

Risk taking by singing males

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The distance at which an individual flees from a potential predator represents a measure of risk taking. If individuals are engaged in another activity that might affect fitness, trade-offs between the fitness benefits of flight and the other activity should determine the nearest distance of approach by a predator. In a comparative analysis of birds, flight distance represented a reliable measure of risk of predation by the sparrowhawk *Accipiter nisus* that increased with decreasing flight distance across species. To test the hypothesis that singing males adjusted their risk taking to the costs and benefits of early flight, we compared the flight distance of singing and nonsinging birds to an approaching human observing with a binocular. Singing birds on average fled at a greater distance than nonsinging birds, implying that singing birds took small risks. We used a standardized measure of difference in flight distance between singing and nonsinging individuals to investigate factors affecting interspecific variation in risk taking. Species that used more exposed song posts (sites used for singing) took smaller risks than species with less exposed song posts. Species that suffered from higher levels of parasitism as reflected by the prevalence of *Plasmodium*, but not by 3 other genera of blood parasites, took greater risks during singing compared with nonsinging activities. Likewise, species with high circulating levels of natural antibodies, and hence a history of natural selection caused by bacteria took relatively greater risks during singing than species with few natural antibodies. These findings suggest that risks taken by singing birds have been molded by natural and sexual selection, and that risk taking represents a compromise between the costs and benefits of flight from a potential predator. *Key words*: malaria, natural antibodies, parasitism, predation, song, song post. [*Behav Ecol* 19:41–53 (2008)]

Predation is an important cause of death in most animals (e.g., Curio 1976; Caro 2005). Therefore, it is not surprising that a large number of different adaptations have evolved to partly reduce the risk of predation (Caro 2005). For example, habitat use, temporal organization of daily routine, amount and kind of food eaten, and the risk taken during foraging or other activities all comprise aspects of adaptations to reduce predation risk. An individual's response to a potential predator may be subject to trade-offs (Dill 1987; Blumstein and Bouskila 1996) because the reduction in risk of predation is traded against risk of starvation or risk of not finding a mate.

Although trade-offs between foraging and other activities such as refuge use or shelter seeking have been described (review in Caro 2005), there is also ample scope for trade-offs between foraging and sexual behavior. Given that sexual signals tend to be condition dependent (reviews in Johnstone 1995; Jennions et al. 2001), such trade-offs should differ among individuals with different condition and hence different expression of secondary sexual characters. State-dependent foraging is commonly reported (Clark 1994), suggesting that species in poor condition often take greater risks (e.g., Bachman 1993; Krause et al. 1998). This argument can also be extended to the interspecific level because individuals of species with exaggerated secondary sexual characters will run disproportionately large risks of predation as shown by comparative analyses of prey eaten by avian predators (Huhta et al. 2003; Møller and Nielsen 2006). Likewise, species differ consistently in risk taking depending on their fecundity and survival prospects (Ghalambor and Martin 2001). Therefore, risk taking should

differ among species reflecting such interspecific differences in risk of predation.

Singing by male (and female) birds is a sexual display performed in a specific site, usually a fixed song post in a bush or tree, or in species with song flight in the air while flying, and such a site may be chosen to optimize the costs and benefits associated with the use of that site. Scherrer (1972), in an early contribution, quantified not only the exposure of singing male birds, finding great differences among species but also effects of habitat, with males in more dense habitats using more secluded song posts, despite exposed song posts also being available in such habitats. Møller et al. (2005) analyzed song post use by males in a community of passerine birds in Europe, showing that species with more exposed song posts fell prey to sparrowhawks *Accipiter nisus* disproportionately often. Furthermore, a path analysis of the causal relationships between predation risk, song post exposure, and sexual coloration, which independently affected predation risk (Huhta et al. 2003; Møller and Nielsen 2006), showed that an increase in song post exposure caused an increase in predation risk. In contrast, there was little evidence of susceptibility to predation driving the evolution of song post exposure (Møller et al. 2005). These findings suggest that it is sexual selection that exaggerates song post exposure, thereby imposing a cost in terms of natural selection on singing males due to predation. This raises the possibility that song post exposure affects risk taking. An elevated risk of predation for males with exposed song posts could partly be ameliorated if such males took small risks by flying off early during the approach of a potential predator. Given that males must sing in order to attract a mate and defend a territory, they may flee sooner than nonsinging males because monitoring of an approaching potential predator is a cognitively costly behavior. If this alternative hypothesis accounted for male flight responses to an approaching potential predator, we would expect that the distance at which a singing individual detected an approaching predator

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Received 25 September 2006; revised 13 August 2007; accepted 23 September 2007.

would be shorter than that of an individual involved in other activities.

