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

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16 Running Head: Colour, size and FID in birds

17

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19

20 **Abstract**

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

38

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

40 **Introduction**

41 Escape behaviour is a critical component of the life history of animals as it allows individuals
42 to minimise the risk of predation. Differences in fearfulness towards potential predators
43 (indexed by flight-initiation distance, FID; see Weston *et al.* 2012) are well known among
44 species of many taxonomic groups, including reptiles and birds (Blumstein 2006; Capizzi *et*
45 *al.* 2007; Glover *et al.* 2015). For example, bird species with larger body sizes are associated
46 with longer FIDs, perhaps because of larger sensory organs and hence earlier detection of
47 predators (e.g. Blumstein 2006; Møller and Erritzøe 2010). Alternatively, larger species may
48 be more readily detected by predators, including human hunters (Holmes *et al.* 1993; Glover
49 *et al.* 2011), or they may have earlier departures to counteract their slower or more
50 cumbersome escapes (Fernández-Juricic *et al.* 2002). Similarly, more colourful species are
51 more readily detected by predators and may struggle to evade predators or hide (e.g. Götmark
52 and Olsson 1997; Stuart-Fox *et al.* 2003). Such species may have longer FIDs. However, the
53 evidence currently available for birds suggests that vividness is not related to escape
54 distances, although such studies have not examined the possibility of within-species variation
55 (Hensley *et al.* 2015) which conceivably may be a more sensitive test of the effect. These
56 patterns might also apply within species, because the functional explanations of FID should
57 apply within as well as across species (see, for example, Gotanda *et al.* 2009). Although there
58 is mounting evidence that, at least in some species, predation risk may differ between the
59 sexes with the more colourful sex being at greater risk (Huhta *et al.* 2003; Thiel *et al.* 2007;
60 Ekanayake *et al.* 2015b; Marshall *et al.* 2015), with few exceptions, escape strategies have
61 been assumed to be consistent between sexes within species, at least in birds (Weston *et al.*
62 2012; Guay *et al.* 2016). Interestingly, studies in lizards have demonstrated that males, the
63 more colourful sex, is both at greater risk of predation and initiates escape behaviour earlier
64 than females (Capizzi *et al.* 2007; Marshall *et al.* 2015; but see Samia *et al.* 2015). A handful
65 of studies have shown that FIDs can vary between the sexes of birds (Thiel *et al.* 2007; Smith
66 2011; Guay *et al.* 2013a). However, whether or not sex differences in escape behaviour in
67 birds are associated with the degree of sexual dimorphism remains unknown.

68 Understanding sex differences in FID could shed light on inter-sexual conflict, mate
69 choice and social systems (Møller *et al.* 2008), as well as inform management of bird
70 disturbance (Weston *et al.* 2012). Currently, there is an absence of comparative studies on
71 FID and dimorphism in birds, partly because of the difficulty of sexing monomorphic species.
72 Here, we examine the influence of plumage (plus bare parts), and body size, dimorphism on
73 the fearfulness of birds. We measured both plumage and size dimorphism as they may both

74 independently influence conspicuousness. We measured FIDs of both males and females in
75 19 species of birds, including both monomorphic and dimorphic species. FIDs were
76 quantified by slowly approaching an individual bird and measuring the distance between the
77 observer and bird at which escape was initiated. We then examined sex differences in size,
78 plumage dimorphism and FID and predicted that intersexual differences in FID would be
79 larger for species with greater size or plumage dimorphism. As more conspicuous species
80 may also be more readily detected by humans, we also tested whether the distance at which
81 observers commenced approaches (the ‘starting distance’) was greater for more colourful or
82 larger species.

83

84 **Materials and methods**

85 *Field measurements*

86 Species were selected on the basis that they were sexable in the field, either because they
87 were sexually dimorphic or because they were monomorphic and had been genetically sexed
88 and fitted with unique marks in previous research (Guay and Mulder 2009; Mulder *et al.*
89 2010; Cardilini *et al.* 2013; Cardilini *et al.* 2015; Ekanayake *et al.* 2015a; Ekanayake *et al.*
90 2015b; Whisson *et al.* 2015; Roche *et al.* 2016) (Table 1).

