



HAL
open science

Flight initiation distance, color and camouflage

Anders Pape Møller, Wei Liang, Diogo S M Samia

► **To cite this version:**

Anders Pape Møller, Wei Liang, Diogo S M Samia. Flight initiation distance, color and camouflage. *Current zoology*, 2019, 65 (5), pp.535-540. 10.1093/cz/zoz005 . hal-02390279

HAL Id: hal-02390279

<https://hal.science/hal-02390279>

Submitted on 3 Dec 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Article

Flight initiation distance, color and camouflage

Anders Pape MøLLER^{a,b,*}, Wei LIANG^c, and Diogo S. M. SAMIA^d

^aLaboratoire d'Ecologie, Systématique et Evolution, CNRS UMR, Université Paris-Sud, Batiment 362, Orsay Cedex, France, ^bMinistry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, College of Life Sciences, Beijing Normal University, Beijing 100875, China, ^cMinistry of Education Key Laboratory for Ecology of Tropical Islands, College of Life Sciences, Hainan Normal University, Haikou, China, and ^dDepartment of Ecology, Federal University of Goiás, Goiania, Brazil

*Address correspondence to Anders Pape Møller. E-mail: anders.moller@u-psud.fr.

Handling editor: David Swanson

Received on 21 October 2018; accepted on 17 February 2019

Abstract

Camouflage is widespread throughout the animal kingdom allowing individuals to avoid detection and hence save time and energy rather than escape from an approaching predator. Thus, camouflage is likely to have co-evolved with antipredator behavior. Here, we propose that camouflage results in dichotomous escape behavior within and among species with classes of individuals and species with cryptic coloration having shorter flight initiation distances (FIDs; the distance at which an individual takes flight when approached by a human). We report the results of 2 tests of this hypothesis. First, bird species with cryptically colored plumage have consistently shorter FID than closely related species without such color. Within species with sexually dimorphic plumage, brightly colored adult male common pheasants *Phasianus colchicus* and golden pheasants *Chrysolophus pictus* have long and variable FID, whereas cryptically colored juveniles and adult females have short and invariable FID. Second, FID in females was predicted by presence or absence of cryptic color, FID in males and their interaction. These findings are consistent with the hypothesis that risk-taking behavior has been attuned to camouflage, and that species with different levels of camouflage differ consistently in their FID.

Key words: anti-predator behavior, birds, camouflage, crypsis, sexual dichromatism

Large birds “do not possess the possibilities of developing skulking habits like grasshopper warblers (especially *Locustella certhiola* [Pall.] and *Locustella lanceolata* [Temm.]), which like the quails or quail-like birds (*Turnix tanki blanfordii* Blyth and *Coturnix c. japonica* Temm. & Schleg.) are sometimes nearly trodden upon even in open country with low grass before being detected.” (Hemmingsen 1951, p. 76).

Camouflage is defined as arising from the use of any combination of materials, coloration or illumination for concealment (Stevens and Merilaita 2011). Camouflage refers to color resemblance, concealment shadow, crypsis, disruptive coloration and pattern blending that reduce the risk of mortality caused by predation. Camouflage is common throughout the animal kingdom, allowing animals to remain hidden from potential predators and only escape at the very last minute thereby conferring a fitness advantage

(Wallace 1889; Trivers 1985; Stevens and Merilaita 2011; Troscianko et al. 2016). Such late departure during predator approach has 2 consequences. First, predators may get scared because they have not yet identified whether the camouflaged individual is a prey or another predator. Such late departure may also be associated with no departure at all. A potential predator may get startled because late flushing is an unusual response by a prey individual. Prey generally flush at long distances, whereas a cryptic individual habitually flushes late (Hemmingsen 1951). Some species may change from immobility to fleeing when approached by a predator (Nishiumi and Mori 2015). A second advantage of camouflage is that individuals can save time and energy by staying put (“freezing”) rather than engaging in frequent and costly escape flight (Hediger 1934; Hemmingsen 1951; Samia et al. 2015).