Diseased and heavily parasitized individuals run elevated risks of predation, as shown by comparisons of the level of parasitism of prey and individuals from the general population (Temple 1986). Likewise, prey differs from random individuals in terms of immune function (Møller and Erritzøe 2000). Differences in predation risk of diseased and healthy species may be attributed to differences in ease of capture or condition (Zuk and Kolluru 1998). However, if diseased or parasitized individuals are more likely to die, they have reduced residual reproductive value (current and future reproductive success multiplied by the likelihood of reaching older age [Fisher 1930]) compared with healthy individuals. Hence, such individuals should take relatively greater risks because their reduced residual reproductive value should change the trade-off between safeguarding against predation and, for example, risks taken during sexual display.

A corollary of the natural selection costs of parasitism is that the immune system has evolved and is maintained as a defense against parasitism. Therefore, the strength of immunity can be considered a measure of the impact of parasites on host fitness (e.g., Møller et al. 1999). Given that strong immune responses would imply strong pressures of natural selection caused by parasitism, immunity should affect risk taking by hosts. More specifically, we would expect species with strong immune responses to take greater risk, simply because individuals of such species would have reduced residual reproductive value. Here, we use interspecific variation in levels of natural antibodies (NAbs) for testing interspecific variation in risk taking. We deliberately chose to use this measure of immunity because it is part of innate immunity and thus not subject to induction by exposure to parasites (Abbas et al. 1994). Constitutive innate immunity represents the first line of defense against parasite attack, with the 2 parts being NAbs and complement. The function of these 2 components is to recognize and initiate the complement enzyme cascade (NAbs) that eventually ends in cell lysis (Carroll and Prodeus 1998). NAbs have been shown to provide resistance to malarial parasites (Congdon et al. 1969) and correlate with the abundance of chewing lice (Whiteman et al. 2006). Naturally occurring concentrations of NAbs can kill bacteria and spirochetes in vivo (Ochsenbein et al. 1999; Belperron et al. 2001) and clear lipopolysaccharides in vitro (Reid et al. 1997).

The objectives of the present study were to test a number of predictions relating to risk taking by singing birds under field conditions. Song plays a central role in male–male competition and female choice (Catchpole and Slater 1995), and the fitness benefits of song are therefore well documented. However, the cost of bird song as a condition signal is debated (Ward et al. 2004 and references therein). Here, we tested the assumption that short flight distances predisposed individuals to an elevated risk of predation, using a unique data set on predation risk. Furthermore, we tested the following predictions. 1) Bird species with more exposed song posts took smaller risks by having relatively longer flight distances. 2) Bird species with high prevalence of malaria caused by the hematozoan blood parasite genus *Plasmodium*, but not other genera of blood parasites that are presumed to be less virulent due to their weaker effects on erythrocytes (Atkinson and Van Riper 1991), took greater risks when singing by having short flight distances when singing relative to those during other activities. 3) Bird species with high levels of NAbs and hence a history of parasite-mediated selection took greater risks when singing by having short flight distances when singing relative to those during other activities.

METHODS

Song flight distance

During March–August 2006, A.P.M. estimated flight distances for birds, using a standardized technique developed by Blumstein (2006). These recordings were made in Ile-de-France, France, and Northern Jutland, Denmark. The method adopted differed from that of Blumstein (2006) in one important respect: to avoid the problem of large species being detected by the observer at a larger distance than small species, thereby producing a relationship between starting distance and body size, we used binoculars to find a target individual and then subsequently walked toward that individual. This approach not only reduced the strength of the relationship between flight distance and starting distance but also the relationship between starting distance, flight distance, and body mass. In brief, when an individual bird had been located while resting, foraging, preening, or singing, the observer moved at a normal walking speed toward the individual, while recording the number of steps (which approximately equals meters). The distance at which the individual took flight was recorded as the flight distance, whereas the starting distance was the distance from where the observer started walking until the position of the bird. If the individual was positioned in the vegetation, the height above ground was recorded to the nearest meter. While recording these distances, A.P.M. also recorded date and time of day, whether the individual was singing or not, and the sex of the individual if external characteristics allowed sexing with binoculars. Flight distance was estimated as the square root of the sum of the squared horizontal distance and the squared height (Blumstein 2006).

