence of compensation is indicative of such species being more vulnerable. If extravagant ornamentation is costly in terms of predation risk, then we should expect sexually dichromatic species to have longer flight initiation distances (FID) than sexually monochromatic species. If ornamentation is acquired as a handicap with only individuals in prime condition being able to display with the smallest viability cost, we should expect sexually dichromatic individuals to have shorter FID than sexually monochromatic individuals. Such differences among individuals should, on an evolutionary time scale, translate into differences in FID being related to differences in sexual dichromatism among species. We investigated the relationship between FID and sexual dichromatism in phylogenetic analyses, while accounting for effects of continent (Australia, North America, and Europe), body mass, the interaction between sexual dichromatism and body mass and the interaction between sexual dichromatism and continent. In an analysis of 447 species we found shorter FID in sexually dichromatic than in sexually monochromatic species (consistent with the handicap hypothesis because sexually dichromatic species took greater risks), especially so at large body size. FID differed among continents and the relative difference in FID between sexually monochromatic and sexually dichromatic species was larger in Europe than in Australia and North America. These differences among continents may be attributed to latitudinal effects of predation. These findings are important for current ideas about the evolution of secondary sexual characters because they imply covarying continental differences in predation, especially for large bodied sexually dichromatic species. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **117**, 823–831.

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*Corresponding author. E-mail: anders.moller@u-psud.fr

INTRODUCTION

Sexual selection is the evolutionary process that arises from mate choice or competition among individuals of the same sex for access to mates (Andersson, 1994). The fitness advantages of sexual selection are either direct material benefits in the current generation or indirect genetic benefits that accrue to offspring in the next generation (Andersson, 1994). Genetic benefits may arise from good genes providing resistance to parasites (Hamilton & Zuk, 1982) or predators (Baker & Parker, 1979) or from increased diversity of genes (Neff & Pitcher, 2005).

Sexual selection may relate to interspecific interactions such as those between predators and prey because only individuals of high quality will be able to signal that they are unprofitable prey (Cott, 1947; Baker & Parker, 1979; Götmark, 1992, 1993). Because secondary sexual characters often are condition dependent, with only healthy individuals in prime condition being able to develop the most exaggerated secondary sexual traits (Andersson, 1994), we should expect that such individuals are better able to escape from predators, a prediction that has been confirmed in three studies (Petrie, 1992; de Lope & Møller, 1994; Møller & Nielsen, 1997).

Conspicuous coloration is widely used in mate choice within species (Andersson, 1994). Nevertheless, several interspecific studies investigating interspecific differences in coloration suggest that bright coloration is positively correlated with risk of predation (Baker & Bibby, 1987; Götmark, 1993; Slagsvold, Dale & Kruszewics, 1995; Götmark & Post, 1996; Rytönen *et al.*, 1998; Huhta, Rytönen & Solonen, 2003; Møller & Nielsen, 2006), while others suggest that there is a negative correlation (Baker & Parker, 1979; Baker & Bibby, 1987). Such contradictory results are commonplace in all sciences including evolutionary biology. They may arise from differences in methods, differences in sampling effort and differences among localities or years.

If sexually dichromatic species suffer from higher risks of predation due to elevated conspicuousness to predators (Baker & Bibby, 1987; Götmark, 1993; Slagsvold *et al.*, 1995; Götmark & Post, 1996; Rytönen *et al.*, 1998; Huhta *et al.*, 2003; Møller & Nielsen, 2006), we should expect such species to take smaller risks and hence have evolved longer flight initiation distances (FID, the predator–prey distance at which prey begins to escape). However, longer FIDs come at a cost because such individuals are disturbed more often, and males with bright plumage coloration need to spend more time foraging to recover the costs. Importantly, Møller & Nielsen (2006) showed that it was the sex difference in

plumage brightness that accounted for the higher susceptibility to predation in sexually dichromatic bird species in Europe, while the difference in plumage brightness of males was not related to susceptibility to predation, nor was the difference in plumage brightness of females.

