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Vivid birds do not initiate flight sooner despite their potential conspicuousness

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Abstract The distance from an approaching threat at which animals initiate flight -- flight-initiation distance (FID) -- is a sensitive metric of variation in risk, but the effects on FID associated with the risk of possessing highly detectable external coloration are unknown. We tested whether variation in the degree of plumage vividness in birds explained variation in flight-initiation distance. After controlling for body mass, the distance at which the experimental approach began, and phylogenetic relatedness, plumage vividness was not a predictor of FID. Contrary to the expectation that vividness affects risk, and therefore risk assessment, these results suggest that birds do not compensate for greater visual conspicuousness by fleeing sooner from approaching threats [*Current Zoology* 61 (4): 773–780, 2015].

Keywords Antipredator behavior, Body size, Coloration, Comparative method, Conspicuousness, Flight Initiation Distance

The distance from an approaching threat at which animals initiate flight (i.e., flight-initiation distance; FID) is a metric of risk assessment that is sensitive to a variety of factors (Blumstein, 2003; Stankowich and Blumstein, 2005; Blumstein, 2006). Birds, mammals, and reptiles are particularly well-studied taxa (Stankowich and Blumstein, 2005; Cooper et al., 2014; Samia et al., 2015). For example, we know that various external factors influence FID, including speed of approach (Stankowich and Blumstein, 2005), habitat type (urban vs. rural; Møller, 2008; Bateman and Flemming, 2014), human activity (Price et al., 2014), and predation pressure (Møller et al., 2008). Factors inherent to organisms ("internal" factors) also influence FID, including body size, body temperature, reproductive status, and both individual and interspecific behavioral variation (Bauwens and Thoen, 1981; Brodie, 1989; Bulova, 1994; Blumstein, 2006, Møller and Garamszegi, 2012).

In addition to the factors just listed, an organism's coloration would be expected to influence its predation risk, and hence its FID, in at least three ways (Cott, 1940). First, coloration may be aposematic and thereby signal unprofitability to potential predators (for a review see Baker and Parker 1979). Second, coloration could be cryptic whereby external coloration generally decreases detectability by predators through background matching (Cott, 1946; Endler, 1978). Third, a color could increase the detectability of an individual while not providing any aposematic benefits, as in the case of social ornaments (Møller and Nielsen, 2006). Many animals have evolved such coloration as signals used in social communication (e.g., through sexual selection; Darwin, 1871), which are adaptive in spite of the survival cost that comes with increased conspicuousness. These outcomes are also influenced by at least two external factors: (1) the background habitats against which these colors are compared, and (2) the ability of receivers (e.g., potential predators, mates, etc.) to discriminate between the signaler and background (Endler, 1978; Endler, 1990). Despite complex visual environments and selection from predators with different visual ecologies, we still may expect conspicuous color to influence escape decisions.

A few studies have examined the relationship between conspicuous coloration and FID. Martín and López (1999) found that the males of the large, sexually dichromatic lizard *Psammodromus algirus* with conspicuous head coloration had larger FIDs than both females and males with less coloration. By contrast, Cooper (2003) did not find that coloration intensity explained variation

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in FID in female *Holbrookia propinqua* lizards (although this conclusion was based on a relatively small sample size). Reports for various other lizards indicate that cryptic coloration affects anti-predator behavior: differing levels of camouflage changes anti-predator tactics in the common chameleon (*Chamaeleo chamaeleon*, Cuadrado et al., 2001), and FID in certain species of *Anolis* lizards is associated with their detectability (Heatwole, 1968; Cooper, 2006). These studies provide some support for the hypothesis that animals can modify their behavior to compensate for conspicuous coloration.

Conspicuous coloration may affect how organisms assess their level of risk, altering the costs and benefits of certain anti-predator behaviors including FID. Theoretical models predict that animals should flee when the costs of flight are surpassed by costs of staying in the presence of a perceived predator (Ydengberg and Dill, 1986) or when costs of fleeing are minimized and the benefits are maximized (Cooper and Frederick, 2007). Conspicuousness may greatly increase the cost of staying by increasing predation risk (Götmark and Olsson, 1996; Huhta et al., 2003; Stuart-Fox et al., 2003), outweighing the benefits of not fleeing. In this scenario, we may expect conspicuous coloration to influence escape behaviors like FID.

