

Original Article

Sexual signals, risk of predation and escape behavior

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Adults of many species display extravagant sexual signals during the reproductive season, apparently evolved as a means of attracting mates or repelling potential competitors, thereby inadvertently also attracting the attention of predators. Many studies have shown predation costs of sexual display. Therefore, we should expect species with the most exaggerated signals to have evolved antipredator behavior that reduces or eliminates predation costs of sexual signaling but also to have evolved behavior that allows for escape from a predator once captured. We quantified 6 aspects of escape behavior in 2105 free-living birds belonging to 80 species when handled after capture for banding. Escape behavior was species specific as demonstrated by significant consistency in behavior among individuals. Escape behavior was significantly related to susceptibility to predation by cats *Felis catus* and goshawks *Accipiter gentilis*, showing that escape behavior is under current selection. Escape behavior was related to the ease of feather loss estimated in a previous study but also to the frequency of tailless individuals recorded in the field. Thus, escape behavior reported here was cross-validated against other aspects of antipredator behavior shown to reflect risk of predation. Aspects of escape behavior differed significantly between males and females (biting, fear screams, and feather loss). Sexually dichromatic species differed in escape behavior from monochromatic species by having a reduced frequency of fear screams and increased tonic immobility. These findings suggest that exposure to risk of predation has modified escape behavior in relation to sexual coloration. **Key words:** alarm calls, escape behavior, fear scream, predation, sex, signaling, tonic immobility. [*Behav Ecol* 22:800–807 (2011)]

INTRODUCTION

Sexual signals have evolved to attract the attention of male and female conspecifics but also as an unintended side effect attract the attention of predators and parasites (Andersson 1994; Zuk and Kolluru 1998). In contrast, there is no evidence that conspicuous color has evolved in birds to display to predators (Darwin 1871; Andersson 1994). Predators often show strong male bias in prey with males outnumbering females to a significant extent (Cade 1960; Lindberg 1983). Many studies have shown that predation significantly has affected the expression of secondary sexual characters. For example, local adaptation in guppies *Poecilia reticulata* reduces risk of predation associated with conspicuous sexual coloration (Endler 1983, 1986). Indeed, the risk of predation due to display of conspicuous sexual signals may be reduced by defenses or restriction of signaling to specific times, places, or contexts (Burk 1982; Magnhagen 1991; Møller, Nielsen, and Erritzøe 2006).

Conspicuous sexual signals are common in males, and males and females are often behaviorally and ecologically different (Andersson 1994). Conspicuous signals can increase the likelihood of predation. It may be that sexually dichromatic species have evolved different antipredator behaviors in the face of such increased predation risk and that males and females may also differ in antipredator behavior. Although there are many examples of sexual display showing evolutionary modifica-

tions by predation (review in Zuk and Kolluru 1998), we are unaware of antipredator behavior having been modified to reflect the different risks of predation of individuals and species with and without extravagant sexual displays. Thus, is it the case that antipredator behavior has evolved to reduce the costs of sexual display?

A special category of antipredator behavior is the behavior that allows an already captured individual to escape. Indeed, “adaptation unto death” occurs as a consequence of prey struggling to escape a predator even after actual capture (Högestedt 1983; Møller and Nielsen 2010). Such behavior will only evolve if there is a nonnegligible probability of evasion. Indeed, tail autotomy in lizards (Edmunds 1974; Vitt et al. 1977; Cooper et al. 2004), feather loss in captured birds (Møller, Nielsen, and Erritzøe 2006), and fear screams by captured animals that attract the attention of secondary predators (Högestedt 1983; Møller and Nielsen 2010) all constitute such escape behavior by potential prey that allow a significant number of individual to survive successful capture by a predator.

The objectives of this study were to test 1) whether escape behavior was related to susceptibility to 2 common predators (cat *Felis catus* and goshawk *Accipiter gentilis*), 2) to which extent the sexes differ in antipredator behavior once captured, and 3) to test if species that are sexually dichromatic differ in antipredator behavior from sexually monochromatic species. For the first hypothesis, we explicitly tested how escape behavior related to an index of susceptibility to predation by 2 common predators (Møller and Nielsen 2007; Møller et al. 2010), thereby providing crucial information about the link between behavior by potential prey and actual risk of predation. Thus, we expected escape behavior to be more exaggerated in species that are more susceptible to predation. Second, comparative analyses of escape behavior assume that behavior differs among species

