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Are the big and beautiful less bold? Differences in avian fearfulness between the sexes in relation to body size and colour.

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Running Head: Colour, size and FID in birds

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Abstract

Conspicuousness towards predators may influence escape behaviour (or 'fearfulness') amongst animals, with more conspicuous species initiating escape behaviour earlier. Amongst birds, for example, body size and colour may influence differences in escape behaviour between species, and possibly between the sexes of dimorphic species. We examined 19 bird species with varying degrees of body size and colour dimorphism (including individually marked and sexed monomorphic species), to examine whether these two potential measures of conspicuousness influence sex differences in flight-initiation distance (FID). Starting Distance (the distance at which an observer commenced approaching a bird, which is an artefact of investigator behaviour; SD) was not correlated with dimorphism, so we used phylogenetically controlled models which explored the correlation between dimorphism and FID. Modelling indicated that only sex differences in SD correlated with sex differences in FID in these birds, and that dimorphism in either plumage or body size does not apparently correlate with sex differences in FID. These results suggest that, amongst the 19 bird species investigated, apparent differences in the conspicuousness to predators between the sexes do not influence escape behaviour. This suggests that either conspicuousness to predators does not influence escape distances in these species, or that sex differences in conspicuousness were too subtle to result in variation in FIDs.

Keywords Colour, Conspicuousness, Escape, Flight-initiation Distance, Sexual selection

Introduction

Escape behaviour is a critical component of the life history of animals as it allows individuals to minimise the risk of predation. Differences in fearfulness towards potential predators (indexed by flight-initiation distance, FID; see Weston *et al.* 2012) are well known among species of many taxonomic groups, including reptiles and birds (Blumstein 2006; Capizzi *et al.* 2007; Glover *et al.* 2015). For example, bird species with larger body sizes are associated with longer FIDs, perhaps because of larger sensory organs and hence earlier detection of predators (e.g. Blumstein 2006; Møller and Erritzøe 2010). Alternatively, larger species may be more readily detected by predators, including human hunters (Holmes *et al.* 1993; Glover *et al.* 2011), or they may have earlier departures to counteract their slower or more cumbersome escapes (Fernández-Juricic *et al.* 2002). Similarly, more colourful species are more readily detected by predators and may struggle to evade predators or hide (e.g. Götmark and Olsson 1997; Stuart-Fox *et al.* 2003). Such species may have longer FIDs. However, the evidence currently available for birds suggests that vividness is not related to escape distances, although such studies have not examined the possibility of within-species variation (Hensley *et al.* 2015) which conceivably may be a more sensitive test of the effect. These patterns might also apply within species, because the functional explanations of FID should apply within as well as across species (see, for example, Gotanda *et al.* 2009). Although there is mounting evidence that, at least in some species, predation risk may differ between the sexes with the more colourful sex being at greater risk (Huhta *et al.* 2003; Thiel *et al.* 2007; Ekanayake *et al.* 2015b; Marshall *et al.* 2015), with few exceptions, escape strategies have been assumed to be consistent between sexes within species, at least in birds (Weston *et al.* 2012; Guay *et al.* 2016). Interestingly, studies in lizards have demonstrated that males, the more colourful sex, is both at greater risk of predation and initiates escape behaviour earlier than females(Capizzi *et al.* 2007; Marshall *et al.* 2015; but see Samia *et al.* 2015). A handful of studies have shown that FIDs can vary between the sexes of birds (Thiel *et al.* 2007; Smith 2011; Guay *et al.* 2013a).However, whether or not sex differences in escape behaviour in birds are associated with the degree of sexual dimorphism remains unknown.

Understanding sex differences in FID could shed light on inter-sexual conflict, mate choice and social systems (Møller *et al.* 2008), as well as inform management of bird disturbance (Weston *et al.* 2012). Currently, there is an absence of comparative studies on FID and dimorphism in birds, partly because of the difficulty of sexing monomorphic species. Here, we examine the influence of plumage (plus bare parts), and body size, dimorphism on the fearfulness of birds. We measured both plumage and size dimorphism as they may both independently influence conspicuousness. We measured FIDs of both males and females in 19 species of birds, including both monomorphic and dimorphic species. FIDs were quantified by slowly approaching an individual bird and measuring the distance between the observer and bird at which escape was initiated. We then examined sex differences in size, plumage dimorphism and FID and predicted that intersexual differences in FID would be larger for species with greater size or plumage dimorphism. As more conspicuous species may also be more readily detected by humans, we also tested whether the distance at which observers commenced approaches (the ‘starting distance’) was greater for more colourful or larger species.