All recordings were made during the breeding season, when most individuals are sedentary, thus preventing the same individual from being recorded in different sites. Only adults were included to avoid problems caused by juveniles having short flight distances. If there was doubt about age, an individual was not recorded. We avoided pseudoreplication by only recording individuals of a given sex and species at a given site. We recorded 2298 flight distances in total, and the present study of flight distance and song is based on data for 40 species for which we had information on flight distance for both singing individuals and individuals involved in other activities.

We cross-validated our estimates of flight distances in 2 different ways. First, we compared our estimates with those published by Blumstein (2006). For 13 species, we found a strongly positive relationship between the 2 series of estimates ($F = 18.12$, degrees of freedom [df] = 1,11, $r^2 = 0.62$, $P = 0.0013$, slope [SE {standard error}] = 0.89 [0.21]), and the means were not significantly different (paired t -test, $t = 0.53$, df = 13, $P = 0.60$). Second, we compared our estimates with those collected by an independent observer (Einar Flensted-Jensen) in the Danish study area where A.P.M. worked. The independent observer had been instructed how to estimate flight distances but otherwise worked independently. Again, for 17 species we found a strongly positive relationship between the 2 series of estimates ($F = 12.86$, df = 1,15, $r^2 = 0.46$, $P = 0.0027$, slope [SE] = 0.92 [0.12]), and the means were not significantly different (paired t -test, $t = 0.04$, df = 16, $P = 0.99$).

Ecological variables

Sparrowhawk predation

We used extensive data on observed and expected abundance of prey of sparrowhawks obtained during 21 years (1977–1997) in a study area of 2417 km² in Northern Denmark

(Møller and Nielsen 2006). A total of 31 745 prey items of 64 species of birds were used, whereas 3178 prey items were excluded because they were mammals, cage birds, or migrants. All nest sites were visited 3–4 times during the breeding season, and sampling effort can therefore be considered to have remained similar across sites.

We calculated the expected number of prey by using information on density of breeding birds (Grell 1998). Maps of the density of breeding birds have been made based on systematic point counts of breeding birds carried out by hundreds of amateurs, providing reliable estimates of breeding bird density as shown by extensive analyses of potential sources of error and bias and by cross-validation with other census methods (see summary in Grell 1998).

We estimated a logarithmic index of prey vulnerability as the observed \log_{10} -transformed number of prey minus the \log_{10} -transformed expected number of prey. The expected number of prey according to abundance was estimated as the proportion of prey individuals of each species multiplied by the total number of prey individuals, according to the results of point counts reported by Grell (1998). This index has a value of zero when prey is taken according to their abundance, with a value of +1 indicating an overrepresentation by a factor 10 with respect to abundance, whereas a value of –1 indicates an underrepresentation by a factor 10. For further details, see Møller and Nielsen (2006, 2007).

Song posts

We estimated song post exposure by determining the height of the song post of common passerine birds relative to the surrounding vegetation or structures such as buildings (see Møller and Nielsen 2006) for further details and data). In brief, song post exposure is estimated as the percentage of all song posts of a given species that are at a height above the surrounding vegetation, ranging from 0 when all song posts are lower than the surrounding vegetation to 100 when all song posts are above the vegetation. This method for describing song posts was first developed by Scherrer (1972), and we found a high degree of consistency in song post exposure estimates between the study of Møller and Nielsen (2006) and that of Scherrer (1972).