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because if individuals do not differ consistently in behavior among species, there is no variation to explain. Thus, we tested this assumption by comparing escape behavior of individuals within and among species. We also tested the assumption that escape behavior reliably reflects behavior related to risk of predation. To this end, we related interspecific differences in escape behavior to interspecific differences in ease of feather loss and the fraction of tailless individuals in nature that by definition must reflect successful escape from previous capture by a predator (Møller, Nielsen, and Erritzøe 2006). Thus, we assumed that escape behavior would correlate with ease of feather loss and the fraction of tailless individuals. We also tested if sexes differed in escape behavior, using a nested design to ensure that comparisons of escape behavior were made between sexes within species, with the prediction that males should suffer more from predation and hence show more extreme escape behavior than females because males are generally more conspicuously colored. For the third hypothesis, we used mean estimates of escape behavior of 80 species of birds in relation to sexual dichromatism because previous studies have shown a positive relationship between sexual dichromatism and risk of predation, even when controlling statistically for potentially confounding variables such as body mass, abundance, and habitat (Huhta et al. 2003; Møller and Nielsen 2006; Møller, Nielsen, Garamszegi 2006). Therefore, we predicted that sexually dichromatic species should have more extreme escape behavior than monochromatic species.

MATERIALS AND METHODS

Study sites

We studied the behavior of adult birds during capture for bird banding in connection with bird monitoring schemes in Denmark, Sweden, and Ukraine during 2008–2010. Breeding birds were studied in Northern Jutland, Denmark and Chernobyl, Ukraine, while birds were studied during migration in Northern Jutland, Denmark and at Ottenby Bird Observatory, Sweden, whereas birds are captured annually during the main migration periods March–June and August–October. Birds were either captured in mist nets or large funnel traps, measured and weighed, and finally scored for 6 aspects of escape behavior as explained in detail below. Birds captured in Ukraine had escape behavior that was only weakly related to background radiation level in statistical models that also included species as a factor, accounting for at most 1% of the variance ($F < 5.94$, degrees of freedom [df] = 1.491, $r^2 < 0.011$, $P > 0.015$). Inclusion of background radiation level in the models presented here did not change any of the conclusions (results not shown). In total, we investigated 2105 individuals belonging to 80 species. Two observers made all measurements, and the first observer carefully instructed the second observer before recording any behavior. The study was not conducted in order to study sexual dichromatism, so it is unlikely that there was any bias in measurements.

All breeding individuals at the 3 study sites were sexed (and aged if possible) using Svensson (2006) as a source, with the structure of the brood patch being the most important sexing criterion in monochromatic species. For all migrating (i.e., non-breeding) individuals at the bird ringing station in Sweden, we were only able to sex the sexually dichromatic species, whereas the sexually monochromatic species were left unsexed. However, these latter individuals were “still” included in the final analyses comparing the behavior of sexually monochromatic and dichromatic species.

Behavioral variables

When we captured a bird, we recorded 6 aspects of escape behavior in the order listed below:

Wriggle score

We scored how much the bird struggled while being held in a hand (a score of 0—no movement, 1—moves rarely, 2—moves regularly, but not always, 3—moves continuously). We considered this variable a measure of the attempt to wriggle loose from a predator, although we are unaware of any previous use of this measure. However, we note that some birds manage to wriggle loose and escape even from trained bird banders, showing the efficiency of this form of escape behavior.

Biting

We held our right hand index finger in front of the beak and gave a score of 0, if the bird did not bite, and 1 if it did. We assumed that a bird biting more frequently or harder would enjoy an elevated probability of escape although that has so far not been tested.

Feather loss

Whether the bird lost feathers (a score of 1) or not (a score of 0) while handled. Møller et al. (2006a) showed that feather loss was significantly related to susceptibility to predation.

Distress call

Whether the bird while handled gave a distress call or fear scream (a score of 1) or not (a score of 0). Högstedt (1983) and Møller et al. (2010) described how loud fear screams attracted the attention of secondary predators and significantly increased the probability of escape once captured by a predator. Distress calls differ from alarm calls in terms of loudness, structure, and function (see Högstedt (1983) for an extensive description).

Tonic immobility

Just before the bird was released, we placed it with our right hand on its back on our flat left hand. When the bird was lying still, we removed the right hand and recorded time until the bird righted itself and flew away. We allowed tonic immobility up to 30 s, and if the bird had not left yet, we terminated the trial. This is a standard measure of fear in poultry research with both environmental and genetic components (Hoagland 1928; Jones 1986; Boissy 1995; Forkman et al. 2007). The longer time a bird stays, the higher its level of fear. Tonic immobility has a strongly bimodal distribution, with most individuals having tonic immobility of 0–5 s, but some 10–20% having 25–30+ s as shown in the present study.

Alarm call

Whether the bird gave an alarm call, when departing from our hand (a score of 1) or not (a score of 0). Birds and mammals give alarm calls in the proximity of a predator, and their function has been hypothesized to be distraction of the predator or a warning signal for kin, mates, or heterospecifics (Marler 1955; Charnov and Krebs 1975; Platzen and Magrath 2004).