Here we took advantage of intra- and interspecific variation in camouflage in birds, namely 1) all sex and age classes of a species being cryptic (i.e., males, females, and juveniles alike) whereas sister taxa are not; and 2) species in which adult females are cryptic whereas adult males are not. We predicted that flight initiation distance (FID) would be consistently shorter in species, age and sex classes with camouflage, FID being the distance at which individuals take flight when approached by a potential predator such as a human (Hediger 1934; Hemmingsen 1951; Blumstein 2006; Weston et al. 2012; Cooper and Blumstein 2016). Empirical evidence shows a positive relationship between FID and the risk of predation (Møller et al. 2006; Møller 2014). Many species are camouflaged against the background of the common habitat with all sex and age classes showing similar inconspicuous coloration (Hemmingsen 1951). Among birds, examples of European species that are generally judged by observers to be cryptic in all sex and age classes are bittern *Botaurus stellaris*, snipes and woodcocks, corncrake *Crex crex*, buttonquails, nightjars, larks, pipits, reed warblers, and leaf warblers among many others. In such camouflaged species, we should expect FID to be consistently short compared with closely related sister taxa without camouflage.

Many bird species differ by 1 sex or age class being camouflaged with respect to the background, whereas the other class is brightly colored (Wallace 1869, 1889). Examples of this category among European species include mallard *Anas platyrhynchos* and other dabbling ducks, scoters, eiders, harriers, capercaillie *Tetrao urogallus*, black grouse *Lyrurus tetrix*, pheasants, ruff *Philomachus pugnax*, yellow wagtail *Motacilla flava*, whinchat *Saxicola rubetra*, redstart *Phoenicurus phoenicurus*, and blackbird *Turdus merula* among many others.

FID should reflect the risk of predation with longer FID implying lower probability of predation (Møller et al. 2006; Møller 2014). Hence, we should expect in species with sexually bright coloration in males, but camouflaged plumage in females or juveniles that FID is shorter in juveniles and females than in males. We tested 1) whether that was the case in a paired comparison of sister taxa with and without cryptic coloration in both sex and age classes. We expected in species with bright coloration in males, but cryptic coloration in females or juveniles that FID is short in juveniles and females, but not in males in which conspicuous coloration allows detection by a predator already at long distances. We also tested whether that was the case in the golden pheasant *Chrysolophus pictus* and the common pheasant *Phasianus colchicus* in which males are brightly colored, whereas females and juveniles have mottled brown coloration that matches a background of withered grass or leaves (Mullarney et al. 2000; Marshall and Gluckman 2015). We only had sufficiently many observations of the 2 pheasant species for this test. Next, we tested 2) whether FID in females was predicted by FID in males, presence or absence of cryptic color and their interaction. We predicted that species with males without cryptic color, but females with cryptic color would respond similarly to a predator at short FID, but not at long FID. Because long FIDs imply frequent disturbances at a given density of predators, there should be considerable advantages from camouflage in adult females in species with the longest FID. We made these tests in birds for which we had information on sex-specific differences in FID and cryptic coloration.

Material and Methods

Study areas and FID

APM estimated FID for birds during February–September 2006–2014, using an experimental field procedure (Hediger 1934;

Hemmingsen 1951; Blumstein 2006). All estimates were collected blindly with respect to the hypothesis on camouflage being tested here, thereby preventing any conscious or unconscious bias, because the data were collected before the hypotheses were formulated. The observations were made in an area of 100 km² in Orsay (48°42'N, 2°11'E), Ile-de-France, France, an area of 800 km² in Northern Jutland (57°12'N, 10°00'E), Denmark, and to a lesser extent elsewhere in Europe. Flight initiation distance (FID) data were also collected by Wei Liang at Foping National Nature Reserve (33°22'N, 107°10'E), Central China in January–March 1996 and Kuankuoshui National Nature Reserve (28°10'N, 107°10'E), and Guizhou, Southwestern China in December 1998–March 1999.