Sexual dichromatism

We scored species as either sexually monochromatic or dichromatic. Species were classified as monochromatic, and given a score of zero, if males and females could not be reliably distinguished based on plumage characters according to field guides (e.g., Svensson 1984; Mullarney et al. 2000). Any sex difference in plumage coloration was considered to represent sexual dichromatism, which was scored as one. 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. Our dichotomous score was strongly positively correlated with quantitative scores from Møller and Birkhead (1994) and Read (1987), suggesting that dichotomous and continuous scores provide similar information (analysis for goshawk: $F = 9.62$, $df = 1,11$, $r^2 = 0.47$, $P = 0.010$, analysis for sparrowhawk: $F = 25.48$, $df = 1,13$, $r^2 = 0.66$, $P = 0.0002$). Therefore, we only report results for sexual dichromatism scored on a dichotomous scale. We did not have information on ultraviolet coloration, and we were therefore restricted to only use sexual dichromatism in the visible domain for humans.

Blood parasites

We used information on prevalence of blood parasites from Europe by relying on information in Møller and Nielsen

(2006). We also extracted information on the number of individuals examined for each of the host species. In total, the study was based on examination of infection level of 18 429 individual juvenile and adult hosts based on blood smears. Blood parasites are typically only present in the blood stream in juvenile and adult hosts but often not in nestlings. Most of the blood parasite information derives from Northern Europe, where the study of flight distance was also conducted. Hence, there was a high degree of overlap between the geographical location of study sites for parasites and predation.

Natural antibodies

Blood was collected from adult birds captured during the breeding season 2005 in the Danish study sites by puncturing the brachial vein and collecting 2 heparinized capillaries of 75- μ l blood that were stored in a cooling box at a temperature just above freezing. In the laboratory, within a period of 2 h, we centrifuged the capillaries for 10 min at 4000 rpm. Plasma and cells were separated and stored at –20 °C until analysis at the laboratory.

To estimate the levels of circulating NABs and complement, we used the procedure developed by Matson et al. (2005) and adjusted by Møller and Haussy (2007). The agglutination part of the assay estimates the interaction between NABs and antigens in rabbit blood producing blood clumping. Quantification of agglutination is achieved by serial dilution in polystyrene 96-well assay plates, with the dilution step at which the agglutination reaction is stopped. We used fresh rabbit blood with Alsever's anticoagulant, 96 round well assay plates, and an EPSON 4490 photo scanner that was set at professional mode, with document-type color film, 48-bit color, and 300 dpi. Whole rabbit blood was stored at 4 °C. After determination of the level of hematocrit, we diluted to obtain a solution of 1% of erythrocytes.

The protocol for hemagglutination was as follows. The plasma samples were thawed and homogenized using a vortex. Subsequently, 25 ml of plasma was pipetted into each column, followed by addition of 25 ml of the solution in all wells. Subsequent wells contained a solution diluted by a factor 2 from a solution of 1 in 2 in the first well to a solution of 1 in 2048 in the 11th well. Well number 12 only contained the dilution of erythrocytes, thus serving as a negative control. Subsequently, 25 ml of the 1% solution of rabbit blood was added to all wells. The assay plate was then covered and shaken for 10 s, followed by incubation for 90 min in a bath at 37 °C. The assay plate was then removed from the bath at left at an inclination of 45 °C at ambient temperature for 20 min. The assay plate was then read and scanned. Scoring was based on negative wells having a small round agglutinate at the bottom thus forming a well-defined red round point and positive wells having a diffuse film at the bottom. See Møller and Haussy (2007) for further details of procedures.

Body mass

Larger species may provide more resources to predators, but may be more difficult to catch, whereas small species may be unprofitable. Accordingly, Götmark and Post (1996) and Møller and Nielsen (2006) showed that prey species of intermediate body size suffered an elevated risk of predation by the sparrowhawk. Therefore, we used body mass and squared body mass of all species as additional predictor variables based on our own field measurements or in the absence of data as reported by Dunning (1993). All data are reported in Appendices 1–2.

Statistical analyses

Flight distance, starting distance, and body mass were \log_{10} transformed before analysis. Song post exposure and prevalence of blood parasites were square root arcsine transformed before analysis.

We tested whether flight distance is a species-specific attribute in a nested analysis of variance with flight distance as the response variable and song behavior (song or other behavior) nested within species, species, and starting distance as predictor variables. A significant species effect would imply that there is significant variation among species as required for comparative analyses.