Residual force required to remove feathers from the rump and frequency of tailless individuals

Birds that are susceptible to predation lose feathers when attacked by a predator, especially from the rump. Thus, the ease of feather loss from the rump is greater than from the back, which is greater than from the breast, and this is more so for species that are disproportionately often attacked by predators. We used information reported in Møller, Nielsen, and Erritzøe (2006) on the residual force required to remove feathers from the rump relative to the back. Birds without tails have been attacked but successfully managed to escape from a predator. Thus, the frequency of tailless individuals represents an estimate of the frequency of successful escape from predation. Møller, Nielsen, and Erritzøe (2006) reported the

frequency of tailless individuals in different species of birds. Both these variables are significantly related to susceptibility to predation (Møller, Nielsen, and Erritzøe 2006).

Sexual dichromatism

We scored prey species as sexually monochromatic or dichromatic, using a dichotomous classification based on human categorization of plumage coloration in field guides. Species were considered to be monochromatic, and given a score of zero, if all males and females could not be reliably distinguished based on plumage characters according to field guides (e.g., Mullaney et al. 2000; Svensson 2006). Any sex difference in plumage coloration that reliably allowed all individuals to be correctly sexed independently of its magnitude was considered to represent sexual dichromatism, which was scored as 1. For example, blue tits *Parus caeruleus*, that can be reliably sexed based on the intensity of the blue coloration of the crown, were scored as dichromatic, whereas coal tits *Parus ater*, that cannot be sexed based on plumage characters, were scored as monochromatic. We did not attempt to quantify the magnitude of the sex difference in coloration because we do not know how predators perceive such differences. However, our dichotomous score was strongly positively correlated with quantitative scores from Møller and Birkhead (1994) and Read (1987), suggesting that both dichotomous and continuous scores provide similar information. Finally, we did not consider plumage brightness of males or females because apparent brightness to a human may be completely cryptic depending on the environment. Because both males and females by definition live in the same environment during reproduction, any difference in plumage brightness between the sexes (i.e., sexual dichromatism) is likely to reflect a difference in coloration between the sexes independent of the environment.

We did not consider ultraviolet (UV) coloration in the present study although avian predators are fully capable of seeing signals in the UV part of the spectrum (Viitala et al. 1995). Previous studies using dichotomous scores of sexual dichromatism have shown predicted relationships (e.g., Møller and Birkhead 1994), and sexual dichromatism is strongly positively related to measures of coloration derived from models based on avian vision (e.g., Armenta et al. 2008; Seddon et al. 2010). We are aware of the potential weaknesses of our approach, although we consider that there is little evidence of human visual scores distorting categorization of sexual dichromatism. We report all data making the study available for reanalysis in the future if other or better methods become available.

Susceptibility to cat and goshawk predation

We estimated susceptibility to predation by cats and goshawks on a logarithmic scale expressed as log-transformed observed number of prey minus log-transformed expected number of prey according to estimated of breeding density assessed using standardized point counts during the breeding season in Northern Denmark (Grell 1998; Møller et al. 2010). Thus, a susceptibility index of 0 implies that prey are consumed according to expectation from their abundance, an index of +1 implies that a given prey species is consumed 10 times more often than expected, and an index of -1 implies that a given prey species is consumed 10 times less often than expected from its abundance. We have previously described these estimates and their reliability in detail elsewhere (e.g., Møller and Nielsen 2007; Møller et al. 2010).

Body mass

We recorded body mass using Pesola spring balances.

Summary statistics for all variables are reported in Supplementary Material 1.

Statistical analyses

We tested for an effect of trapping method on behavioral variables but found no significant effects, so this variable was not considered further in the analyses. We developed best-fit statistical models by reducing full models until the final model only contained factors with an associated $P < 0.10$ (Sokal and Rohlf 1996). To assess possible problems of collinearity, we calculated variance inflation factors that in all cases were less than 3, which is much less than the commonly accepted levels for significant collinearity of 5–10 (McClave and Sincich 2003).

Closely related species may have more similar behavior than species that are more distantly related due to shared ecology rather than common phylogenetic descent (Harvey and Pagel 1991). We controlled for similarity in phenotype among species due to common phylogenetic descent by calculating standardized independent linear contrasts (Felsenstein 1985), using CAIC (Purvis and Rambaut 1995). We tested the statistical and evolutionary assumptions of the continuous comparative procedure (Garland et al. 1992) by regressing absolute standardized contrasts against their standard deviations. In order to reduce the consequent problem of heterogeneity of variance, 1) outliers (contrasts with Studentized residuals > 3) were excluded from subsequent analyses (Jones and Purvis 1997) and 2) analyses were repeated with the independent variable expressed in ranks. In neither case, did these new analyses change any of the conclusions. Thus, we report the analyses based on all independent contrasts.

The composite phylogeny used in the analyses was modified from Davis (2008) (Supplementary Material 2). Because information for the composite phylogeny came from different sources using different methods, consistent estimates of branch lengths were unavailable. Therefore, branch lengths were transformed assuming a gradual model of evolution with branch lengths being proportional to the number of species contained within a clade. Results based on these branch lengths were compared with those obtained using constant branch lengths (a punctuated model of evolution). Finally, we used a standard bird taxonomy (Howard and Moore 1991) to test for consistency in findings independent of phylogenetic hypothesis. Nowhere were the results qualitatively different (results not shown).