FID was recorded when an individual bird had been located with a pair of binoculars. Subsequently, APM and WL moved at a normal walking speed towards the individual, whereas recording the number of steps (which approximately equals the number of meters [Møller 2008a]). The horizontal distance at which the individual took flight was recorded as the FID, whereas the starting distance was the distance from where the observer started walking up to the bird. In most cases, this was chosen as a fixed distance of ~30 m to avoid a correlation between FID and starting distance. If birds started moving when the observer was longer than 30 m away, we used a longer starting distance (this amounted to <2% of all observations). The use of a constant starting distance also prevented any problems of collinearity between starting distance and FID. APM and WL also recorded information on date and time of day, and with binoculars sex and age, if possible, based on plumage characteristics or behavior during copulation or reproduction (Mullarney et al. 2000). FID was estimated as the Euclidian distance, which equals the square-root of the sum of the squared horizontal distance and the squared height above ground level (Blumstein 2006). Repeatability analyses have previously indicated that estimates of FID are consistent across studies (Blumstein 2006; Møller 2008a, 2008b, 2008c), observers (Møller 2008a, 2008b, 2008c; Guay et al. 2013), countries (Møller 2008c), and seasons (Møller 2008c).

The number of FID observations is reported in ESM Table S1 (93 species with 2 to 748 observations, mean [SE] number of observations = 40.3 [9.6]) and Table S2 (12 pairs of species with 4 to 219 observations, mean [SE] number of observations 87.3 [22.4]). All observations of FID were made during the breeding season. APM and WL wearing neutral clothes avoided any effects of pseudo-replication by only observing a single individual of a given sex, age, and species at a given site. Only 1 individual was observed when birds were in a flock to avoid that dependent observations were entered into the same analysis.

We performed 2 separate studies that were performed slightly differently, 1 on common and golden pheasants in Europe and China (these data are reported in Figure 3A and B) and a second study of FID in Europe (ESM Table S1 and ESM Table S2).

Camouflage and FID

For the paired comparison of FID in relation to camouflage with color of the species resembling the color of the natural habitat (Mullarney et al. 2000) we searched for independent observations of camouflage in both sexes and sister taxa without crypsis relying on the phylogeny by Jetz et al. (2012) with the only restriction being that we had information on FID.

In a second test of the relationship between camouflage color and FID, we identified all 93 species for which we had sex-specific FID. All species were classified as having female-specific camouflage

Table 1. OLS regression of mean female FID in relation to presence or absence of camouflage, male FID and the 2-way interaction for different species of birds, and a second analysis excluding 2 extreme values

Term	Sum of squares	df	F	P	Estimate	SE
Intercept				0.036	0.159	0.074
Camouflage	0.76	1	0.87	0.35	0.016	0.017
Male FID	87.70	1	101.01	<0.0001	0.771	0.077
Camouflage × Male FID	5.86	1	6.75	0.011	0.199	0.077
Error	77.27	89				

Term	Sum of squares	df	F	P	Estimate	SE
Intercept				0.256	0.966	0.845
Camouflage	360.22	1	15.81	<0.0001	2.021	0.508
Male FID	6520.16	1	286.09	<0.0001	0.800	0.047
Camouflage × Male FID	514.67	1	22.58	<0.0001	0.225	0.047
Error	77.27	87				

The first model had the statistics $F = 34.98$, $df = 3, 89$, $r^2 = 0.53$, $P < 0.0001$, whereas the second model had the statistics $F = 193.86$, $df = 3, 87$, $r^2 = 0.87$, $P < 0.0001$.

based on whether females of the species had similar color as the background in the habitat in which they live (Mullarney et al. 2000). We tested for the repeatability of this classification for which we had sex-specific FID by asking 2 students to classify the 93 species as having a color that resembled the color of the natural background based on their own field experience without providing the students with further information that could potentially affect the outcome of their classification. One of these students had a classification that differed from ours' but only for 1 species *Phylloscopus collybita*. Hence, we consider the classification to be reliable and repeatable. All data are reported in Electronic Supplementary Material Tables S1–S2.

Statistical analyses

The analyses were made with JMP (SAS 2012). We compared FID among the 3 classes (male, female and juvenile) in the 2 species of pheasants using a Welch ANOVA for unequal variances with a Levene's test for differences in variance.

We compared FID between species with camouflage and sister species without camouflage relying on a paired comparison using a matched-pairs signed-ranks test (Møller and Birkhead 1992). We did not use parametric tests because of the skewed distributions of mean FID.

