

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

**Bhukya Prameela**

Department of Zoology, AK Navajivan Women's PG College, Hyderabad, Telangana State, India

## ABSTRACT

Conspicuousness towards predators may influence escape behaviour (or 'fearfulness') among animals, with more conspicuous species initiating escape behaviour earlier. Among 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, among 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 behaviour; flight-initiation distance; sexual selection; fearfulness; sexual dimorphism.

## INTRODUCTION

Escape behaviour is a critical component of the life history of animals as it allows individuals to minimize 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, Luiselli & Vignoli, 2007; Glover, Guay & Weston, 2015). For example, bird species with larger body sizes have longer FIDs, perhaps because of larger sensory organs and hence earlier detection of predators (e.g. Blumstein, 2006; Møller & 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 (Fernandez-Juricic, Jimenez & Lucas, 2002). Similarly, more colourful species are more readily detected by predators and may struggle to evade predators or hide (e.g. Gotmark & 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, Turgeon & Kramer, 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, Ryttonen & Solonen, 2003; Thiel et al., 2007; Ekanayake et al., 2015b; Marshall, Philpot & Stevens, 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 on lizards have demonstrated that males, the more colourful sex, are at greater risk of predation and initiate 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, Nielsen & Garamszegi, 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 & Mulder, 2009; Mulder et al., 2010; Cardilini et al., 2013, 2015; Ekanayake et al., 2015a,b; Whisson, Weston & Shan-non, 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 it is 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 0.970.17.

### Comparative data

For each species we compiled two body size measurements, body mass (g; Dunning, 2008) and wing length (mm; Marchant & Higgins, 1990, 1993; Higgins, 1999; Higgins, Peter & Steele, 2001; Higgins & Peter, 2002; Higgins, Peter & Cowling, 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. Fernandez-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 calculate 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 & Higgins, 1990 for body region diagram). While we recognize 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 & Higgins, 1990, 1993; Higgins, 1999; Higgins et al., 2001, 2006; Higgins & Peter, 2002), 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 ultra-violet (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, Cuthill & Norris, 1994). While some, but not all, avian predators have been demonstrated to use UV light cues for foraging (e.g. Viitala et al., 1995; Koivula, Korpimäki & Viitala, 1997), most mammalian predators are not able to see in the UV range (Honka-vaara 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 (Gedde & Hastad, 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 summed for all seven body regions to obtain one dimorphism score per species. Whilst it is recognized 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](http://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 Villemeireuil 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 (Lindfors, Revell & Nunn, 2010). We then constructed a series of phylogenetic generalized least squares (PGLS) models (Symonds & 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. 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 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.

## 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 generalized least squares analyses revealed no significant effect of Plumage-DI, mass-DI or body

Table 1 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)	1	SD-DI	0.739	1.024 (0.418 to 1.630)
	Mass-DI	0.201	0.157 ( 0.867 to 0.552)		Plumage-DI	0.016	0.019 ( 0.075 to 0.036)
	Body mass	0.197	0.034 ( 0.288 to 0.220)		Mass-DI	0.154	0.004 ( 0.853 to 0.845)
2	Plumage-DI	0.213	0.009 ( 0.032 to 0.050)	2	Body mass	0.034	0.006 ( 0.218 to 0.231)
	Wing-DI	0.239	0.690 ( 2.533 to 1.154)		SD-DI	0.766	1.086 (0.465 to 1.709)
	Wing length	0.288	0.257 ( 0.831 to 0.317)		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)

investigation. Overall, 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 generalized 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 (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 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 detectable 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; 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, Lill & Price, 2010) and for a diversity of birds examined comparatively at the species scale males as females. It is also possible that individual non-sexual differences in FID exist (Runyan & 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 & 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, Aen & Fox, 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 among 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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