Regressions based on contrasts were forced through the origin because the comparative analysis assumes that there has been no evolutionary change in a response “variable” when the predictor variable has not changed (Purvis and Rambaut 1995). That is, for $x = 0$, $y = 0$ due to any effects of x , although obviously other factors may influence the value of y .

A common underlying assumption of most statistical analyses is that data points provide equally precise information about the deterministic part of total process variation, i.e., the standard deviation of the error term is constant over all values of the predictor variable(s) (Sokal and Rohlf 1995). The standard solution to violations of this assumption is to weight each observation by sampling effort in order to use all data, giving each datum a weight that reflects its degree of precision due to sampling effort (Draper and Smith 1981; Neter et al. 1996; Garamszegi and Møller 2010). Comparative analyses (just as any other analysis) may be confounded by sample size if sampling effort is important, and if sample size varies considerably among taxa (Garamszegi and Møller 2010). Therefore, we weighted statistical models by sample size. In order to weight models by sample size in the analysis of contrasts, we calculated weights for each contrast by calculating the mean sample size for the taxa immediately subtended by that node (Møller and Nielsen 2007).

We evaluated the magnitude of associations between escape behavior and predictor variables based on effect sizes using Cohen's (1988) criteria for small (Pearson $r = 0.10$, explaining 1% of the variance), intermediate (Pearson $r = 0.30$, 9% of the variance) and large effects (Pearson $r = 0.50$, 25% of the variance).

Results

Susceptibility to predation and escape behavior

The 6 aspects of escape behavior were only weakly correlated with each other, with maximum correlations being between wriggle and fear scream (Pearson $r = 0.40$, $t = 3.67$, $df = 75$, $P < 0.001$), feather loss and fear scream ($r = 0.32$, $t = 2.87$, $df = 75$, $P < 0.001$) and biting and fear scream ($r = 0.23$, $t = 2.03$, $df = 75$, $P < 0.05$). These effects are so small that problems of collinearity are not a cause of concern.

Susceptibility to goshawk predation was only weakly positively correlated with susceptibility to cat predation ($F = 2.70$, $df = 1, 34$, $r^2 = 0.07$, $P = 0.11$). Susceptibility to goshawk predation was explained by escape behavior, accounting for 87% of the variance (Table 1). Susceptibility increased with intensity of wriggle behavior and duration of tonic immobility (Table 1).

Escape behavior accounted for 66% of the variance in susceptibility to cat predation (Table 1). Again, the only 2 factors accounting for significant variation were intensity of wriggle behavior and duration of tonic immobility (Table 1).

Species-specific component of escape behavior

Escape behavior varied significantly among species, with the amount of variance ranging from 12% for tonic immobility to 59% for biting (Table 2).

Testing if escape behavior is related to predation

In a first analysis of predictors of residual force required to remove feathers from the rump in different species of birds, 4 of 6 escape behaviors explained significant variation, with an

Table 1

Susceptibility to goshawk and cat predation in relation to escape behavior and body mass and body mass squared of prey

Variable	Sum of squares	df	F	P	Slope (SE)
Goshawk predation					
Wriggle	83.64	1	9.36	0.0057	1.88 (0.61)
Biting	0.24	1	0.03	0.87	-0.07 (0.42)
Fear scream	3.25	1	0.36	0.55	0.54 (0.89)
Feather loss	29.64	1	3.32	0.082	-1.60 (0.88)
Tonic immobility	86.16	1	9.64	0.0052	2.08 (0.67)
Alarm call	7.67	1	0.86	0.36	0.40 (0.43)
Error	196.53	22			
Cat predation					
Wriggle	226.20	1	18.72	0.0002	1.94 (0.45)
Biting	3.25	1	0.27	0.61	0.23 (0.44)
Fear scream	20.88	1	1.73	0.20	-1.38 (1.05)
Feather loss	2.39	1	0.20	0.66	-0.52 (1.16)
Tonic immobility	91.80	1	7.60	0.011	1.70 (0.62)
Alarm call	5.74	1	0.48	0.50	0.34 (0.49)
Error	314.20	26			

The 2 models had the statistics $F = 18.25$, $df = 8, 22$, $r^2 = 0.87$, $P < 0.0001$ and $F = 6.40$, $df = 8, 26$, $r^2 = 0.66$, $P < 0.0001$.