91 Fieldwork was conducted between 28 March 2013 and 21 August 2013. Standard field
92 methods were used to measure FIDs in the field (Guay *et al.* 2013a; McLeod *et al.* 2013). For
93 each approach we recorded the start distance (SD; distance at which the direct approach
94 towards the focal bird started), the FID, the species and the sex of the focal bird. SD was
95 recorded because is it a very strong predictor of FID (e.g. Blumstein 2003; Symonds *et al.*
96 2014). Even though datasets from different observers can be combined without problems
97 (Guay *et al.* 2013b; van Dongen *et al.* 2015a), all approaches were performed by the same
98 observer to avoid any biases and all targeted birds were evidently non-breeding (or at least
99 away from the nest). All approaches were conducted at locations within 150 km of
100 Melbourne, Australia, and all approaches for any given species were conducted at the same
101 location to account for any spatial variation in habituation. Sampling was evenly spread
102 between the sexes; the average sex ratio (male/female \pm Standard Deviation) across species
103 was 0.97 ± 0.17 .

104

105 *Comparative data*

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

108 1999; Higgins *et al.* 2001; Higgins and Peter 2002; Higgins *et al.* 2006), which we analysed
109 separately. We used both measurements of size since mass is known to be very labile and can
110 vary enormously between seasons in some species (e.g. Briggs 1988). Furthermore, some
111 measurements of wing shape and size are known to be correlated with FID (e.g. Fernández-
112 Juricic *et al.* 2006; Møller 2014). We also calculated indices of dimorphism in size and
113 plumage. Size (body mass and wing length) dimorphism were indexed by calculating $Mass -$
114 $DI = 1 - \frac{mass(male)}{mass(female)}$ and $Wing - DI = 1 - \frac{wing\ length(male)}{wing\ length(female)}$ (after Lovich and
115 Gibbons 1992). Plumage dimorphism (Plumage-DI) was indexed using the technique of Chen
116 *et al.* (2013), whereby seven broad body regions were scored for sexual dimorphism,
117 including bill (including upper and lower mandibles), head (including nape), back (including
118 rump), wing, underparts (including breast, belly and flanks), tail and legs (see Marchant and
119 Higgins 1990 for body region diagram). Whilst we recognise that bare parts (bill and legs) are
120 not part of the plumage we included them in our scoring of plumage dimorphism because,
121 like any part of the plumage, they can be used as cues by predator for prey detection. For each
122 body region, we scored dimorphism, based on colour plates (Marchant and Higgins 1990;
123 Marchant and Higgins 1993; Higgins 1999; Higgins *et al.* 2001; Higgins and Peter 2002;
124 Higgins *et al.* 2006), as either no difference (0 points), difference in colour intensity or pattern
125 (1 point) or difference in pattern and colour (2 points). This measurement of dimorphism
126 focuses on reflection in the visible light spectrum to the exclusion of reflection in the
127 ultraviolet (UV) range. It is well documented from studies on sexual selection that birds have
128 the capacity to see in the UV range and that measurements of plumage brightness should
129 include the UV component (e.g. Bennett *et al.* 1994). Whilst some, but not all, avian predators
130 have been demonstrated to use UV light cues for foraging (e.g. Viitala *et al.* 1995; Koivula *et*
131 *al.* 1997), most mammalian predators are not able to see in the UV range (Honkavaara *et al.*
132 2002). Furthermore, analyses of the violet and ultraviolet light absorbing opsin present on the
133 retina of raptors (Accipitridae and Falconidae) indicate that unlike Passeriformes, they are not
134 sensitive in the short wavelength UV range (Ödeen and Håstad 2003). Thus, focus on the
135 visible light spectrum in this study is unlikely to have influenced the results. Since the
136 species targeted use a wide array of different habitat, it was not possible to assess
137 conspicuousness against background habitat which could impact in the sexual
138 dimorphism as detected by predators. The dimorphism scores were then summed for all 7
139 body regions to obtain one dimorphism score per species. Whilst it is recognised that the
140 particular body regions exposed can influence predation risk in given circumstances (e.g. the

141 legs of a duck swimming are not exposed), we took the conservative approach of giving equal
142 weight to all body regions.

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

149

150 *Comparative analysis*

151 As morphological and behavioural traits may be more similar in closely-related species due to
152 phylogenetic effects, we employed a phylogenetic comparative approach to our data. We
153 obtained phylogenies for the species in our analysis from the “Global Phylogeny of Birds”
154 website – www.birdtree.org (Jetz *et al.* 2012). Specifically, we downloaded a set of 2000
155 possible trees for our species from the distribution of trees on that site. All trees have the
156 same basic Hackett *et al.* (2008) phylogeny as a ‘backbone’ (results obtained using an
157 alternative Ericson *et al.* (2006) backbone were nearly identical and are not presented).
158 Studies have demonstrated that more reliable estimates of evolutionary coefficients can be
159 obtained when multiple phylogenies are used as the basis for analysis (De Villemereuil *et al.*
160 2012; Rubolini *et al.* 2015). We therefore carried out analyses using all 2000 trees as the basis
161 for analysis, producing averaged values for parameter estimates, with associated confidence
162 intervals and weights.