Møller, Christiansen & Mousseau (2011) investigated six aspects of anti-predator behaviour in 80 species of birds showing that such behaviour was indeed related to risk of predation by the two most common predators, cats *Felis catus* and sparrowhawks *Accipiter nisus*. Anti-predator behaviour was related to sexual dichromatism with a reduced frequency of fear screams and an increased duration of tonic immobility in sexually dichromatic species, implying that anti-predator behaviour has evolved in response to sexual coloration (Møller *et al.*, 2011). Although FID was not related to sexual dichromatism in a previous study of European birds (Møller, 2009), there is evidence that secondary sexual characteristics are linked to other kinds of anti-predator behaviour, implying that sexual selection has affected the evolution of predator–prey communication (Møller, Nielsen & Garamszegi, 2008).

Wallace (1889) emphasized the strength of interspecific interactions in the tropics compared with his temperate homeland (UK). A higher biodiversity and a longer evolutionary time scale of interspecific interactions have resulted in a greater impact of biotic compared to abiotic factors in the tropics. This observation has been consistently confirmed in numerous studies since then (Schemske *et al.*, 2009; Díaz *et al.*, 2013). Interspecific interactions such as those among predator–prey, parasite–host, herbivore–plant and pollinator–plant show consistent latitudinal variation with more intense interactions at lower latitudes (Schemske *et al.*, 2009). Such interactions imply that not only attack, but also defenses have evolved to high levels at low latitudes. That is the case for chemical defenses, secondary compounds of plants and aposematic coloration (Schemske *et al.*, 2009). There is also evidence that anti-predator defences are stronger at lower latitudes such as in tadpoles of *Rana temporaria* in Scandinavia (Laurila, Lindgren & Laugen, 2008), and birds of the same species in temperate Europe and in tropical China (Møller & Liang, 2013).

FID increases strongly with body size (Holmes *et al.*, 1993; Laursen, Kahlert & Frikke, 2005; Blumstein, 2006; Fernández-Juricic *et al.*, 2006; Møller, 2008a), as expected from larger species requiring longer time to get airborne and hence avoid capture (Møller, 2008a; Møller, Vágási & Pap, 2013). This effect of body size may also relate to predation risk because species of intermediate body size are preferred as prey over small species (Götmark & Post,

1996; Møller & Nielsen, 2006). Small species may be easier to catch, but they will provide less food for a given hunting effort causing the prey preference to converge towards prey of intermediate size. It is important therefore to consider body size as a potentially confounding variable when analysing the relationship between sexual dichromatism and susceptibility to predation.

The objectives of this study were to test: (1) if FID is related to sexual dichromatism among species; (2) whether FID and the strength of the relationship between FID and sexual dichromatism differ among species differs among continents; and (3) whether the difference in FID between sexually monochromatic and sexually dichromatic species increases with body size. We did so by analysing 17 791 FID measurements made on 447 species, studied on three continents – Australia, Europe, and North America.

MATERIAL AND METHODS

FLIGHT INITIATION DISTANCE

We recorded FID for a total of 447 species during the breeding season by using a standard procedure developed by Blumstein (2006). Eighteen of these species occurred in two continents and one species (*Pluvialis squatarola*) occurred in all three, resulting in 467 estimates of mean species FID (Supporting Information, Table S2). In Europe FID was recorded in Norway during 2009–2010, Denmark during 2006–2015, France during 2006–2015 and Spain during 2007–2012 (latitude 49–58°N, longitude 5°W–10°E). In North America, FID was recorded in the United States during 2001–2002 (southern California and western Colorado; latitude 33–39°N, longitude 107–119°W). In Australia, most FIDs were collected from southeastern Australia during 1999–2002 and 2011–2015 (latitude 28–38°S, longitude 113–153°E). In brief, we walked at a slow pace ($\sim 0.5 \text{ m s}^{-1}$) directly towards a bird recording the distance (measured in number of steps, or using a Bushnell® Elite 1500 Laser Rangefinder) from the bird when we started walking, the distance at which the birds initiated escape, and the bird's height in the vegetation as judged from the height of the observer (Blumstein, 2006; Møller, 2008b, 2015; Weston *et al.*, 2012; Guay *et al.*, 2013; McLeod *et al.*, 2013). To account for the height at which individuals were perched, FID was calculated as the Euclidian distance between the approaching human and the focal bird (which equals the square-root of the sum of the squared flight distance and the squared height in the vegetation). We also recorded starting distance (i.e. the predator–prey distance when the approach begins), although we did not report starting distances here for simplicity.