Within birds, coloration has been well characterized. Plumage coloration across birds is recognized as a balance between natural selection favoring cryptic colors with sexual selection favoring highly dimorphic colors between the sexes (Baker and Parker, 1979; Dunn et al., 2015). Therefore most instances of highly detectable coloration should be costly. Some species may have aposematic coloration to signal unprofitability, like poisonous birds of the genus *Pithohui* (Dumbacher and Fleischer, 2001) or as suggested by the Unprofitable Prey Hypothesis (Baker and Parker, 1979). However, these examples are rare: there is only one genus of poisonous birds discovered to date, and the Unprofitable Prey Hypothesis is widely debated (Baker and Hounsome, 1983; Baker, 1985; Lyon and Montgomerie, 1985; Götmark, 1992; Götmark, 1993; Slagsvold et al., 1994; Götmark and Olsson, 1997). As such, natural selection should favor anti-predator behaviors that compensate for, and coadapt with, increased conspicuousness. For instance, a recent comparative study of birds in the Virgin Islands demonstrated that more vivid species are more responsive to playbacks of avian predator calls than less vivid species (Journey et al., 2013).

We tested the hypothesis that avian plumage vividness, as measured by humans (see Journey et al., 2013), is positively associated with FID. This hypothesis relies on the assumption that such conspicuous coloration translates into increased predation risk (Møller and Nielsen, 2006). Despite the rich literature, which demonstrates that increased predation risk usually translates into compensatory anti-predatory behavior, few studies explicitly test the hypothesis that organisms with conspicuous coloration are warier or more sensitive to predation risk. Using vividness as a proxy for conspicuousness, we tested the prediction that, after controlling for body size, individuals of more vivid species initiate flight sooner than individuals of less vivid species.

1 Materials and Methods

1.1 Flight-initiation distance

Measurement of flight-initiation distance (FID) came directly from Blumstein (2006), following the methods of Blumstein (2003). Briefly, calm, non-endangered, non-nesting birds were experimentally approached by a trained observer at a practiced pace of ~0.5 m/s. Observers noted distance at the start of approach (starting distance) and the distance at which a focal subject either walked or flew away (FID). Participants minimized resampling by approaching birds in different locations and by not re-sampling locations. Species (n = 136) included for analyses had a minimum of 10 observations and FID was averaged within species across all observations. We included FIDs of birds of both sexes regardless of whether or not they were dimorphic at the time of study. Thus, our inferences use the average species' FID, making our analyses conservative.

1.2 Vividness

We measured vividness of birds by having participants score images in surveys created using QuestionPro (Question Pro, 2009) following the methods described in (Journey et al., 2013). The surveys randomized the order of the images, which we compiled from several field guides (details in Supplementary Material). When plumage varied between the breeding and non-breeding season, we used images from the breeding season. For sexually dichromatic species, we only included data from males, since images of males were most readily available and in most instances of dichromatism, were more vivid.

Observers (number of participants per image, mean = 16.25, range = 5–25) ranked the vividness of the plumage of each species from the field guides by giving a score from a range of 1–5 ((1) dull; entirely neutral col-

ors, (2) overall dull, but some small amount of color that stands out slightly against neutral background, (3) slightly bright; mostly neutral/dull colors, but fair amount of subtle coloration or prominent amounts of white, (4) bright; plumage mostly bright colors, but some dull/neutral colors, (5) very bright; no dull/neutral plumage, all plumage bright/neon). The participants were unaware of the definition of brightness employed by scientists who study color (Endler, 1990; Armenta et al., 2008), which we acknowledge is distinct from its colloquial use and therefore use 'vividness' to capture this colloquial meaning hereafter. We calculated the mean vividness score for each species.

Although this method does not use spectrophotometric data, a previous study has corroborated the strength of human-assessed visual conspicuousness ("vividness") as compared to those of spectral data (see Journey et al., 2013) in similar models. We concur with previous investigators (Karubian, 2013; Santos et al., 2014) that for a large comparative study like this one, our methodology is more feasible than spectrophotometric methods. Recent studies have also found that human visual assessment of bird plumage coloration is comparable to spectrophotometric measurements in the range visible to humans (Seddon et al., 2010; Journey et al., 2013), which lends credence to the argument that vividness scored by humans is a reasonable approximation of vividness as perceived by birds and potentially by some of their predators.

1.3 Dichromatism

We scored each bird species as either being dichromatic with a '1' for dimorphic coloration differences, or a '0' for monomorphic. We scored species that are dichromatic only seasonally as dimorphic. Likewise, for species that are sexually dichromatic, seasonal or not, we scored as dimorphic. In this way, we were conservative by collapsing both seasonal and sexual variation in our measure of dichromatic coloration. For further discussion on our conservative scores of bird dichromatism, see the Supplementary Materials (section "Validating dichromatism scores").