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

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

175 Anderson 2002; Symonds and Moussalli 2011). In each analysis we evaluated the AIC scores
176 for the five best approximating models along with model weights, and averaged these weights
177 across the most common ordering of models across the 2000 phylogenies. Model averaging
178 was also employed to derive predictor weights (the summed Akaike weights of all models in
179 which that predictor featured), model-averaged estimates and associated 95% confidence
180 intervals for each predictor. The predictor weights can be considered analogous to the
181 probability that that predictor really does feature in the best approximating model. As
182 described above, final predictor weights, estimates and confidence intervals were obtained by
183 averaging results from all 2000 phylogenies. For statistical analysis we used the R framework
184 (R Core Team 2015), and the associated packages *phytools* (Revell 2012), *ape* (Paradis *et al.*
185 2004) and *AICcmodavg* (Mazerolle 2015).

186

187 **Results**

188 *Starting distance*

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

196

197 *FID*

198 A preliminary GLM with SD, sex and species as predictors of FID revealed a significant
199 interaction between species and sex ($F_{18,371} = 2.076$, $P = 0.006$; $R^2 = 0.803$). This justified
200 further investigation. Overall, male and female FID did not differ significantly between the
201 sexes (phylogenetically controlled paired t-test, $t = -0.205$, $p = 0.840$, average from 2000
202 trees). Across 2000 phylogenetic generalised least squares models, only SD-DI positively and
203 consistently explained variation in FID-DI, whereas body mass and wing length and the
204 dimorphism in these traits were only weakly associated with FID-DI (Tables 4 and 5). In
205 analyses with SD-DI, the model with that as a single predictor was consistently and
206 unambiguously returned as the best model, otherwise the null model was the strongest (Tables
207 6 and 7).

208

209 **Discussion**

210 While differences in escape distances between sexes have been reported for a broad range of
211 taxa, including birds (Thiel *et al.* 2007; Smith 2011; Guay *et al.* 2013a) and reptiles (Capizzi
212 *et al.* 2007), fearfulness as indexed by FID did not differ between the sexes for the bird
213 species we examined. This is in line with the results obtained in magpie-lark (*Grallina*
214 *cyanoleuca*; Kitchen *et al.* 2010) and for a diversity of birds examined comparatively at the
215 species scale (Hensley *et al.* 2015). Only a handful of reports of sexual differences in bird FID
216 exist (Smith 2011; Guay *et al.* 2013a), and some of these come from areas where one sex is
217 hunted (Thiel *et al.* 2007). Thus, sexual differences in FID among birds might be rare or even
218 absent. Neither Plumage-DI nor size dimorphism were significantly associated with
219 differences in FID between the sexes, despite a wide gradient of dimorphism tested. This
220 result suggests either that the sexes do not significantly adjust their escape behaviour to their
221 conspicuousness to predators or that the relatively slight sexual differences in size or
222 colouration do not result in detectable differences in conspicuousness towards predators. It is
223 important to note that we did not investigate sex differences in colour in the UV range, but
224 sexual differences in the UV range would be unlikely to have resulted in sex differences in
225 FID because whilst some avian predators can use UV cues for foraging, unlike passerines,
226 most raptors are not well adapted to detect short wavelength UV light and most mammalian
227 predators cannot detect UV light (Viitala *et al.* 1995; Honkavaara *et al.* 2002; Ödeen and
228 Håstad 2003). The potential explanation that the predator environment was relatively benign
229 in the study area seems unlikely (many predators occur in the area; Cardilini *et al.* 2013;
230 Ekanayake *et al.* 2015c). When sexing birds in the field, some errors can occur due to
231 juveniles first acquiring female-like plumage (e.g., robins, *Petroica* spp; Higgins and Peter
232 2002) or adult males acquiring an eclipse plumage reminiscent of females at certain times of
233 the year (e.g. Chestnut Teal, *Anas castanea*; Marchant and Higgins 1990). Moulting thus can
234 cause plumage variation across seasons and errors in sexing in some species, but care was
235 taken not to target family groups with juveniles or large groups of ducks with female-like
236 plumage to avoid the risk of sexing eclipse plumaged males as females. It is also possible that
237 individual non-sexual differences in FID exist (Runyan and Blumstein 2004) and these may
238 mask subtler sexual differences in FID. In fact, large differences in FID can be observed
239 between individuals of the same species living in different habitats (e.g. Ikuta and Blumstein
240 2003; McGiffin *et al.* 2013; van Dongen *et al.* 2015b). This cannot be a factor in our study
241 because all approaches on each species were conducted at the same site. Clearly, further
242 investigation of dimorphism and FID across a larger taxonomic sample would be desirable.