We subsequently developed a linear model of \log_{10} mean female FID for the different species as a response variable with camouflage or not in females, \log_{10} mean male FID and the interaction between these 2 variables as predictors. We used female rather than male FID as the response variable because sexual dichromatism is often due to loss of bright color in females rather than gain of bright color in males (Dale et al. 2015). The present analysis was weighted by sample size to account for the fact that sample sizes were skewed ranging from 2 to 748 (Garamszegi and Møller 2010, 2011).

Closely related species are more likely to have similar phenotypes because of their shared ancestry, which may result in data points based on species-specific values being statistically dependent by producing more similar residuals from a least squares regression (Felsenstein 2004). A commonly used technique to account for the phylogenetic structure in residuals is the Phylogenetic Generalized Least Squares (PGLS) regression (Grafen 1989). However, the use of PGLS in the absence of phylogenetic signal in residuals is to be avoided because, among other reasons, it can substantially increase the Type I error rate of tests (Revell 2010; Garamszegi 2014). We tested for the presence of

phylogenetic signal in residuals of our comparative model by using Pagel's λ (Pagel 1997, 1999) as implemented using the R package "phytools" (Revell 2012). $\lambda = 0$ indicates an absence of phylogenetic signal in residuals (justifying the use of Ordinary Least Squares [OLS] models), whereas $\lambda = 1$ indicates the strongest phylogenetic signal in residuals (demanding application of phylogenetically informed models, as PGLS) (Symonds and Blomberg 2014). We used the most recent phylogenetic avian hypothesis (Jetz et al. 2012; Electronic Supplementary Material Figure S1).

Results

Camouflage and FID

Mean FID was consistently shorter in all 12 taxa with camouflage than in their matched 12 sister taxa without camouflage (Figure 1; binomial test: $P = 0.00024$; Wilcoxon signed-ranks test, $U = 39$, $P < 0.0005$). This finding was not confounded by differences in body mass which did not differ in the 12 paired observations (paired t -test, $t = 0.41$, $df = 11$, $P = 0.69$).

FID in species with female camouflage color or not

There was no phylogenetic signal in residuals of an OLS model (Pagel's $\lambda \ll 0.001$, $P = 1$), indicating that OLS was an adequate model to be fitted. Female FID increased with male FID, whereas there was no main effect of camouflage on female FID in an OLS regression (Figure 2 and Table 1). There was a significant male FID by camouflage interaction implying that males and females did not differ between species with and without camouflage at short FID, but did so at long FID (Figure 2; Table 1). This model fitted the data as shown by a goodness of fit test ($F = 4.05$, $df = 87, 2$, $P = 0.22$). Exclusion of 2 extreme FID values in Figure 2 did not change the conclusions (Table 1).

Mean FID for species without camouflage after back-transformation of means from the full model was 12.26 m, whereas it was only 8.44 m for species with camouflage, or a reduction by 31.16%.

Pheasants and FID

The variance in FID was much greater in adult males than in adult females or juveniles of either sex (Levene's test: $F = 4.99$, $df = 2, 73$, $P = 0.0093$). There was a significant difference in mean FID among the 3 age and sex classes of common pheasant (Figure 3A; Welch

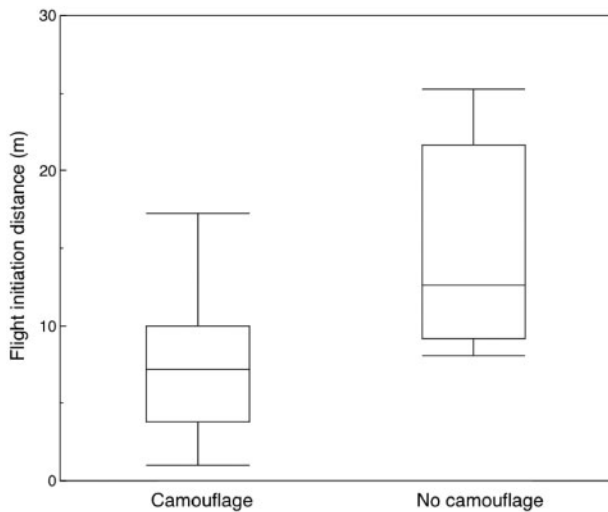


Figure 1. Box plots of FID (m) in bird species with and without camouflage color. The box plots show medians, quartiles, 5- and 95-percentiles and extreme values.