Observers wore neutral colored clothes and behaved quietly as normal pedestrians. FIDs were recorded in a representative range of habitats by searching systematically for birds in all available habitats. FID was measured by a number of trained observers and therefore data were pooled for analysis because there was little evidence of observer effects on FID estimates (Guay *et al.*, 2013). The FID estimates were initially reported in Blumstein (2006), Møller (2008b), and Weston *et al.* (2012). There is an extensive literature on methodology of studies of FID showing consistency among methods (number of steps vs. range finder), observers, vehicles for approach and other causes of variation in FID showing a high degree of consistency (McLeod *et al.*, 2013; Cooper & Blumstein, 2015; Møller, 2015). Humans are widely used to study risk assessment because animals often perceive humans as potential predators (Frid & Dill, 2002). We know that FID varies according to the costs and benefits of escape; thus, other potential predators may elicit different FIDs. Nonetheless, humans walking at a constant pace provide a standardized stimulus with which to study perception of predation risk.

The field studies did not involve endangered or protected species and Blumstein (2006), Møller (2008b), and Weston *et al.* (2012) provide further details. FID data collection only required behavioural observations and did not involve capture, collection or sacrifice of specimens.

ECOLOGICAL VARIABLES

We selected three variables in our models:

1. Continent. All species were scored with respect to continent (Australia, North America or Europe).
2. Sexual dichromatism. We provided bird species with a dichotomous score of sexual dichromatism, based on categorization of plumage coloration in field guides. Species were given a score of zero, if males and females could not be reliably distinguished based on plumage characters according to field guides and handbooks (e.g. Cramp & Perrins, 1977–1994; Poole, Stettenheim & Gill, 1993–2002; Higgins & Davies, 1996–2006; Mullarney *et al.*, 2000; Svensson, 2006), while all other species were scored as 1. For example, blue tits *Parus caeruleus*, that can be reliably sexed based on the intensity of the blue coloration of the crown, were scored as 1, whereas coal tits *P. ater*, that cannot be sexed based on plumage characters, were scored as 0. We did not attempt to quantify the magnitude of the sex difference in coloration because we do not know how any predators perceive such differences, nor could we readily pool such information from different

predators. However, our dichotomous score was strongly positively correlated with quantitative scores from Møller & Birkhead (1994) and Read (1987) (Spearman $r = 0.89$, $N = 24$, $P < 0.001$), suggesting that both dichotomous and continuous scores provide similar information. Finally, we did not consider plumage brightness of males or females because apparent brightness to a human may be completely cryptic depending on the environment. Because both males and females by definition live in the same environment during reproduction, any difference in sexual dichromatism is likely to reflect a difference in coloration between the sexes independent of the environment. We did not consider ultraviolet (UV) coloration in this study, although avian predators are fully capable of seeing signals in the UV (Viitala *et al.*, 1995). Previous studies using dichotomous scores of sexual dichromatism have shown predicted relationships with other variables (e.g. Møller & Birkhead, 1994), and sexual dichromatism is strongly positively related to measures of coloration derived from models based on avian vision (e.g. Armenta, Dunn & Whittingham, 2008; Seddon *et al.*, 2010). We are aware of the potential weaknesses of our approach, although we consider that there is little evidence of human visual scores distorting categorization of sexual dichromatism (Armenta *et al.*, 2008; Seddon *et al.*, 2010).