Once having shown that flight distance is species specific, we tested whether mean flight distance differed between singing males and individuals involved in other activities, using a paired *t*-test weighted by sample size to account for interspecific differences in sampling effort.

Once having shown that flight distance on average differed between singing males and males with other activities, we developed an index of relative flight distance when singing for all species. This was simply \log_{10} -transformed mean flight distance of nonsinging males minus \log_{10} -transformed mean flight distance of singing males. This index has a value of zero when singing males do not differ from individuals with other activities with respect to flight distance, whereas positive values imply that singing individuals take smaller risks and negative values imply that singing individuals take greater risks relative to individuals engaged in other activities. Blumstein (2006) has shown that flight distance is influenced by starting distance, and, therefore, we adjusted for starting distance in the analyses by using that variable as an additional independent variable.

We analyzed factors explaining variation in predation risk to the sparrowhawk by relying on factors previously identified as explaining such risk (Møller and Nielsen 2006). These factors included abundance, sexual dichromatism, and a polynomial effect of body mass of prey, reflecting the fact that predators prefer prey of intermediate body size.

All analyses were weighted by sample size to adjust for uneven sampling effort among species under the assumption that estimates based on larger sample sizes were closer to the true population estimate.

Comparative analyses

Closely related species are more likely to have similar phenotypes than species that are more distantly related. Therefore, species cannot be treated as statistically independent observations in comparative analyses because apparent phenotypic correlations among species may result from species sharing a common ancestor rather than convergent evolution. Initially, we tested if there was a significant phylogenetic signal in the data by calculating the parameter λ (Freckleton et al. 2002). In the 3 tests (Tables 2–4), we did not find a significant λ ($\lambda < 0.81$, $P > 0.38$), and the results based on generalized least squares (Pagel 1997) and the species-specific data were the same. Therefore, we present analyses of the species-specific data and the analyses controlled for similarity in phenotype among species due to common phylogenetic descent based on standardized independent linear contrasts (Felsenstein 1985), using the software CAIC (Purvis and Rambaut 1995). We tested the statistical and evolutionary assumptions of the comparative analyses (Garland et al. 1992) by regressing absolute standardized contrasts against their standard deviations. In order to test for effects of problems of heterogeneity in variance, 1) we excluded outliers (contrasts with Studentized residuals > 3) in a second series of analyses

(Jones and Purvis 1997) and 2) analyses were repeated with the independent variable expressed in ranks. These analyses are conservative tests of the null hypothesis, explicitly investigating the robustness of the conclusions. In neither case did these new analyses change any of the conclusions, and they are therefore not reported here.

The composite phylogenies used in the comparative analyses were based on Sibley and Ahlquist (1990), combined with information from other sources (Sheldon et al. 1992; Blondel et al. 1996; Slikas et al. 1996; Badyaev 1997; Helbig and Seibold 1999; Barker et al. 2001, 2004; Voelker and Spellman 2004) (Supplementary Figure 1A,B). Because information for the composite phylogenies originated from different studies using different molecular and phylogenetic 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. The results from the phylogenetic analyses were also qualitatively similar when making the calculations using the taxonomy of Sibley and Monroe (1990).

We used sexual dichromatism as continuous variables in the analyses despite the fact that it was defined as a dichotomous variable because intermediate states of this variable are biologically meaningful. Using variables as continuous variables in statistical analyses is similar to using a dichotomous variable as a dummy variable in standard regression analyses (Sokal and Rohlf 1995).

A common underlying assumption of most statistical approaches is that each data point provides equally precise information about the deterministic part of total process variation, that is, the standard deviation of the error term is constant over all values of the predictor or explanatory variables (Sokal and Rohlf 1995). The standard solution to this problem is to weight each observation by sampling effort in order to use all data, while giving each datum a weight that reflects its degree of precision due to sampling effort (Sokal and Rohlf 1995). Violation of this assumption and its implications has only recently been considered in comparative analyses by weighting contrasts by sample size (Møller and Nielsen 2006, 2007). In order to weight regressions 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 2006, 2007).