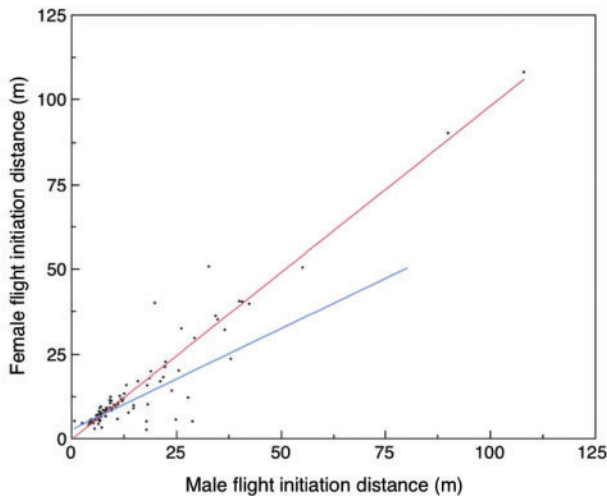


Figure 2. Mean FID (m) in female birds in relation to mean FID (m) in male birds for species without (red line) and with camouflage color (blue line).

ANOVA: $F = 8.52$, $df = 2$, 35.27 , $P = 0.001$). While juveniles of both sexes and adult females had similar short FID, adult males had much longer FID than the 2 other categories (Figure 3A; Tukey post-hoc test).

Likewise, there was a significant difference in FID among the 3 age and sex classes of common pheasant (Figure 3B; Welch ANOVA: $F = 7.94$, $df = 2$, 162.67 , $P = 0.0005$). Adult males had much longer FID than the 2 other categories (Figure 3B). In addition, the variance in FID was much greater in adult males than in adult females or juveniles of either sex (Levene's test: $F = 16.70$, $df = 2$, 436 , $P < 0.0001$).

Discussion

The main findings of this study were that bird species with camouflage had consistently shorter FID than sister taxa without camouflage. Furthermore, female camouflage was related to male FID. Finally, adult males of the common pheasant and the golden