243 Broad taxonomic studies of birds have revealed a positive allometric relationship
244 between the extent of sexual size dimorphism and overall size (e.g. Dale *et al.* 2007).
245 Furthermore, the positive relationship between FID and size is well established (Blumstein
246 2006; Bregnballe *et al.* 2009; Glover *et al.* 2011; Guay *et al.* 2013c). It therefore follows that
247 any differences in FID between the sexes were expected to be greater in larger species. In
248 contrast, we found no significant correlation between FID-DI and body size within our
249 dataset. Given the lack of evidence of sexual dimorphism in escape behaviour between the
250 sexes, this may not be unexpected.

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

258

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264

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476
477

478 **Table 1** Species chosen for this research, the Starting Distance and Flight-initiation Distance, and their plumage and body size dimorphism
 479 scores (see text). Means \pm 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 <i>Biziura lobata</i> (22)	136.3 \pm 13.2	99.4 \pm 8.0	109.9 \pm 12.2	92.1 \pm 10.2	2	-0.546	1975	-0.205	204
Cape Barren goose <i>Cereopsis novaehollandiae</i> (23)	54.6 \pm 6.5	21.3 \pm 3.8	67.3 \pm 7.4	32.3 \pm 5.2	0	-0.403	4530	-0.065	456
Black swan <i>Cygnus atratus</i> (27)	39.4 \pm 2.8	8.8 \pm 1.8	39.4 \pm 3.6	4.6 \pm 2.2	0	-0.229	5685	-0.022	464
Australian wood duck <i>Chenonetta jubata</i> (26)	43.3 \pm 3.0	24.2 \pm 1.5	43.9 \pm 3.2	28.6 \pm 1.6	4	-0.019	808	-0.023	269
Australasian shoveler <i>Anas rhynchotis</i> (12)	170.0 \pm 13.2	118.7 \pm 15.6	171.7 \pm 5.3	126.3 \pm 10.0	8	-0.003	666	-0.004	239
Chestnut teal <i>Anas castanea</i> (25)	62.3 \pm 7.2	36.9 \pm 4.3	56.2 \pm 4.0	38.6 \pm 3.8	4	-0.152	638	-0.071	210
Hardhead <i>Aythya australis</i> (22)	160.1 \pm 15.7	113.5 \pm 11.0	139.8 \pm 12.1	107.7 \pm 9.4	6	-0.076	870	0.009	216
Blue-billed duck <i>Oxyura australis</i> (21)	147.8 \pm 13.9	97.3 \pm 11.0	114.8 \pm 15.3	78.1 \pm 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 <i>Charadrius ruficapillus</i> (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 <i>Vanellus miles</i> (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 <i>Psephotus haematonotus</i> (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 <i>Malarus cyaneus</i> (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 <i>Epthianura albifrons</i> (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 <i>Cracticus tibicen</i> (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 <i>Grallina cyanoleuca</i> (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)
<i>Petroica boodang</i> (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
<i>Petroica phoenicea</i> (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
<i>Turdus merula</i> (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
<i>Passer domesticus</i> (19)									

480

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

484

Model	Predictor	Weight	Estimate ($\pm 95\% \text{CI}$)
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)

485

486

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

491

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

492

493 **Table 4** Results of the effect of plumage dimorphism, SD-DI, mass and body mass on FID-DI
 494 using 1) body mass and 2) wing length as control variables. Averaged cumulative parameter
 495 weights and coefficients are presented.
 496

Model	Predictor	Weight	Estimate ($\pm 95\%$ 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)

497
 498

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

502

Model	Predictor	Weight	Estimate ($\pm 95\% \text{CI}$)
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)

503

504

505 **Table 6** The most consistently returned top five best approximating models predicting Flight
 506 Initiation dimorphism (FID-DI) from the PGLS analyses across 2000 phylogenies, including
 507 SD-DI as a predictor and using 1) body mass and 2) wing length as control variables. Average
 508 delta AIC and Akaike weights for each model are presented.
 509

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

510

511

512 **Table 7** The most consistently returned top five best approximating models predicting Flight
 513 Initiation dimorphism (FID-DI) from the PGLS analyses across 2000 phylogenies, *without*
 514 including SD-DI as a predictor and using 1) body mass and 2) wing length as control
 515 variables. Average delta AIC and Akaike weights for each model are presented.
 516

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

517