Table 2

Variation in escape behavior of individual birds among species

Variable	Sum of squares	df	F	r^2	P
Wriggle	175.491	77	4.60	0.15	<0.0001
Error	993.178	2005			
Biting	263.204	77	37.20	0.59	<0.0001
Error	184.253	2005			
Fear scream	55.444	77	9.83	0.27	<0.0001
Error	146.818	2005			
Feather loss	78.685	77	16.19	0.38	<0.0001
Error	126.535	2005			
Alarm	80.83	77	8.23	0.24	<0.0001
Error	255.680	2005			
Tonic immobility	94.092	77	3.69	0.12	<0.0001
Error	663.148	2005			

additional marginal effect of body mass (Table 3). We predicted a priori that it would be easier to remove feathers when feather loss was common, when fear screams were common, when individuals gave alarm calls when released, and when tonic immobility only lasted a short time, as we found (Table 3). The fraction of individuals emitting fear screams and the duration of tonic immobility were most strongly related to residual force required to remove feathers from the rump (Figure 1). Effect sizes for the different kinds of behavior were intermediate to strong accounting for 15% to 29% of the variance (based on F -statistics in Table 3).

In a second analysis, the fraction of tailless individuals was positively related to the frequency of feather loss during handling for capture but not significantly to any of the other escape behavior variables, with a marginal effect of body mass (Table 4; Figure 2). The effect was strong accounting for 40% of the variance.

Escape behavior of males and females

Nested analyses showed significant sex differences in behavior for biting with more females biting than males, males giving fear screams less often than females, and males losing feathers more often than females (Table 5). Effect size was 0.21, 0.24, and 0.23, respectively, implying intermediate effects. In contrast, there were no significant differences between sexes for wriggle behavior, alarm calls, and tonic immobility (Table 5).

Table 3

Residual force required for removal of feathers from the rump in relation to escape behavior and body mass in different species of birds

Variable	Sum of squares	df	F	P	Slope (SE)
Feather loss	0.376	1	5.45	0.026	-0.135 (0.058)
Fear scream	0.882	1	12.79	0.0011	-0.185 (0.052)
Alarm call	0.380	1	5.50	0.025	-0.080 (0.034)
Tonic immobility	0.839	1	12.16	0.0014	0.155 (0.045)
Body mass	0.226	1	3.28	0.08	0.073 (0.040)
Error	2.208	32			

The model had the statistics $F = 11.34$, $df = 5, 32$, $r^2 = 0.64$, $P < 0.0001$.

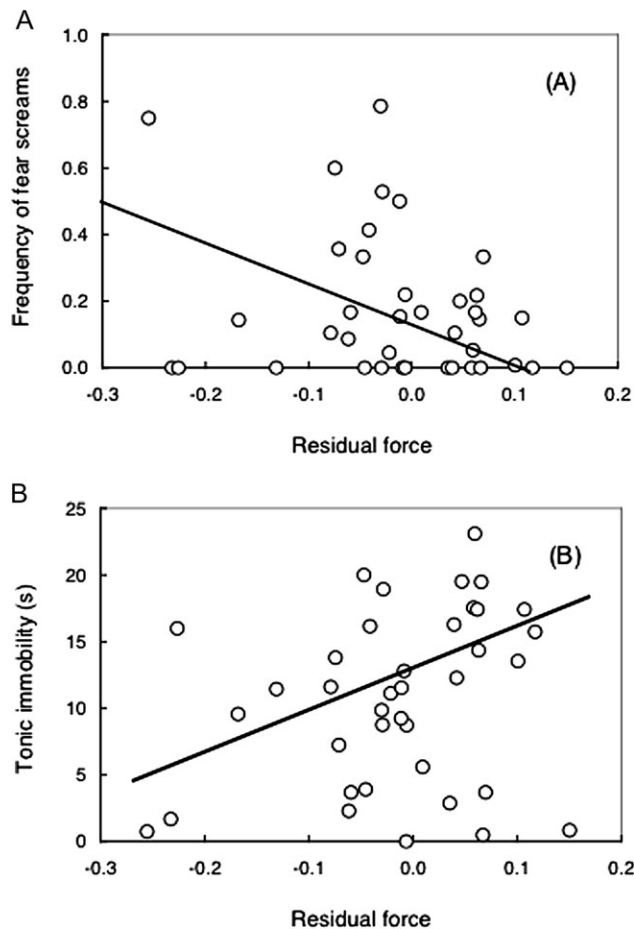


Figure 1
(A) Fraction of individuals giving fear screams and (B) tonic immobility (s) in relation to residual force required to remove feathers from the rump in different species of birds. The lines are the linear regression lines.

Escape behavior and sexual dichromatism

Sexual dichromatism was significantly related to escape behavior (Table 6; Figure 3). Phylogenetic analysis revealed that significantly fewer individuals gave fear screams in dichromatic species and the duration of tonic immobility was longer in dichromatic than in monochromatic species (Table 6). For the other 4 kinds of behavior, the differences between sexes for the species-specific analyses were not upheld in phylogenetic analyses because similarity among species was due to common phylogenetic descent rather than convergent evolution.