1.4 Body Mass and Location

Maximum bird body masses were taken from Blumstein (2006) and originally derived from multiple sources (see available supplement for data [Supplementary Materials 2] and for references). Continent-level species distributions were also obtained from these sources.

1.5 Phylogeny

Using birdtree.org (Jetz et al., 2012), we downloaded ultrametric phylogenetic trees for the 136 species. Trees were sourced from Hackett (all species; set of 10,000 trees with 9,993 OTUs each) as selected from the drop-down menu. A total of 1,000 trees were generated and we used TreeAnnotator (v. 1.6.1; Drummond and Rambaut 2007) with default settings (burnin = 0, posterior probability limit = 0.5, tree type = maximum clade credibility, node heights = median heights) to generate a rooted consensus phylogeny with branch lengths. The tree used for these analyses is available in the supplement as a NEXUS file (Supplementary Material 1).

1.6 Statistical analysis

We regressed log FID on vividness, log body mass, log start distance, a binary dimorphism character state, and an interaction between log vividness and dimorphism. We also included two other categorical, independent variables: a continent variable, coded by region, to account for geographic variation in FID, and a clade variable to assess whether differences in FID could be explained by major differences among evolutionary lineages. To control for potential phylogenetic effects and to test the sensitivity of our results, we performed the same regression four times under different evolutionary scenarios. These scenarios were calculated using transformations of the variance-covariance structures of the residuals (Garland and Ives, 2000; Lavin et al., 2008; Rezende and Diniz-Filho, 2012) using the 'ape' package (v. 3.1–2; Paradis et al., 2004) in R. First, we used non-phylogenetic, ordinary least squares (OLS). Then, we used phylogenetic least squares (PGLS), which assumes a Brownian motion model of trait evolution (Pagel's $\lambda = 1$) implemented with the "corBrownian" function. We also fitted regressions with the branch lengths transformed using the restricted maximum likelihood (REML) value of Pagel's λ (RegLambda; Pagel, 1994) as calculated using the "corPagel" function, which allowed the tree to mirror the strength of the phylogenetic signal in the residuals (Freckleton et al., 2002). Finally, we performed a regression with the REML estimate of the paramater mimicking the Ornstein-Uhlenbeck (RegOU) model of trait evolution, which simulates stabilizing selection, to transform the tree. This analysis was calculated by the "corMartins" function that allowed the α parameter to vary with the strength of the phylogenetic signal (Butler and King, 2004).

The "global" model with all 7 predictor variables was constructed using the "gls" function in the 'nlme' package (v.3.1–117; Pinheiro et al., 2014) and calculated using REML estimation of the regression parameters. The correlation structures were implemented in the

"correlation" option of the "gls" function. All models were weighted using the inverse square-root of sample size to account for variation in sampling effort ("weights" option of "gls" function; Garamszegi and Møller 2010). Taking this global model, and using the 'MuMIn' package (v. 1.10.0; Barton, 2014), we used the "dredge" function to iterate through all variable combinations to explain variation in FID. All models considered included log body mass and log starting distance because these explained significant variation in FID in previous studies (Blumstein, 2003; Blumstein, 2010; Samia et al., 2013); other variables were systematically included/excluded in a particular iteration. We used log-transformed values to normalize the distribution of residuals. All models are reported in Supplementary Material 3. We also report the same analyses without weighting by sampling effort in Supplementary Material 4.

For our collection of models, three procedures were used in an attempt to identify outlying or statistically influential data points. First, we checked the distribution of standardized residuals for values > |3.0| in our "global" models and the best supported models for each of the four evolutionary scenarios mentioned (OLS, PGLS, RegLambda, and RegOU). For values so noted, we then applied the outlier test described by Cook and Weisberg (1999). Finally, we checked for large effects on P values or parameter estimates if values noted in step one were removed. In the end, these procedures did not lead us to delete any data points from the final analyses.

We compared models with the Akaike Information Criterion statistic corrected for sample size (AICc), in all cases based on repeating our analyses using maximum likelihood estimation instead of REML. We interpreted AICc values within 2 units of the smallest AICc value as providing the best support (Burnham and Anderson, 2002). We also looked at two other ways to quantify relative model support: the evidence ratio (ER) and Akaike weights (acc_w). ER is used between models to estimate how relatively favored one model is over others. Acc_w is a model probability indicating how likely it would be for any given model to be the best fitting model given the data. These acc_w values are additive and can be used to determine which variables are most influential in predicting variation in FID (Dlugosz et al., 2013). All raw data are reported fully in Supplementary Materials 2.