3. Body mass. We used information on body mass of adults relying on standard handbooks averaging the body mass of males and females if body masses were reported separately for the two sexes (Cramp & Perrins, 1977–1994; Poole *et al.*, 1993–2002; Higgins & Davies, 1996–2006). All data for different species in different continents are reported in Supporting Information (Table S2).

COMPARATIVE ANALYSES

Closely related species are more likely to have similar phenotypes because of common ancestry, which makes data points statistically dependent (Felsenstein, 2004). Therefore, we fitted Phylogenetic Generalized Least Squares models (PGLS; Garland & Ives, 2000) to account for the phylogenetic non-independence on the relationship between FID and the predictor variables. PGLS models were fitted using the 'gls' function of the R package 'nlme' (Pinheiro *et al.*, 2011). The strength of the phylogenetic signal on residuals, measured as Pagel's λ , was optimized by the maximum likelihood method (Freckleton, Harvey & Pagel, 2002). The models were weighted by sample size to account for differences in sample size among

species (Garamszegi & Møller, 2010, 2011; Garamszegi, 2014). Exclusion of species with less than a certain number of observations would be arbitrary, it could cause bias by exclusion of rare species that may differ from the overall sample, and it could even be considered unethical because individuals were disturbed to no avail (Garamszegi & Møller, 2010, 2011; Garamszegi, 2014). To weight the samples, we used the inverse of the sample size as a proxy of variance to be used in the variation function structure (argument 'weights' of the 'gls' function [Paradis, Claude & Strimmer, 2004]).

We used the most recent avian super-tree (Jetz *et al.*, 2012; <http://birdtree.org/>) to reconstruct the evolutionary history of the species included in our data set. We used two phylogenetic trees in our analyses to test if our conclusions were sensitive to the choice of phylogeny: the Ericson backbone and the Hackett backbone phylogenies (Supporting Information, Figs S1, S2). The models presented in the main text were yielded using the Ericson phylogeny. The models using the Hackett phylogeny are available in the Supporting Information (Table S1). A very short phylogenetic distance (0.0000001 Myr) was assigned to the same species occurring on different continents. Although the use of only a single phylogeny in a statistical model does not account for uncertainty in the estimate of the structure of the tree, previous studies have reported robustness of regression estimates from phylogenetic analyses (Rohlf, 2006; Stone, 2011; Hadfield *et al.*, 2014).

We evaluate the degree of support of 13 candidate models comprising all possible combination among the main effect of the three predictors: continent, body mass, and sexual dichromatism. We tested for an interaction between body mass and sexual dichromatism because we hypothesized that the effect of sexual dichromatism on FID may vary with body mass. We tested for an interaction between continent and sexual dichromatism because we hypothesized that the strength of the relationship between FID and sexual dichromatism may increase at higher latitudes. We also included an intercept-only model to be used as a null model. A constant term (intercept) was included in all models. Our candidate models respected 'marginality constraints' so that models containing interactions were not included without their respective main effects. FID and body mass were log₁₀ transformed before analyses.

We used an information-theoretic approach based on Akaike's criteria corrected for small sample size (AIC_c) to evaluate the set of candidate models. AIC_c is a measure of distance of putative model from full reality (Burnham & Anderson, 2002). The candidate models were ranked by their AIC_c values, and models with the lowest AIC_c values are the best models

(Burnham & Anderson, 2002). Models with $\Delta AIC_c < 2$ are considered equally good as models with the lowest AIC_c . Given the high relative likelihood of our best model as indicated by its Akaike weight ($w_i = 0.89$; Table 1), we did not employ multi-model inference based on model averaging as recommended by Burnham & Anderson (2002).

We assessed the importance of each predictor in the best model based on effect sizes calculated as partial correlation coefficients, quantifying the effect of a given predictor while controlling for the effects of other covariates included in the model (Nakagawa and Cuthill 2007). We emphasize that there was no strong collinearity among predictor variables, and hence effect sizes were unbiased. We followed criteria listed by Cohen (1988) for small ($r = 0.10$, explaining 1% of the variance), intermediate ($r = 0.3$, explaining 9% of the variance) or large effect sizes ($r = 0.5$, explaining 25% of the variance). All analyses were conducted using the R programming language (R Development Core Team, 2011).