Discussion

We quantified 6 aspects of escape behavior in free-living birds when handled after capture for banding. Escape behavior ex-

Table 4
Fraction of tailless individuals in different species of birds in relation to feather loss during capture and body mass

Variable	Sum of squares	df	F	P	Slope (SE)
Feather loss	0.000012	1	9.41	0.0084	0.0040 (0.0013)
Body mass	0.000005	1	4.21	0.059	-0.0018 (0.0009)
Error	0.000031	14			

The model had the statistics $F = 5.12$, $df = 2, 14$, $r^2 = 0.42$, $P = 0.022$.

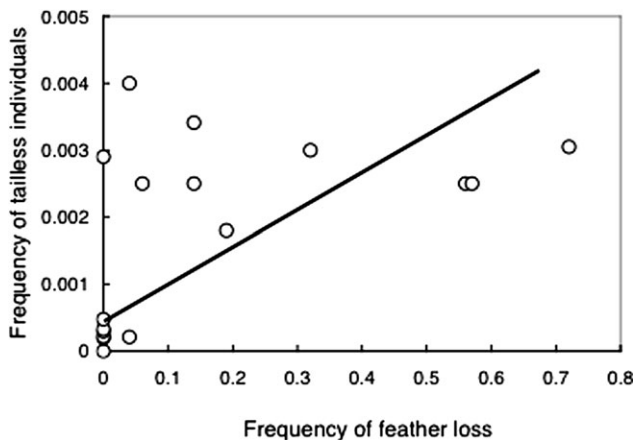


Figure 2
Fraction of tailless individuals in relation to fraction of individuals with feather loss in different species of birds. The lines are the linear regression lines.

plained significant variation in susceptibility to 2 common predators of birds, the cat and the goshawk. Escape behavior was species-specific providing evidence for the assumption that individuals belonging to different species have evolved specific kinds of escape behavior, apparently as an adaptation to interspecific differences in predation risk. Escape behavior was related to 2 previously identified behavioral responses to capture by a predator, the ease of feather loss and the frequency of tailless individuals recorded in the field (Møller, Nielsen, and Erritzøe 2006). Aspects of escape behavior differed significantly between males and females (biting, fear screams, and feather loss). Sexually dichromatic species differed in escape behavior from monochromatic species by less often emitting fear screams and having higher tonic immobility. These findings suggest that sex and sexual signaling are related to escape behavior, and by inference that exposure to risk of predation has shaped antiescape behavior in relation to sexual coloration.

We recorded escape behavior in a standardized way under the assumption that this would reflect important aspects of behavior concerning the ability of captured birds to successfully evade predators once captured. Individuals belonging to bird species that were particularly susceptible to 2 common predators wriggled more intensely and showed longer duration of tonic immobility when captured by a human. Therefore, we can conclude that escape behavior when birds are handled by a human reliably reflects predation risk. We tested this assumption by relating escape behavior to 2 other measures of prey behavior during capture: the ease of feather loss as reflected by how easy it is to remove feathers from the rump relative to the back (Møller, Nielsen, and Erritzøe 2006) and the fraction of tailless individuals observed in the field, individuals that apparently successfully have avoided death when captured by a predator (Møller, Nielsen, and Erritzøe 2006). Residual force required to remove feathers from the rump relative to the back provides an estimate of the force that a prey individual would need for its feathers to loosen from the grip of a predator (Møller, Nielsen, and Erritzøe 2006). A weak force implies that feathers are easily lost and that individuals of such a species have evolved elevated escape ability from predators (Møller, Nielsen, and Erritzøe 2006). Indeed, this measure has previously been shown to be related to susceptibility to predation by the sparrowhawk *Accipiter nisus*. Likewise, Møller, Nielsen, and Erritzøe (2006) showed that the frequency of tailless individuals, that thus must have

Table 5
Nested analyses of variance of the relationship between escape behavior and sex

Variable	Sum of squares	df	F	P	Male mean (SE)	Female mean (SE)
Wriggle	0.82	45, 1564	0.82	0.80	0.925 (0.095)	0.971 (0.086)
Biting	6.96	45, 1564	1.72	0.0022	0.403 (0.065)	0.437 (0.067)
Fear scream	5.95	45, 1564	2.07	< 0.0001	0.169 (0.040)	0.205 (0.040)
Feather loss	5.28	45, 1564	2.03	< 0.0001	0.141 (0.038)	0.099 (0.024)
Alarm	3.31	45, 1564	0.63	0.98	0.182 (0.043)	0.168 (0.043)
Tonic immobility	18.45	45, 1564	1.31	0.084	0.868 (0.068)	0.866 (0.072)

survived a capture attempt by a predator, was inversely related to the force required to remove feathers from the rump. Here, we extended such cross validations by showing that residual force required to remove feathers from the rump was less when the fraction of individuals with any feather loss during capture was high, when the fraction of individuals emitting fear screams and alarm calls was high, and when the duration of tonic immobility was short. Tonic immobility provides a behavioral measure of fearfulness commonly used in poultry studies (Hoagland 1928; Jones 1986; Boissy 1995; Forkman et al. 2007). The simplest interpretation of the results for tonic immobility is that when there is a high probability of escape from a predator once an individual has been captured, prey attempt to escape immediately by showing little hesitation. Thus, fearfulness can be considered a behavior under selection by predators. The second test based on the fraction of tailless individuals showed that when tailless individuals were common, a large fraction of individuals lost feathers when handled during capture. These findings suggest that different aspects of escape behavior are coherent, and that they contain biologically meaningful information.