Materials and methods

Field measurements

Species were selected on the basis that they were sexable in the field, either because they were sexually dimorphic or because they were monomorphic and had been genetically sexed and fitted with unique marks in previous research (Guay and Mulder 2009; Mulder *et al.* 2010; Cardilini *et al.* 2013; Cardilini *et al.* 2015; Ekanayake *et al.* 2015a; Ekanayake *et al.* 2015b; Whisson *et al.* 2015; Roche *et al.* 2016) (Table 1).

Fieldwork was conducted between 28 March 2013 and 21 August 2013. Standard field methods were used to measure FIDs in the field (Guay *et al.* 2013a; McLeod *et al.* 2013). For each approach we recorded the start distance (SD; distance at which the direct approach towards the focal bird started), the FID, the species and the sex of the focal bird. SD was recorded because is it a very strong predictor of FID (e.g. Blumstein 2003; Symonds *et al.* 2014). Even though datasets from different observers can be combined without problems (Guay *et al.* 2013b; van Dongen *et al.* 2015a), all approaches were performed by the same observer to avoid any biases and all targeted birds were evidently non-breeding (or at least away from the nest). All approaches were conducted at locations within 150 km of Melbourne, Australia, and all approaches for any given species were conducted at the same location to account for any spatial variation in habituation. Sampling was evenly spread between the sexes; the average sex ratio (male/female ± Standard Deviation) across species was 0.97 ± 0.17.

Comparative data

For each species we compiled two body size measurements, body mass (g; Dunning 2008) and wing length (mm; Marchant and Higgins 1990; Marchant and Higgins 1993; Higgins

1999; Higgins *et al.* 2001; Higgins and Peter 2002; Higgins *et al.* 2006), which we analysed separately. We used both measurements of size since mass is known to be very labile and can vary enormously between seasons in some species (e.g. Briggs 1988). Furthermore, some measurements of wing shape and size are known to be correlated with FID (e.g.Fernández-Juricic *et al.* 2006; Møller 2014). We also calculated indices of dimorphism in size and plumage. Size (body mass and wing length) dimorphism were indexed by calculating $Mass - DI = 1 - \frac{mass\ (male)}{mass\ (female)}$ and $Wing - DI = 1 - \frac{wing\ length\ (male)}{wing\ length\ (female)}$ (after Lovich and Gibbons 1992). Plumage dimorphism (Plumage-DI) was indexed using the technique of Chen *et al.* (2013), whereby seven broad body regions were scored for sexual dimorphism, including bill (including upper and lower mandibles), head (including nape), back (including rump), wing, underparts (including breast, belly and flanks), tail and legs (see Marchant and Higgins 1990 for body region diagram). Whilst we recognise that bare parts (bill and legs) are not part of the plumage we included them in our scoring of plumage dimorphism because, like any part of the plumage, they can be used as cues by predator for prey detection. For each body region, we scored dimorphism, based on colour plates (Marchant and Higgins 1990; Marchant and Higgins 1993; Higgins 1999; Higgins *et al.* 2001; Higgins and Peter 2002; Higgins *et al.* 2006), as either no difference (0 points), difference in colour intensity or pattern (1 point) or difference in pattern and colour (2 points). This measurement of dimorphism focuses on reflection in the visible light spectrum to the exclusion of reflection in the ultraviolet (UV) range. It is well documented from studies on sexual selection that birds have the capacity to see in the UV range and that measurements of plumage brightness should include the UV component (e.g. Bennett *et al.* 1994). Whilst some, but not all, avian predators have been demonstrated to use UV light cues for foraging (e.g. Viitala *et al.* 1995; Koivula *et al.* 1997), most mammalian predators are not able to see in the UV range (Honkavaara *et al.* 2002). Furthermore, analyses of the violet and ultraviolet light absorbing opsin present on the retina of raptors (Accipitridae and Falconidae) indicate that unlike Passeriformes, they are not sensitive in the short wavelength UV range (Ödeen and Håstad 2003). Thus, focus on the visible light spectrum in this study is unlikely to have influenced the results. Since the species targeted use a wide array of different habitat, it was not possible to assess conspicuousness against background habitat which could impact in the sexual dimorphism as detected by predators. The dimorphism scores were then summed for all 7 body regions to obtain one dimorphism score per species. Whilst it is recognised that the particular body regions exposed can influence predation risk in given circumstances (e.g. the legs of a duck swimming are not exposed), we took the conservative approach of giving equal weight to all body regions.