RESULTS

The results of model selection searching for the best model to explain variation in FID are presented in Table 1. The full model had the highest weight among the candidate models (i.e. that model included the three main effects, the interaction between sexual dichromatism and body mass, and the interaction

Table 2. The best Phylogenetic Generalized Least Squares model to explain variation in flight initiation distance in species from three continents (Europe, Australia, and North America)

Predictor	d.f.	F	P	Effect size
Intercept	1	7092.59	< 0.001	
Sexual dichromatism	1	46.02	< 0.001	0.30
Continent	2	24.10	< 0.001	0.22
Body mass	1	238.10	< 0.001	0.58
Sexual dichromatism*body mass	1	32.07	< 0.001	0.25
Sexual dichromatism*continent	2	4.19	0.016	0.09

d.f., *F*-statistic, *P*-value, and the partial correlation coefficients (*r*) as measures of effect sizes are shown.

between sexual dichromatism and continent; Table 2). All other models only had marginal support according to Akaike weight and AIC_c (Table 1). The best model (Table 2) indicated that FID was consistently shorter for sexually dichromatic compared with sexually monochromatic species with an intermediate effect size (Fig. 1). FID increased with body mass with a large effect size (Fig. 2, Table 2). Yet, the relative difference in FID between sexually monochromatic and sexually dichromatic species increased with body mass with a small to intermediate effect

Table 1. Intercepts, continent, species body mass, sexual dichromatism, species body mass by sexual dichromatism, and continent by sexual dichromatism as predictors of flight initiation distance according to Phylogenetic Generalized Least Squares models

Intercept	Continent	Body mass	Sexual dichromatism	Sexual dichromatism: continent	Sexual dichromatism: body mass	AIC_c	ΔAIC_c	w_i
0.625	+	0.231	+	+	+	166.40	0	0.89
0.608	+	0.238	+		+	170.49	4.09	0.11
0.591	+	0.252	+	+		195.24	28.84	< 0.001
0.583	+	0.254	+			198.38	31.99	< 0.001
0.560		0.251	+		+	204.37	37.98	< 0.001
0.560	+	0.266				210.56	44.17	< 0.001
0.546		0.262	+			219.91	53.51	< 0.001
0.523		0.274				231.93	65.53	< 0.001
1.099	+		+	+		366.52	200.13	< 0.001
1.093	+		+			377.12	210.72	< 0.001
1.092	+					401.57	235.18	< 0.001
1.070			+			403.90	237.50	< 0.001
1.066						427.76	261.36	< 0.001

The AIC_c , ΔAIC_c and Akaike weight (w_i) are shown for each model. ‘+’ Symbol indicates factors with more than one level.

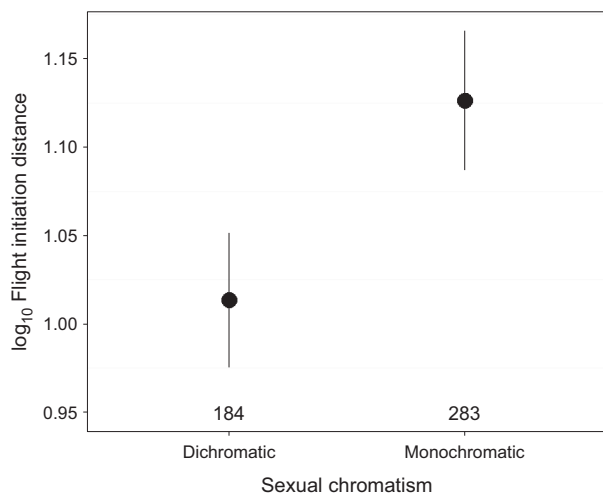


Figure 1. Mean and 95% confidence intervals of flight initiation distance for sexually dichromatic and sexually monochromatic species. Number of species for each category is shown at the bottom of the figure.