We used multiple regression to find the best fit model, using the software JMP (2000). The best fit model was determined using Akaike's information criterion (AIC) as an estimate of the improvement in fit for addition of variables (Burnham and Anderson 1998). We started out by using the best fit models and then adding factors according to their delta AIC values, using the criterion that a change in AIC of more than 2.00 would be considered biologically meaningful (Burnham and Anderson 1998). These analyses were repeated using Mallows' C_p criterion for choice of the best fit model (JMP 2000), which is the model with a C_p value closest to the number of parameters p in the model. There was no evidence of collinearity between variables. Green (1979) suggested that any correlation less than 0.70 will eliminate serious problems of collinearity.

Regressions of standardized linear contrasts were forced through the origin because the comparative analyses assume that there has been no evolutionary change in a character when the predictor variable has not changed (Purvis and Rambaut 1995).

We report effect sizes estimated as Pearson's product-moment correlation coefficients, using the conventions of Cohen (1988) that a small effect equals $r = 0.10$, intermediate

Table 1
Nested analysis of variance of flight distance in relation to species, singing, and starting distance

| Variable | Sum of squares | df | <i>F</i> | <i>P</i> | Pearson <i>r</i> (95% CI) |
|-------------------------|----------------|------|----------|----------|---------------------------|
| Species (singing) | 109.52 | 130 | 12.11 | <0.0001 | 0.67 (0.64, 0.69) |
| Singing | 2.71 | 1 | 39.00 | <0.0001 | 0.04 (0.00, 0.08) |
| Log (starting distance) | 0.75 | 1 | 10.83 | 0.0010 | 0.02 (0.01, 0.02) |
| Error | 131.99 | 1897 | | | |

Pearson's correlation coefficient *r* is given as a standardized estimate of effect size. The overall model had the statistics $F = 15.53$, $df = 132, 1897$, $r^2 = 0.52$, $P < 0.0001$. CI, confidence interval.

effect equals $r = 0.30$, and a large effect equals $r = 0.50$. Effect sizes in biology are typically on average $r = 0.25$ (Møller and Jennions 2002). We used equations in Rosenthal (1994) for estimating effect sizes. We also present 95% confidence intervals as suggested recently (Nakagawa 2004; Garamszegi 2006).

RESULTS

Flight distance of singing and nonsinging birds

A nested analysis of variance revealed a highly significant effect of singing on flight distance (Table 1). The main factor explaining variation in flight distance was species, with additional variation attributed to variance among activities and starting distance (Table 1). This suggests that flight distance was related to song. The significant species effect suggests that flight distance is a species-specific attribute showing greater variation among than within species.

The mean index of risk taking by singing compared with nonsinging individuals was $+0.092$ (SE = 0.027, range = -0.231 to $+0.509$, $N = 40$ species). The mean of $+0.092$ deviated significantly from zero (Figure 1; one-sample *t*-test weighted by sample size, $t = 3.36$, $df = 39$, $P = 0.0017$). Most species fled a longer distance when singing than when not singing (Figure 1). However, 16 out of 40 estimates were negative, showing shorter flight distance when singing in some species and hence large heterogeneity among species.

Flight distance and sparrowhawk predation

The most common predator of small passerine birds in the study area is the sparrowhawk. We tested if flight distance

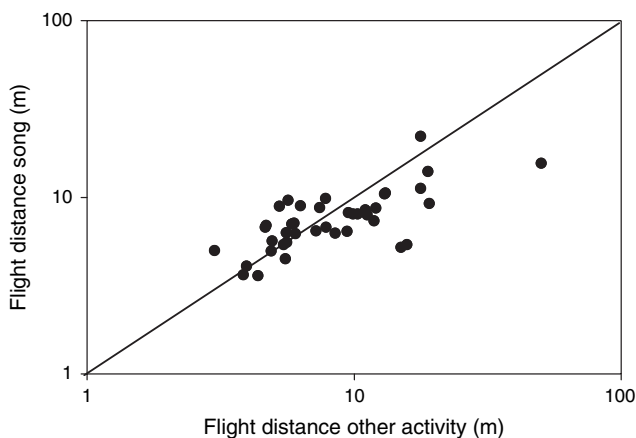


Figure 1
Mean flight distance (m) of singing and nonsinging birds of different species. The line indicates when singing and nonsinging birds have similar flight distance.