The sexes differed in escape behavior with respect to the frequency of biting, fear screams, and feather loss. If males attracted more attention from predators because of their sexual signals, we should expect males more often to fall prey to predators, as actually observed (e.g., Cade 1960; Lindberg 1983; Nielsen 2004). Therefore, we should also expect males to show more exaggerated escape behavior than females. Alternatively, females play a greater role in parental care in dichromatic than in monochromatic species (e.g., Verner and Wilson 1969), and this may have increased escape behavior in females over that of males. Consistent with this suggestion, comparative analyses of birds have shown that sex differences in both parental care and sexual dichromatism are associated with sex differences in survival prospects (Liker and Székely 2005). Here, we found that males showed a lower frequency of biting and less often emitted fear screams than females but showed a higher frequency of feather loss. There was no sig-

nificant sex effect for the 3 other kinds of behavior showing that all aspects of escape behavior did not evolve in unison. The function of fear screams has been hypothesized to be attraction of a secondary predator that potentially could allow escape by the captured individual (Högestedt 1983; Møller and Nielsen 2010), attraction of conspecifics including close kin or reciprocating individuals that could interfere with and hence disrupt a predation attempt (Rohwer et al. 1976; Møller and Nielsen 2010), or warning kin of predation (Perrone 1980). Observations of predation attempts and comparative analyses have provided evidence for successful escape due to interference by a kleptoparasitic predator or conspecifics (Högestedt 1983; Møller and Nielsen 2010). In addition, kin may play a role in the evolution of fear screams because fear screams are more common when co-occurring individuals share more genes (Møller and Nielsen 2010). The fact that males show a lower frequency of fear screams at first seems inconsistent with kin-based hypotheses because males generally disperse less than females (Greenwood 1980). However, a higher certainty of maternity than paternity would render fear screams more important to kin of a captured female than a captured male. Feather loss can be considered an escape response that allows captured individuals to evade a predator (Møller, Nielsen, and Erritzøe 2006). Thus, a higher frequency of feather loss in males would imply an evolved ability to better escape predator attacks than females. Møller, Nielsen, and Erritzøe (2006) have previously shown that feather loss and fear screams are positively correlated among species.

Sexual dichromatism was significantly related to escape behavior with fewer individuals giving fear screams and tonic immobility lasting longer in dichromatic than in monochromatic species. We used a dichotomous score of sexual dichromatism because this score predicts probability of extrapair paternity (Møller and Birkhead 1994) and susceptibility to predation (Huhta et al. 2003; Møller and Nielsen 2006; Møller, Nielsen, and Garamszegi 2006), although such sexual signals may be more sensitive to the UV-tuned visual system of conspecific

Table 6
Sexual dichromatism in birds in relation to escape behavior

Variable	df	Wald χ^2	P	Slope (SE)	F	P	Slope (SE)
Wriggle	1	79.52	0.0001	2.241 (0.251)	1.13	0.29	0.159 (0.150)
Biting	1	148.01	0.0001	-4.527 (0.372)	1.37	0.25	0.272 (0.232)
Feather loss	1	43.72	0.0001	3.146 (0.476)	1.75	0.19	0.405 (0.307)
Fear scream	1	84.24	0.0001	6.996 (0.762)	16.62	<0.0001	-1.290 (0.316)
Alarm call	1	29.98	0.0001	-2.243 (0.410)	2.56	0.16	0.363 (0.255)
Tonic immobility	1	24.57	0.0001	-2.309 (0.466)	20.00	<0.0001	0.037 (0.008)

The logistic model had the statistics $\chi^2 = 543.91$, $df = 6$, $r^2 = 0.27$, $P < 0.0001$, whereas the phylogenetic model had the statistics $F = 6.66$, $df = 6, 73$, $r^2 = 0.08$, $P < 0.0001$.