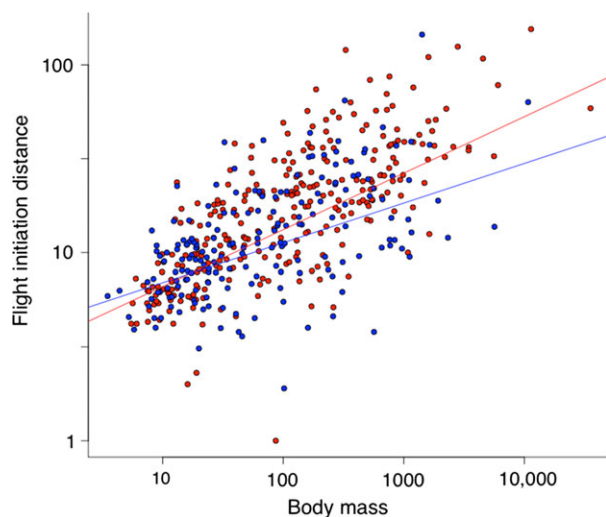


Figure 2. Flight initiation distance in relation to body mass and sexual dichromatism. The two lines are the regression lines for sexually monochromatic (red circles and red line) and sexually dichromatic species (blue circles and blue lines).

size (Fig. 2, Table 2). Finally, FID showed a consistent geographic pattern: FID differed among continents, and this effect had a small to intermediate effect size (Fig. 3, Table 2). However, the relative difference in FID between sexually monochromatic and sexually dichromatic species was larger in Europe than in Australia and North America with a small effect size (Fig. 4, Table 2).

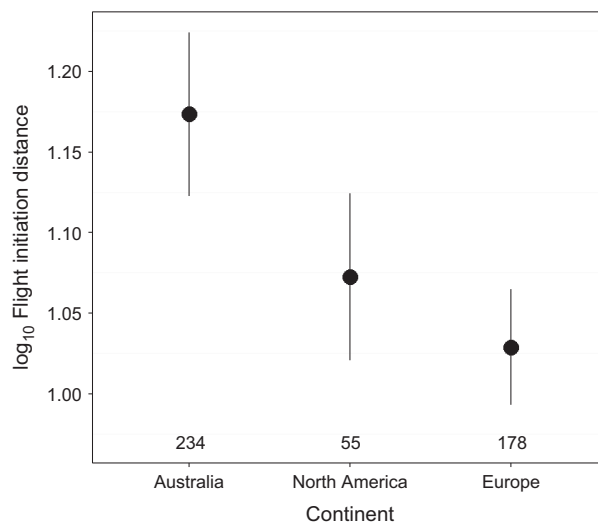


Figure 3. Mean and 95% confidence intervals of flight initiation distance for species from Europe, North America, and Australia. Number of species sampled in each continent is shown at the bottom of the figure.

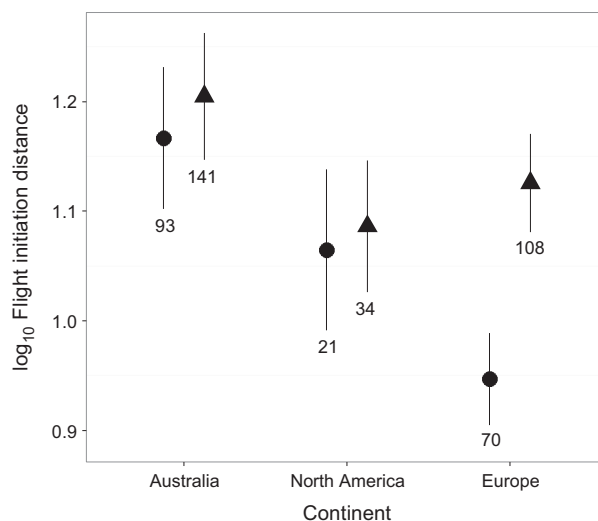


Figure 4. Mean and 95% confidence intervals of flight initiation distance of sexually dichromatic (circle) and sexually monochromatic (triangle) species in Europe, North America, and Australia. Number of species sampled is shown at the bottom of the figure.