For both FID and SD, we calculated sex difference indices (FID-DI and SD-DI) as described above for size. SD is a distance defined by an investigator and is therefore subject to human bias, specifically brighter or bigger birds may have been detected by the observer more readily and therefore associated with longer SDs. We therefore examined whether a difference in SD occurred between the sexes, and ran models with and without SD-DI to ensure SD-DI did not influence our results.

Comparative analysis

As morphological and behavioural traits may be more similar in closely-related species due to phylogenetic effects, we employed a phylogenetic comparative approach to our data. We obtained phylogenies for the species in our analysis from the “Global Phylogeny of Birds” website – www.birdtree.org (Jetz *et al.* 2012). Specifically, we downloaded a set of 2000 possible trees for our species from the distribution of trees on that site. All trees have the same basic Hackett *et al.* (2008) phylogeny as a ‘backbone’ (results obtained using an alternative Ericson et al. (2006) backbone were nearly identical and are not presented). Studies have demonstrated that more reliable estimates of evolutionary coefficients can be obtained when multiple phylogenies are used as the basis for analysis (De Villemereuil *et al.* 2012; Rubolini *et al.* 2015). We therefore carried out analyses using all 2000 trees as the basis for analysis, producing averaged values for parameter estimates, with associated confidence intervals and weights.

For estimation of sexual differences in SD and FID generally we employed phylogenetic paired t-tests (Lindenfors *et al.* 2010). We then constructed a series of phylogenetic generalized least squares (PGLS) models (Symonds and Blomberg 2014) examining the response variables of FID-DI or SD-DI against Plumage-DI and a measure of body size, either mass or wing length. We included indices of dimorphism in mass or wing length as well as absolute mass or wing length (respectively) as covariates in models, since sexual size dimorphism increases with size (Rensch 1950) and thus larger species may be more size dimorphic which may result in increased FID-DI. We also weighted the analyses relative to sample size (N) for each species.

We used an information theoretic approach to analyse the explanatory power of our predictor variables in determining FID-DI. For each phylogeny, all model combinations of the predictor variables were compared using Akaike’s Information Criterion (Burnham and

Anderson 2002; Symonds and Moussalli 2011). In each analysis we evaluated the AIC scores for the five best approximating models along with model weights, and averaged these weights across the most common ordering of models across the 2000 phylogenies. Model averaging was also employed to derive predictor weights (the summed Akaike weights of all models in which that predictor featured), model-averaged estimates and associated 95% confidence intervals for each predictor. The predictor weights can be considered analogous to the probability that that predictor really does feature in the best approximating model. As described above, final predictor weights, estimates and confidence intervals were obtained by averaging results from all 2000 phylogenies. For statistical analysis we used the R framework (R Core Team 2015), and the associated packages *phytools* (Revell 2012), *ape* (Paradis *et al.* 2004) and *AICcmodavg* (Mazerolle 2015).

Results

Starting distance

We obtained 411 SDs and FIDs from known-sex individuals of 19 species (51% were female) (Table 1). SD did not significantly differ between the sexes (phylogenetically controlled paired t-test, t = 0.622, $P = 0.543$, average from 2000 trees), and phylogenetically generalised least squares analyses revealed no significant effect of Plumage-DI, mass-DI or body mass itself on SD-DI (Table 2). The null model was consistently and unambiguously returned as the best model explaining SD-DI (Table 3). Thus, no adjustments of FIDs in relation to SD were required for the examination of FID versus sex.

FID

A preliminary GLM with SD, sex and species as predictors of FID revealed a significant interaction between species and sex ($F_{18,371} = 2.076$, $P = 0.006$; $R^2 = 0.803$). This justified further investigation. Overall, male and female FID did not differ significantly between the sexes (phylogenetically controlled paired t-test, t = -0.205, p = 0.840, average from 2000 trees). Across 2000 phylogenetic generalised least squares models, only SD-DI positively and consistently explained variation in FID-DI, whereas body mass and wing length and the dimorphism in these traits were only weakly associated with FID-DI (Tables 4 and 5). In analyses with SD-DI, the model with that as a single predictor was consistently and unambiguously returned as the best model, otherwise the null model was the strongest (Tables 6 and 7).