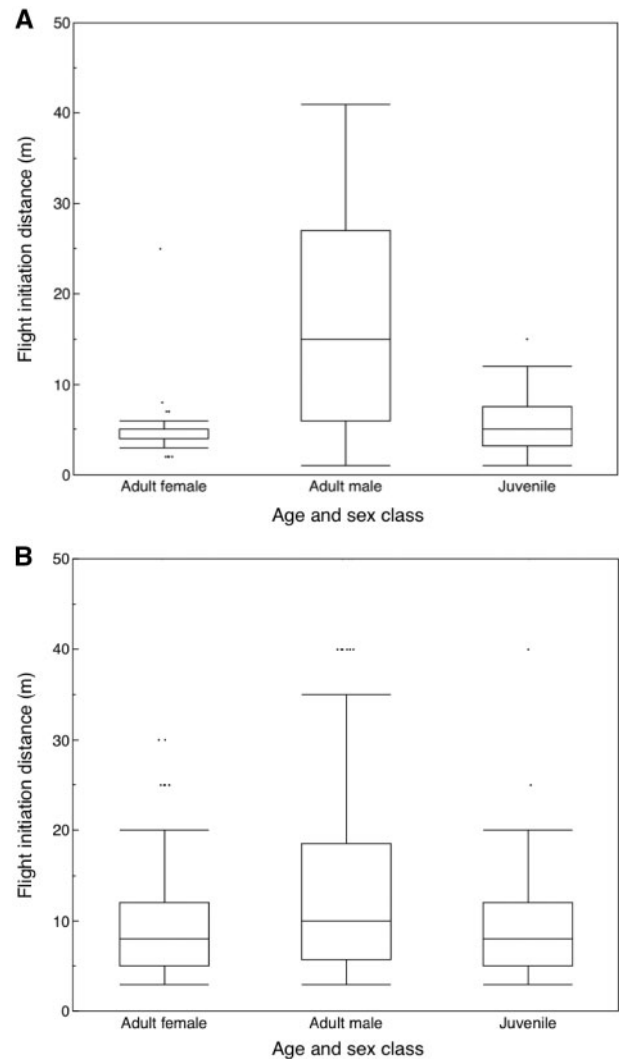


Figure 3. Box plots of FID (m) in adult female, adult male, and juvenile (A) common pheasants and (B) golden pheasants. The box plots show medians, quartiles, 5- and 95-percentiles and extreme values. Sample sizes for common pheasants were 31 adult females, 17 adult males, and 28 juveniles, whereas sample sizes for golden pheasants were 216 adult females, 158 adult males, and 65 juveniles.

pheasant with bright coloration had consistently longer FID than camouflaged adult females and juveniles of either sex. These novel findings are the first to report how camouflage relates to FID.

The evolution of camouflage was emphasized by Wallace (1869, 1889) as a predominant feature of tropical animals resulting in his emphasis on the role of predation as an evolutionary driving force. Trivers (1985) defined camouflage as a deceitful signal, whereas Endler (1991) and Caro (2005) emphasized the diversity of anti-predator signals and mechanisms for understanding the evolution of camouflage. Thus, individuals with cryptic coloration enjoy a survival advantage compared with conspicuous individuals of the same species in the same environment (Cain and Sheppard 1954; Kettlewell 1965; Cuadrado et al. 2001; Cook 2003). The traditional benefit of camouflage is the viability benefit of being hidden against a specific background (Cain and Sheppard 1954; Kettlewell 1965; Cook 2003). Here, we have proposed 2 additional fitness benefits of camouflage: 1) flexible surprise escapes when behavior changes

from immobility to flight, and 2) time and energy savings from reduced frequency of reactions to disturbance by potential predators. First, being hidden against a given background can be flexible as shown by Hemmingsen (1951) demonstrating changes from immobility to flight. More recently, Nishiumi and Mori (2015) showed for frogs that some species may change from immobility to fleeing when approached by a predator. Second, time and energy savings may arise from reduced frequency of reactions to disturbance by potential predators. The underlying fitness benefit of surprise escape is that individuals can remain camouflaged for longer time.

Camouflage may provide time and energy savings from reduced disturbance (Ydenberg and Dill 1986). Studies of urban birds have shown that short FID may confer an advantage in terms of fewer disturbances and hence reduced energy expenditure compared with nearby rural conspecifics (Cooke 1980; Møller 2008a; Glover et al. 2011; Díaz et al. 2013). These benefits vary among latitudes due to differences in abundance and composition of the community of predators (Díaz et al. 2013). In addition, prey may benefit disproportionately from close proximity to humans compared with predators that are known to maintain long FID to human (Møller 2012; Díaz et al. 2013). Here, we hypothesize that species or sex and age classes with camouflage may benefit from reduced time and energy expenditure from predator escape or fewer cases of displacement.

Differential expression of camouflage in adult females and juveniles of either sex implies age- and sex-specific patterns of selection as already noticed by Wallace (1869, 1889), who inferred that sexual dimorphism in plumage was due to exaggeration of the drab female plumage to bright male coloration and/or loss of bright coloration in females. Independent of the causation of these age and sex patterns here we have shown a large difference in FID between ages and sexes. Indeed, adult male common pheasants and golden pheasants, but not adult females or juveniles of either sex have longer and more variable FID. However, that was not the case as shown by the similarity in FID for adult females and juveniles. Males also had much larger variances in FID than females and juveniles combined suggesting that FID in males is a mixture of behavior of individuals with different distances. A remarkable example of the ability to maintain matching with a changing background environment occurs in the willow ptarmigan *Lagopus lagopus* in which individuals with white winter plumage stay in areas covered with snow, whereas changing to habitats at the border between snow and bare ground in spring and summer when their plumage is molted to become partially pigmented (Steen et al. 1992).