2 Results

Table 1 presents the three best models based on AICc. These three models account for 62% of the cumulative evidence (cumulative weight, Table 1) and are significantly better than intercept-only models (Supplementary Table 1). In all three models, the estimate of λ was substantially greater than zero (~0.43), indicating phylogenetic signal in the residual FID (Table 1). Vividness appears only in the third-best of the models (Table 1, Aikake weighting = 0.134), and here it was not statistically significant ($P = 0.555$). When considering variable weights, vividness only appears in 30% of all our models.

Of variables present in the top three models, only 'continent' and log-transformed starting distance were statistically significant (Table 1). Within the 'continent' variable in all three top models, only the species with a

Table 1 Results from the three best supported models fitted to explain variation in $\log_{10}$(FID)

Model	Intercept	Continent	$\log_{10}$(Mass)	$\log_{10}$(Starting Distance)	Passerine	Vividness	
RegLambda 1	-0.1615*	+***	0.0358†	0.8377***			
RegLambda 2	-0.1880*	+***	0.0394†	0.8444***	+		
RegLambda 3	-0.1398	+***	0.0333	0.8383***		-0.0064	
	RSE	Pagel's λ (REML)	logLik (ML)	AICc (ML)	Aikake weight	Cumulative weight	ER
RegLambda 1	0.2363	0.4347	134.1953	-248.9619	0.3488	0.3488	1
RegLambda 2	0.2378	0.4448	134.4212	-247.0823	0.1363	0.4851	2.5595
RegLambda 3	0.2357	0.4217	134.4029	-247.0457	0.1338	0.6189	2.6067

Independent variable trait estimates significantly different from 0 are indicated with asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, † $P < 0.077$). Categorical variables present in any given model are denoted by "+". RegLambda, a regression which incorporates some degree of phylogenetic signal; Continent, the location of a species's natural range with values of (1) Australia (2) Australia & North America (3) Australia & Europe (4) North America (5) Europe; $\log_{10}$(mass), $\log_{10}$ transformation of mass; $\log_{10}$ transformation of starting distance; Passerine, a binary variable describing whether a species is in the passerine clade or not; Vividness, a averaged score of 1–5 of coloration; RSE, residual squared error; Pagel's Lambda, a measure of phylogenetic signal strength for variation in FID estimated via restricted estimate maximum likelihood (REML); logLik, log of the maximum likelihood (ML); AICc, Aikake information criterion corrected for small sample size; ER, evidence ratio.

"Europe" designation significantly explained variation in FID (N_{Europe} = 11, $P < 0.001$); both categories "North America" and "Australia & Europe" were never significant (but note that there is only one species in "Australia & Europe").

In our top three models, body mass was not a statistically significant predictor (all $P > 0.05$). Other variables did no better in explaining variation in FID (see Supplementary Material 3 for details). A binary coding for Passerine performed similarly to vividness (appearing in ~30% of models), but was still not significant in the models ($P = 0.532$).

3 Discussion

Our results do not support the hypothesis that birds compensate for plumage vividness by fleeing more quickly from approaching humans. This result, based on many species of birds, contrasts with a previous report that within a single species, more vivid lizards initiate flight at relatively greater distances (Martín and López, 1999). Our results are notable because some animals have been shown to compensate for increased risk in a variety of ways. Individual frogs (*Craugastor* spp.), even when approached rapidly by perceived predators, remain immobile, presumably to enhance crypsis (Cooper et al., 2008), whereas conspicuous male rock ptarmigan *Lagopus mutus* soil their white plumage to increase crypsis (Montgomerie et al., 2001). Comparative studies of birds have demonstrated that vivid birds are more responsive to vocalizations from their predators (Journey et al., 2013), and Bailey et al. (2015) showed that captive, nesting zebra finches *Taeniopygia guttata* actively selected nesting material that matched their cage colors over more conspicuous materials. These previous studies indicate that some form of compensation for increased risk associated with vivid coloration occurs in a variety of species. Thus, it was surprising that vivid birds did not compensate by initiating flight at greater distances.

Behaviors other than escape may also have evolved to compensate for conspicuous morphological features. For example, Journey et al. (2013) showed that birds with vivid plumage increased their rate of vigilance in response to playbacks of predator vocalizations. Increased vigilance in conspicuous organisms may represent an alternative evolutionary "solution" allowing for shorter FID (sensu Garland et al., 2011; Losos, 2011). By increasing the distance at which a prey responds by looking at the predator (alert distance), prey could better monitor a potential threat. There is some evidence that animals can alter their escape behavior so as to continually monitor a potential threat without fleeing *per* Cooper (2008). By increasing vigilance and predator monitoring, potential prey may sufficiently decrease the cost of remaining. This would result in conspicuous coloration being more tightly correlated to anti-predator behaviors other than FID, like vigilance. Future studies should examine the prevalence and potential trade-offs (Garland, 2014) of these types of alternative anti-predator behaviors in vivid and non-vivid species to test this hypothesis.