Discussion

While differences in escape distances between sexes have been reported for a broad range of taxa, including birds (Thiel *et al.* 2007; Smith 2011; Guay *et al.* 2013a) and reptiles (Capizzi *et al.* 2007), fearfulness as indexed by FID did not differ between the sexes for the bird species we examined. This is in line with the results obtained in magpie-lark (*Grallina cyanoleuca*; Kitchen *et al.* 2010) and for a diversity of birds examined comparatively at the species scale (Hensley *et al.* 2015). Only a handful of reports of sexual differences in bird FID exist (Smith 2011; Guay *et al.* 2013a), and some of these come from areas where one sex is hunted (Thiel *et al.* 2007). Thus, sexual differences in FID among birds might be rare or even absent. Neither Plumage-DI nor size dimorphism were significantly associated with differences in FID between the sexes, despite a wide gradient of dimorphism tested. This result suggests either that the sexes do not significantly adjust their escape behaviour to their conspicuousness to predators or that the relatively slight sexual differences in size or colouration do not result in detectible differences in conspicuousness towards predators. It is important to note that we did not investigate sex differences in colour in the UV range, but sexual differences in the UV range would be unlikely to have resulted in sex differences in FID because whilst some avian predators can use UV cues for foraging, unlike passerines, most raptors are not well adapted to detect short wavelength UV light and most mammalian predators cannot detect UV light (Viitala *et al.* 1995; Honkavaara *et al.* 2002; Ödeen and Håstad 2003). The potential explanation that the predator environment was relatively benign in the study area seems unlikely (many predators occur in the area; Cardilini *et al.* 2013; Ekanayake *et al.* 2015c). When sexing birds in the field, some errors can occur due to juveniles first acquiring female-like plumage (e.g., robins, *Petroica* spp; Higgins and Peter 2002) or adult males acquiring an eclipse plumage reminiscent of females at certain times of the year (e.g. Chestnut Teal, *Anas castanea*; Marchant and Higgins 1990). Moult thus can cause plumage variation across seasons and errors in sexing in some species, but care was taken not to target family groups with juveniles or large groups of ducks with female-like plumage to avoid the risk of sexing eclipse plumaged males as females. It is also possible that individual non-sexual differences in FID exist (Runyan and Blumstein 2004) and these may mask subtler sexual differences in FID. In fact, large differences in FID can be observed between individuals of the same species living in different habitats (e.g. Ikuta and Blumstein 2003; McGiffin *et al.* 2013; van Dongen *et al.* 2015b). This cannot be a factor in our study because all approaches on each species were conducted at the same site. Clearly, further investigation of dimorphism and FID across a larger taxonomic sample would be desirable.

Broad taxonomic studies of birds have revealed a positive allometric relationship between the extent of sexual size dimorphism and overall size (e.g. Dale *et al.* 2007). Furthermore, the positive relationship between FID and size is well established (Blumstein 2006; Bregnballe *et al.* 2009; Glover *et al.* 2011; Guay *et al.* 2013c). It therefore follows that any differences in FID between the sexes were expected to be greater in larger species. In contrast, we found no significant correlation between FID-DI and body size within our dataset. Given the lack of evidence of sexual dimorphism in escape behaviour between the sexes, this may not be unexpected.

Overall, the findings of our study fail to support one of the ‘basic principles’ of escape theory, namely that colour influences detection by, and response to, an approaching threat (see also Hensley *et al.* 2015). In terms of sexual dimorphism amongst the bird species we examined, these effects are not apparent. It may be fruitful to conduct larger-scale studies on individuals from species displaying more extensive sexual size or plumage dimorphism to evaluate whether any individual differences between individuals are driven by differences in individual body size or plumage brightness.

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Table 1 Species chosen for this research, the Starting Distance and Flight-initiation Distance, and their plumage and body size dimorphism scores (see text). Means ± SE are shown. Taxonomy after Christidis and Boles (2008).