We further investigated the relationship between male and female FID in species with and without camouflage. We showed an interaction between camouflage and FID, implying a larger difference in FID between species with and without camouflage at long than at short FID. Journey et al. (2013) showed that birds with bright colors were more responsive to the sound of predators than dull colored species. This implies that individuals of the brightly colored sex have longer FID than individuals of the camouflaged sex, and that individuals of the brightly colored sex run smaller risks in terms of susceptibility to predation (Møller et al. 2006; Møller 2014).

The novel findings on camouflage and FID that we report here have general implications for the coevolution of anti-predator behavior. Endler (1991) showed that different defenses are ordered hierarchically with defenses occurring earlier during the interaction between predators and prey taking priority. This general principle of interspecific interactions also applies to camouflage and FID. Individuals with camouflage more often avoid approach by a

predator altogether whereas conspicuously colored individuals will have to avoid the greater risks of predation by taking flight at a longer distance. This is the pattern that we found in golden and common pheasants, but also among bird species with long FID.

In conclusion, we have shown that FID is related to camouflage of plumage within and among species of birds, and that camouflage may convey a number of benefits in terms of surprise escape and time and energy savings from reduced disturbance.

Acknowledgments

We are grateful to Associate Editor, Dr David Swanson and 2 anonymous referees for their constructive comments. We thank Foping and Kuankuoshui National Nature Reserves for access to field sites in China.

Funding

W.L. was supported by the National Natural Science Foundation of China (Nos 30860044, 31472013, and 31772453). D.S.M.S was supported by Coordenação de Aperfeiçoamento de Pessoal de Ensino Superior.

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>

Conflict of Interest

The authors declare that they have no competing interests.

References

- Blumstein DT, 2006. Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Anim Behav* 71:389–399.
- Cain AJ, Sheppard PM, 1954. Natural selection in *Cepaea*. *Genetics* 39: 89–116.
- Caro T, 2005. *Antipredator Defenses in Birds and Mammals*. Chicago (IL): University of Chicago Press.
- Cook LM, 2003. The rise and fall of the carbonaria form of the peppered moth. *Q Rev Biol* 78:399–417.
- Cooke AS, 1980. Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. *Biol Cons* 18: 85–88.
- Cooper WE Jr, Blumstein DT, 2016. *Escaping from Predators: An Integrative View of Escape Decisions and Refuge Use*. Cambridge: Cambridge University Press.
- Cuadrado M, Martín J, López P, 2001. Camouflage and escape decisions in the common chameleon *Chamaeleo chamaeleon*. *Biol J Linn Soc* 72: 547–554.
- Dale J, Dey CJ, Delhey K, Kempnaers B, Valcu M, 2015. The effects of life history and sexual selection on male and female plumage colouration. *Nature* 527:367.
- Díaz M, Møller AP, Flensted-Jensen E, Grim T, Ibáñez-Álamo JD et al., 2013. The geography of fear: a latitudinal gradient in anti-predator escape distances of birds across Europe. *PLoS ONE* 8:e64634.
- Endler JA, 1991. Interactions between predators and prey. In: Krebs JR, Davies NB, editors. *Behavioural Ecology*. Oxford: Blackwell. 169–196.
- Felsenstein J, 2004. *Inferring Phylogenies*. 1st edn. Sunderland (MA): Sinauer Associates, Inc.
- Garamszegi LZ, 2014. *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice*. New York: Springer.