Vividness might differentially affect the costs and benefits of fleeing. Vivid coloration may increase the cost of remaining by increasing detectability, but it may not necessarily do so in a consistent manner across species. In species where vivid coloration is also a sexual signal, the cost of fleeing may be substantially higher and individuals may tolerate higher risk, fleeing later (Cooper, 1999). This differential effect on risk assessment may vary across species, obscuring the relationship between vividness and FID. Quantifying the relative costs, with respect to fleeing and remaining, of vividness on predation, as well as the benefits of such coloration in order to assess how this potential trade-off may affect FID is an important avenue for future research.

Our results also demonstrate that broad-scale geographical differences are associated with variation in flight-initiation distance. In our study, birds in Europe had significantly shorter FIDs than those observed on other continents. Møller et al. (2014) also recently reported a relationship between FID and continent-level population trends, where the effect of FID on population decline differed across continents. Together, these studies suggest that observed patterns in FID vary across large geographic scales; we do not attempt to provide any mechanistic explanation for the evolution of such variable responses.

We used humans to rate plumage coloration. Several other investigators have also used human assessments of coloration in other taxa (Cooper, 2006; Santos et al., 2014), including in sexually dimorphic species of birds (Armenta et al., 2008; Møller, 2008; Johnson et al., 2013; Karubian, 2013). However, two of these studies implemented a binary coding system to easily record coloration status (i.e., cryptic vs. non cryptic, sexually dimorphic or not). We used a method that created a continuous scale on which finer differences in coloration could be assessed, which previously was validated in a study of risk compensation (Journey et al., 2013). Fu-

ture studies could apply this methodology to other taxa (e.g., lizards, mammals) for which considerable FID data exist.

We acknowledge that our methods rely on a human assessment of coloration and that this does not fully represent the spectral sensitivities of all avian predators (e.g., snakes, other birds, etc.). However, during final revisions of this manuscript, we performed our analyses again using a subset of spectrophotometric plumage data for 90 species from Dunn et al. (2015) with qualitatively similar results (unpublished). We also acknowledge that this method does not account for any ecological variation that may contribute to an animal's conspicuousness such as micro-habitat type. However, because our measured response is a proxy for risk assessment, our ability to discriminate an individual's conspicuousness against a fixed background does not influence the bird's own assessment of the danger level it perceives. And, previous models using these data did not find any ecologically relevant correlates that explained variation in FID (Blumstein, 2006). Thus our results, and our interpretations of them, remain generally sound. In either case, because our human visual ability differs from that of some predators, these caveats should be borne in mind when interpreting our results.

Although a number of previous studies have reported phylogenetic signal (Blomberg et al., 2003) in FID (e.g., Blumstein et al., 2005; Møller, 2008; Møller and Garamszegi, 2012), ours is one of the few to formally compare regression models that do and do not incorporate phylogenetic information by use of an information-theoretic approach (e.g., Cooper et al., 2014; Møller et al., 2014; Samia et al., 2015). Cooper et al. (2014) recently reported that FID variation among species of lizards was best explained by statistical models using a star phylogeny, indicating no phylogenetic signal in residual FID, and thus suggesting rapid evolution of FID (but see Revell et al., 2008). In contrast, our analyses indicate the presence of phylogenetic signal in residual FID, i.e., that some intermediate level of hierarchical structure (see Pagel's λ, Table 1) best explains the residual variation in FID.

The observation that flight-initiation distance demonstrates a variable level of phylogenetic signal, depending on the organisms considered and/or the potential predictive variables considered, could be attributable to a variety of evolutionary processes (see Revell et al., 2008), as well as more mundane factors, such as the amount of measurement error (Blomberg et al., 2003; Ives et al., 2007). One possible explanation for the lack of phylogenetic signal in FID may be that strong selection for more specific anti-predatory behavioral responses erases the footprint of shared evolutionary history. If so, then we would expect that variation in FID would be best explained by contemporary ecological and contextual factors (e.g., predation level). Some evidence supports this idea in lizards, for which anti-predator behaviors are best predicted by predator diversity (Brock et al., 2015) or the lack thereof (Cooper et al., 2014). More explicit tests of the strength of selection on FID in contemporary populations would shed further light on these issues. With various studies (including our own) reporting contrasting differences in the phylogenetic signal of FID, our current understanding indicates that the evolution of escape decisions is both complex and idiosyncratic, e.g., varying among lineages.

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