when approached by a human reflected risk taking during real predation attempts by relying on information on susceptibility to sparrowhawk predation from the same Danish study area where most of the flight distances were recorded. Indeed, species of birds particularly susceptible to predation took flight at short distances (Figure 2), and that was also the case in an analysis of contrasts (Figure 2). Next, we added a number of potentially confounding variables to the analyses but still found a significant negative relationship between susceptibility to predation and flight distance (Table 2A). Body mass and body mass squared were entered as predictors to reflect the fact that the sparrowhawk prefers prey of intermediate body size (Møller and Nielsen 2006). Indeed, sparrowhawks preferred prey of intermediate size as shown by the polynomial effect of body mass on flight distance (Table 2A). The effect of starting distance was not significant ($F = 0.55$, $df = 1, 30$, $P = 0.46$). An analysis of contrasts, weighted by sample size, revealed a similar conclusion (Table 2B). This shows that actual risk of predation to a real predator increased with decreasing flight distance.

Relative flight distance and song post exposure

Singing individuals of species with more exposed song posts took smaller risks than species with less exposed song posts, with information on song posts recorded in the same Danish study areas as where most of the information on flight distance was recorded (Figure 3). Starting distance did not enter as a significant predictor in this model ($F = 0.71$, $df = 1, 32$, $P = 0.41$) or in any of the following models, implying that we did not detect species with exposed song posts further away than species with less exposed song posts, implying that starting distance cancelled out in the calculations. By inference, individual birds should be able to detect the approaching observer independent of song post exposure because observers were able to see the individual birds. This implies that as song posts became exposed, individuals reduced their risk-taking behavior or they simply detected a potential danger earlier. This relationship between song post exposure and flight distance was not confounded by habitat or sexual dichromatism that were both previously shown to predict song post exposure (Møller et al. 2005). Partial regressions for these variables were small and statistically nonsignificant (Table 3). In contrast, the effect for song post exposure remained significant (Table 3). An analysis of contrasts, weighted by sample size showed a similar effect for song post exposure (Table 3), and this effect was not confounded by sexual dichromatism or habitat (Table 3).

Song post exposure was independently related to vulnerability to sparrowhawk predation (Møller et al. 2005), as was relative flight distance to vulnerability to predation (this study). Therefore, we tested if relative flight distance after controlling for vulnerability to predation was related to song post exposure. Indeed, this multiple regression was statistically significant

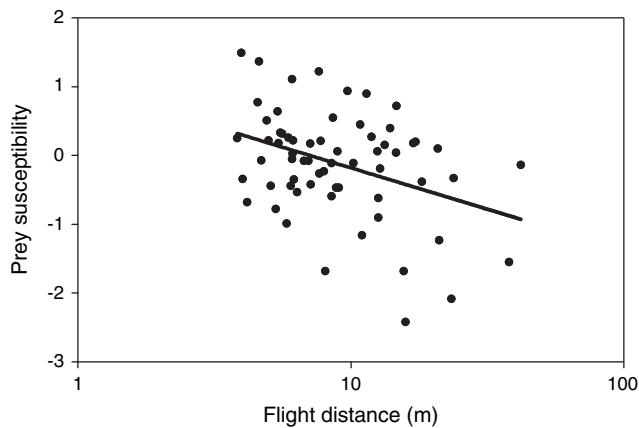


Figure 2

Vulnerability to predation by the sparrowhawk in relation to flight distance (m) by different species of birds. Analysis of species-specific data: $F = 9.48$, $df = 1,62$, $r^2 = 0.13$, $P = 0.0031$, slope (SE) = -1.13 (0.37); analysis of contrasts: $F = 13.11$, $df = 1,62$, $r^2 = 0.17$, $P = 0.0006$, slope (SE) = -1.37 (0.38). The line is the linear regression line.

(Table 4A), and the partial regression for song post exposure was statistically significant (Table 4A). A similar conclusion was reached in an analysis of contrasts (Table 4B).