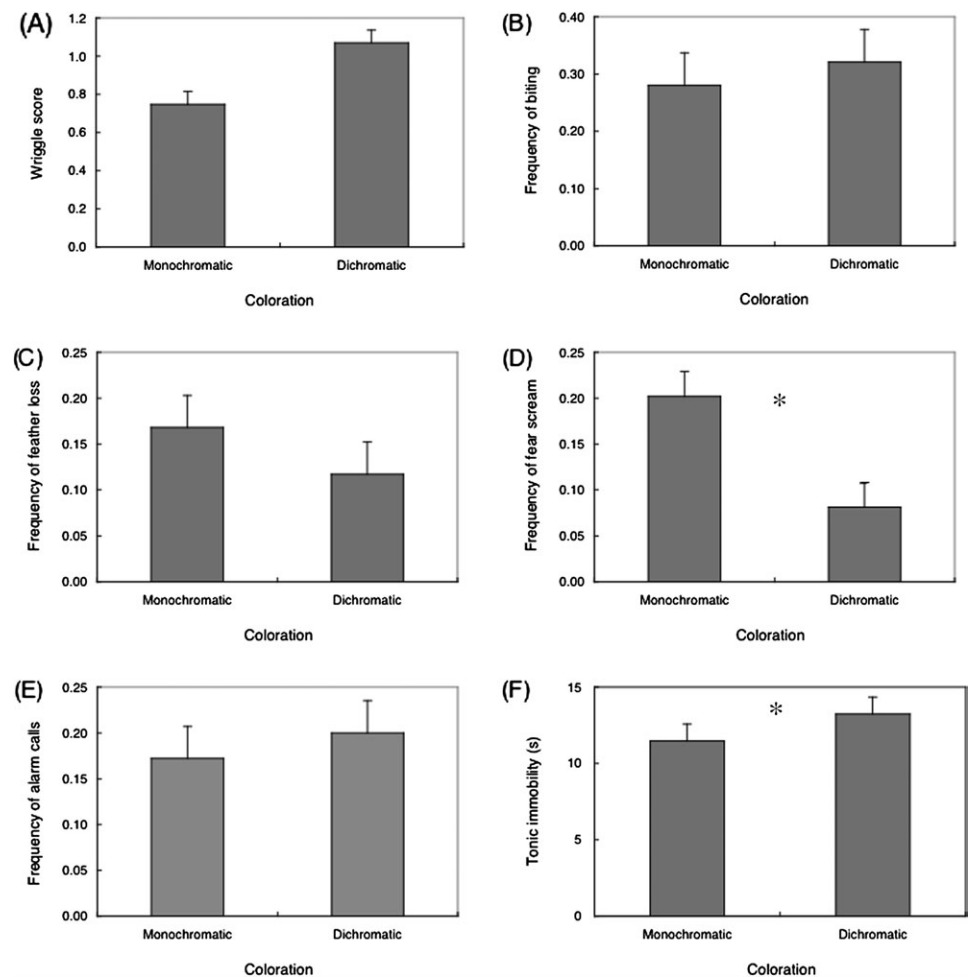


Figure 3

(A) Wriggle score, (B) fractions of individuals biting, (C) fractions of individuals having feather loss, (D) fractions of individuals emitting fear screams, (E) fractions of individuals giving alarm calls, and (F) duration of tonic immobility (s) in sexually monochromatic and dichromatic species of birds. *Indicates statistically significant differences. See Table 6 for statistical tests.

songbirds than to that of raptors and corvids that is a violet-tuned system (Håstad et al. 2005). We do not know if the additional information in a continuous compared with a dichotomous color score would add any biologically relevant information. Hence, we restricted the analyses to the dichotomous variable that is known to contain biologically meaningful information. This approach may suffer from weaknesses although there is to the best of our knowledge, no evidence suggesting that human visual scores distort categorization of sexual dichromatism. Because dichromatic species fall prey to predators more often than monochromatic species by almost a factor 2 (Huhta et al. 2003; Møller and Nielsen 2006; Møller, Nielsen, and Garamszegi 2006), we should have expected a higher frequency of fear screams in dichromatic species, unless fear screams constitute a less efficient antipredator behavior in such species. One possibility is that a lower frequency of fear screams in dichromatic species may relate to lower kin-selected benefits. Indeed, comparative studies of local genetic variation have shown that sexually dichromatic species have lower genetic similarity among individuals in a population than monochromatic species (Petrie et al. 1997; Møller et al. 2008), consistent with our interpretation. We also showed that tonic immobility lasted longer in dichromatic than in monochromatic species. Tonic immobility is a measure of fearfulness in poultry research with both environmental and genetic components (Hoagland 1928; Jones 1986; Boissy 1995; Forkman et al. 2007). Longer tonic immobility in dichromatic than in monochromatic species would imply that individuals belonging to dichromatic species are

more fearful, which could be an evolved response to an elevated risk of predation.

In conclusion, we have shown that behavior of captured birds is antipredator behavior. Because males and females differed in escape behavior and because sexually dichromatic and monochromatic species differed in escape behavior, we can conclude that predation risk has modified escape behavior in relation to degree of sexual signaling. The implications are that spatial and temporal variation in predation risk may affect males and females differently, depending on their sexual coloration, and that such coloration may potentially evolve in response to risk of predation.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>.

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