DISCUSSION

Flight initiation distance was consistently shorter in sexually dichromatic than in sexually monochromatic species, this difference increased with body mass, and both FID and the strength of the relationship between FID and sexual dichromatism differed among continents. These findings are broadly consistent with the handicap hypothesis: sexual dichromatism is a reliable indicator of escape ability by prey. The findings

also suggest a latitudinal trend in predation risk. These findings are inconsistent with the alternative hypothesis that species with sexual dichromatism are unprofitable prey, and they provide no support for a compensation hypothesis that would have predicted that more vulnerable prey compensates for increased risk of predation by initiating flight at greater distances (e.g. Hensley *et al.*, 2015). If FID in sexually dichromatic species simply reflected the risk of predation, we should have found sexually dichromatic species to have shorter FID than sexually monochromatic species, as we actually found.

Predation has been hypothesized to play a role in the evolution of unprofitable prey that signal the difficulty of capture to the predator and hence their unprofitability (Cott, 1947; Baker & Parker, 1979; Götmark, 1992, 1993). Here we have shown that sexually dichromatic species have shorter FID than sexually monochromatic species. Thus sexually dichromatic species should be easier to catch, selecting for reduced susceptibility to predation caused by increasing FID (Møller *et al.*, 2008). Indeed, individuals with more exaggerated secondary sexual characters less often fall prey to predators implying that they are of superior quality (Petrie, 1992; Møller & Nielsen, 1997), consistent with the handicap hypothesis (Zahavi, 1975). Moreover, the significant interaction between body mass and sexual dichromatism implies that risk of predation is higher in species with larger body mass (Møller, 2008a). Comparative analyses have shown that sexual dichromatism is associated with reduced adult survival rate (Promislow, Montgomerie & Martin, 1992, 1994), and that is even the case when controlling for parental effort (Promislow *et al.*, 1994). Hence, the present paper adds to this evolutionary scenario by proposing a possible mechanism emphasizing a reduction in FID in sexually dichromatic species at large body masses.

The difference in FID between sexually monochromatic and sexually dichromatic species was the largest in Europe (by 2.78 m on average) compared to 2.61 m in Australia and 1.08 m in the North America. It may merit discussion whether such small differences of a few meters will make a difference in terms of survivorship. In fact the difference between life and death is often a question of a few metres or less. Barn swallows *Hirundo rustica* that fell prey to sparrowhawks had an average FID that was 7 m shorter than that of survivors (Møller, 2014), even when controlling for a range of potentially confounding variables. Likewise, Møller *et al.* (2008) showed for birds in Europe that susceptibility to sparrowhawk predation was strongly negatively related to FID adjusted for body size, implying that susceptibility to predation and anti-predator behaviour are negatively correlated.

This study has important implications for future studies of FID. Because nest predation on eggs and nestlings plays a key role in the evolution of life histories (Martin, 1995), and because predation on adult birds apparently plays an equally important role as judged from the present and previous studies (Møller & Liang, 2013), there is scope for further synthesis. In particular, the relative role of nest predation and predation on adults, as reflected by anti-predator behaviour such as FID, in structuring the evolution of life histories remains to be assessed. We suggest that effects of predation and anti-predator behaviour would have stronger impact on vital rates in Australia than in North America and especially in Australia than in Europe.

In conclusion, we have shown that: (1) sexually dichromatic species have shorter FID than sexually monochromatic species; (2) this difference is more pronounced in species with relatively large body masses; (3) mean FID decreases with increasing latitude; and (4) the strength of the relationship between FID and sexual dichromatism is stronger in Europe than in Australia and North America.

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ETHICAL STANDARDS

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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SUPPORTING INFORMATION

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

Figure S1. Phylogeny of the bird species based on Ericson backbone.

Figure S2. Phylogeny of the bird species based on Hackett backbone.

Table S1. Model selection of the Phylogenetic Generalized Least Squares models using the Hackett backbone phylogeny.

Table S2. Full dataset used in the analyses.