Species (number of approaches)	**♀ SD (m)**	**♀ FID (m)**	**♂ SD (m)**	**♂ FID (m)**	**PlumageD**	**MassI**	**Body mass (g)**	**Wing I**	**Wing Length (mm)**
Musk duck *Biziura lobata* (22)	136.3 ± 13.2	99.4 ± 8.0	109.9 ± 12.2	92.1 ± 10.2	2	-0.546	1975	-0.205	204
Cape Barren goose *Cereopsis novaehollandiae* (23)	54.6 ± 6.5	21.3 ± 3.8	67.3 ± 7.4	32.3 ± 5.2	0	-0.403	4530	-0.065	456
Black swan *Cygnus atratus* (27)	39.4 ± 2.8	8.8 ± 1.8	39.4 ± 3.6	4.6 ± 2.2	0	-0.229	5685	-0.022	464
Australian wood duck *Chenonetta jubata* (26)	43.3 ± 3.0	24.2 ± 1.5	43.9 ± 3.2	28.6 ± 1.6	4	-0.019	808	-0.023	269
Australasian shoveler *Anas rhynchotis* (12)	170.0 ± 13.2	118.7 ± 15.6	171.7 ± 5.3	126.3 ± 10.0	8	-0.003	666	-0.004	239
Chestnut teal *Anas castanea* (25)	62.3 ± 7.2	36.9 ± 4.3	56.2 ± 4.0	38.6 ± 3.8	4	-0.152	638	-0.071	210
Hardhead *Aythya australis* (22)	160.1 ± 15.7	113.5 ± 11.0	139.8 ± 12.1	107.7 ± 9.4	6	-0.076	870	0.009	216
Blue-billed duck *Oxyura australis* (21)	147.8 ± 13.9	97.3 ± 11.0	114.8 ± 15.3	78.1 ± 11.4	9	0.047	832	-0.046	157

Species (number of approaches)	**♀ SD (m)**	**♀ FID (m)**	**♂ SD (m)**	**♂ FID (m)**	**PlumageD**	**MassI**	**Body mass (g)**	**Wing I**	**Wing Length (mm)**
Red-capped plover *Charadrius ruficapillus* (22)	44.9 ± 5.0	30.3 ± 3.8	44.3 ± 4.0	27.3 ± 3.0	2	0.008	37.5	-0.004	105
Masked lapwing *Vanellus miles* (20)	49.0 ± 4.4	33.3 ± 2.3	50.2 ± 3.2	29.8 ± 3.1	0	-0.060	360	-0.020	250
Red-rump parrot *Psephotus haematonotus* (21)	42.5 ± 5.3	10.0 ± 1.2	49.1 ± 6.3	18.9 ± 5.9	7	0.002	61.5	-0.041	128
Superb fairy-wren *Malarus cyaneus* (29)	30.2 ± 2.6	13.1 ± 1.2	31.4 ± 3.5	11.3 ± 1.0	6	-0.065	9.6	-0.032	50.7
White-fronted chat *Epthianura albifrons* (19)	40.5 ± 6.1	24.8 ± 2.8	38.1 ± 4.1	26.5 ± 2.5	5	-0.008	13.3	-0.023	68.9
Australian magpie *Cracticus tibicen* (21)	53.1 ± 9.2	11.6 ± 2.2	50.2 ± 8.6	14.8 ± 3.3	1	-0.055	336	-0.042	272
Magpie-lark *Grallina cyanoleuca* (20)	45.6 ± 4.4	17.8 ± 2.8	47.9 ± 4.6	18.3 ± 2.1	2	-0.127	86.5	-0.048	177
Scarlet robin	18.1 ± 2.6	10.6 ± 1.9	23.5 ± 3.9	11.8 ± 2.5	7	0.030	13.1	-0.027	74.4

Species (number of approaches)	♀ SD (m)	♀ FID (m)	♂ SD (m)	♂ FID (m)	PlumageD	MassI	Body mass (g)	Wing I	Wing Length (mm)
Petroica boodang (19)									
Flame robin	32.5 ± 2.6	16.1 ± 1.6	31.0 ± 2.9	18.5 ± 2.5	7	-0.021	14.3	-0.032	79.0
Petroica phoenicea (21)									
Common blackbird	32.4 ± 3.2	17.5 ± 1.9	42.4 ± 5.4	24.2 ± 4.0	6	-0.049	92.0	-0.036	129
Turdus merula (22)									
House sparrow	26.6 ± 3.6	11.4 ± 1.1	33.1 ± 3.2	13.0 ± 1.2	4	0.025	27.4	-0.057	74.3
Passer domesticus (19)									

Table 2 Results of the effect of plumage and body size dimorphism, and body size on SD-DI using 1) body mass and 2) wing length as control variables. Averaged cumulative parameter weights and coefficients are presented.