- Garamszegi LZ, Møller AP, 2010. Effects of sample size and intraspecific variation in phylogenetic comparative studies: a meta-analytic review. *Biol Rev* 85:797–805.
- Garamszegi LZ, Møller AP, 2011. Nonrandom variation in within-species sample size and missing data in phylogenetic comparative studies. *Syst Biol* 60:876–880.
- Glover HK, Weston MA, Maguire GS, Miller KK, Christie BA, 2011. Towards ecologically meaningful and socially acceptable buffers: response distances of shorebirds in Victoria, Australia, to human disturbance. *Landsc Urban Plan* 28:1203–1212.
- Grafen A, 1989. The phylogenetic regression. *Phil Trans R Soc of Lond B* 326: 119–157.
- Guay P-J, McLeod EM, Cross R, Formby AJ, Maldonado SP et al., 2013. Observer effects occur when estimating alert but not flight-initiation distances. *Wildl Res* 40:289–293.
- Hediger H, 1934. Zur biologie und Psychologie der Flucht bei Tieren. *Biol Zblatt* 54:21–40.
- Hemmingsen AM, 1951. The relation of shyness (flushing distance) to body size. *Spolia Zool Mus Hauniensis* 11:74–76.
- Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO, 2012. The global diversity of birds in space and time. *Nature* 491:444–448.
- Journey L, Drury JP, Haymer M, Rose K, Blumstein DT, 2013. Vivid birds respond more to acoustic signals of predators. *Behav Ecol Sociobiol* 67: 1285–1293.
- Kettlewell HBD, 1965. Insect survival and selection for pattern. *Science* 148: 1290–1296.
- Marshall KLA, Gluckman TL, 2015. The evolution of pattern camouflage strategies in waterfowl and game birds. *Ecol Evol* 5:1981–1991.
- Møller AP, 2008a. Flight distance of urban birds, predation and selection for urban life. *Behav Ecol Sociobiol* 63:63–75.
- Møller AP, 2008b. Flight distance and population trends in European breeding birds. *Behav Ecol* 19:1095–1102.
- Møller AP, 2008c. Flight distance and blood parasites in birds. *Behav Ecol* 19: 1305–1313.
- Møller AP, 2012. Urban areas as refuges from predators and flight distance of prey. *Behav Ecol* 23:1030–1035.
- Møller AP, 2014. Life history, predation and flight initiation distance in a migratory bird. *J Evol Biol* 27:1105–1113.
- Møller AP, Birkhead TR, 1992. A pairwise comparative method as illustrated by copulation frequency in birds. *Am Nat* 139:644–656.
- Møller AP, Nielsen JT, Garamszegi LZ, 2006. Risk taking by singing males. *Behav Ecol* 19:41–53.
- Mullarney T, Svensson L, Zetterström D, Grant PJ, 2000. *The Complete Guide to the Birds of Europe*. London: Harper Collins.
- Nishiumi N, Mori A, 2015. Distance-dependent switching of anti-predator behavior of frogs from immobility to fleeing. *J Ethol* 33:117–124.
- Pagel M, 1997. Inferring evolutionary processes from phylogenies. *Zool Scripta* 26:331–348.
- Pagel M, 1999. Inferring the historical patterns of biological evolution. *Nature* 401:877–884.
- Revell LJ, 2010. Phylogenetic signal and linear regression on species data. *Methods Ecol Evol* 1:319–329.
- Revell LJ, 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol Evol* 3:217–223.
- Samia DSM, Blumstein DT, Stankowich T, Cooper WE, 2015. Fifty years of chasing lizards: new insights advance optimal escape theory. *Biol Rev* 91: 349–366.
- SAS Institute Inc, 2012. *JMP Version 10.0*. Cary (NC): SAS Institute Inc.
- Steen JB, Erikstad KE, Hoidal K, 1992. Cryptic behaviour in moulting hen willow ptarmigan *Lagopus lagopus* during snow melt. *Ornis Scand* 23:101–104.
- Stevens M, Merilaita S, 2011. *Animal Camouflage: Mechanisms and Function*. Cambridge: Cambridge University Press.
- Symonds MRE, Blomberg SP, 2014. A primer on phylogenetic generalised least squares. In: Garamszegi LZ editor. *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice*. New York: Springer. 105–130.
- Trivers RL, 1985. *Social Evolution*. Menlo Park (CA): Benjamin Cummins.
- Troscianko J, Wilson-Aggarwal J, Stevens M, Spottiswoode CN, 2016. Camouflage predicts survival in ground-nesting birds. *Sci Rep* 6:19966.
- Wallace AR, 1869. *The Malay Archipelago*. London: Macmillan.
- Wallace AR, 1889. *Darwinism*. London: Macmillan.
- Weston MA, McLeod EM, Blumstein DT, Guay P-J, 2012. A review of flight-initiation distances and their application to managing disturbance to Australian birds. *Emu* 112:269–286.
- Ydenberg RC, Dill LM, 1986. The economics of fleeing from predators. *Adv Study Behav* 16:229–247.