Model	**Predictor**	**Weight**	**Estimate (±95%CI)**
1	Plumage-DI	0.225	0.012 (-0.029 to 0.054)
	Mass-DI	0.201	-0.157 (-0.867 to 0.552)
	Body mass	0.197	-0.034 (-0.288 to 0.220)
2	Plumage-DI	0.213	0.009 (-0.032 to 0.050)
	Wing-DI	0.239	-0.690 (-2.533 to 1.154)
	Wing length	0.288	-0.257 (-0.831 to 0.317)

Table 3 The most consistently returned top five best approximating models predicting Starting Distance dimorphism (SD-DI) from the PGLS analyses across 2000 phylogenies, using 1) body mass and 2) wing length as control variables. Average delta AIC and Akaike weights for each model are presented.

Model set	Model structure	Delta AIC	Akaike weight
1	(null model)	0	0.487
	Plumage-DI	2.344	0.151
	Body mass	2.629	0.131
	Mass-DI	2.804	0.120
	Plumage-DI + Mass-DI	4.713	0.047
2	(null model)	0	0.418
	Wing length	1.024	0.222
	Wing-DI	2.161	0.139
	Plumage-DI	2.603	0.121
	Plumage-DI + Wing-DI	4.659	0.044

Table 4 Results of the effect of plumage dimorphism, SD-DI, mass and body mass on FID-DI using 1) body mass and 2) wing length as control variables. Averaged cumulative parameter weights and coefficients are presented.

Model	**Predictor**	**Weight**	**Estimate (±95%CI)**
1	SD-DI	0.739	1.024 (0.418 to 1.630)
	Plumage-DI	0.016	-0.019 (-0.075 to 0.036)
	Mass-DI	0.154	-0.004 (-0.853 to 0.845)
	Body mass	0.034	0.006 (-0.218 to 0.231)
2	SD-DI	0.766	1.086 (0.465 to 1.709)
	Plumage-DI	0.014	-0.023 (-0.075 to 0.029)
	Wing-DI	0.398	0.926 (-2.473 to 4.324)
	Wing length	0.202	-0.084 (-0.637 to 0.469)

Table 5 Results of the effect of plumage dimorphism mass and body mass (without SD-DI) on FID-DI using 1) body mass and 2) wing length as control variables. Averaged cumulative parameter weights and coefficients are presented.

Model	**Predictor**	**Weight**	**Estimate (±95%CI)**
1	Plumage-DI	0.185	0.021 (-0.321 to 0.363)
	Mass-DI	0.225	0.319 (-0.701 to 1.340)
	Body mass	0.187	0.001 (-0.114 to 0.116)
2	Plumage-DI	0.189	-0.002 (-0.068 to 0.063)
	Wing-DI	0.211	0.772 (-2.108 to 3.653)
	Wing length	0.232	-0.316 (-1.253 to 0.621)

Table 6 The most consistently returned top five best approximating models predicting Flight Initiation dimorphism (FID-DI) from the PGLS analyses across 2000 phylogenies, including SD-DI as a predictor and using 1) body mass and 2) wing length as control variables. Average delta AIC and Akaike weights for each model are presented.

Model set	**Model structure**	**Delta AIC**	**Akaike weight**
1	SD-DI	0	0.694
	(null model)	3.139	0.144
	SD-DI + Mass-DI	4.027	0.093
	Mass-DI	6.065	0.033
	SD-DI + Body Mass	8.047	0.012
2	SD-DI	0	0.448
	SD-DI + Wing-DI	0.748	0.308
	(null model)	3.134	0.094
	Wing-DI	3.607	0.074
	Wing length	5.598	0.028

Table 7 The most consistently returned top five best approximating models predicting Flight Initiation dimorphism (FID-DI) from the PGLS analyses across 2000 phylogenies, *without* including SD-DI as a predictor and using 1) body mass and 2) wing length as control variables. Average delta AIC and Akaike weights for each model are presented.

Model set	**Model structure**	**Delta AIC**	**Akaike weight**
1	(null model)	0	0.508
	Mass-DI	2.405	0.153
	Plumage-DI	2.833	0.123
	Mass	2.848	0.122
	Plumage-DI + Mass-DI	5.467	0.033
2	(null model)	0	0.486
	Wing length	2.321	0.152
	Wing-DI	2.533	0.137
	Plumage-DI + Wing-DI	2.815	0.119
	Wing length + Wing-DI	5.149	0.037