Relative flight distance and parasitism

Singing individuals took greater risks than nonsinging individuals when the prevalence of *Plasmodium* was high in a given species (Figure 4A). We emphasize that the blood parasite data derived from across Europe (see Methods), although Scheuerlein and Ricklefs (2004) have shown that estimates of prevalence are repeatable across study sites in Europe. In contrast, partial regressions for prevalence of *Haemoproteus*, *Leucocytozoon*, and *Trypanosoma* did not reach statistical signif-

icance ($F < 0.64$, $df = 1,33$, $P > 0.43$). This result was confirmed by an analysis of contrasts (Figure 4A).

Singing individuals of species with higher levels of NAb took greater risks than did singing individuals in species with low levels of NAb (Figure 4B). NAb were quantified from blood samples taken in the same Danish study site as that where most of the flight distances were recorded.

Finally, we tested whether prevalence of *Plasmodium* and levels of NAb independently explained variation in relative flight distance. Indeed, a multiple regression analysis that also took body mass into account, weighted by sample size, was statistically significant (Table 5). An analysis of contrasts showed that the effect of prevalence of *Plasmodium* remained significant, whereas that was not the case for NAb (Table 5).

DISCUSSION

The main findings of this study of risk taking were that singing birds generally took smaller risks than birds involved in other activities, as reflected by their longer flight distances. Short flight distances can have dire consequences for survival, as shown by species with short flight distances suffering from elevated risks of predation by the sparrowhawk. Singing birds as compared with other individuals took smaller risks if they had more exposed song posts. Health status accounted for additional variation in risk taking, as the relative flight distance of singing individuals compared with individuals involved in other activities decreased with increasing prevalence of *Plasmodium* infection and levels of NAb. There were qualitatively small differences in conclusions when analyses were based on species-specific data or independent contrasts, but given that we found no evidence of significant phylogenetic signal in the data, we consider the species-specific analyses to be fully adequate. We will briefly discuss our findings.

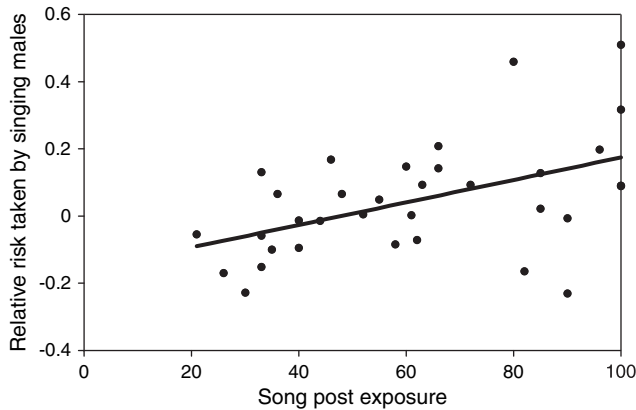
The risk taken by animals in the presence of a predator can have important fitness consequences. Here, we used flight distance to an approaching human being as a measure of risk taking. Mean estimates for different species were cross-validated using 2 different sets of estimates. Estimates

Table 2

Prey vulnerability to the sparrowhawk in relation to mean flight distance (m), body mass (g), body mass squared, and sexual dichromatism in a multiple regression model, weighted by sample size

| Variable | Sum of squares | df | F | P | Slope (SE) | Pearson <i>r</i> (95% CI) | Delta AIC |
|-------------------------|----------------|----|-------|---------|--------------|---------------------------|-----------|
| (A) Species | | | | | | | |
| Log (flight distance) | 41.42 | 1 | 8.11 | 0.0061 | -0.85 (0.30) | 0.35 (0.11, 0.55) | 6.23 |
| Log (body mass) | 8.30 | 1 | 1.62 | 0.21 | 0.23 (0.18) | 0.16 (-0.09, 0.38) | 2.63 |
| Log (body mass) squared | 112.64 | 1 | 22.04 | <0.0001 | -1.40 (0.30) | 0.52 (0.32, 0.68) | 18.31 |
| Sexual dichromatism | 25.78 | 1 | 5.05 | 0.028 | 0.30 (0.13) | 0.28 (0.04, 0.50) | 3.25 |
| Error | 301.51 | 59 | | | | | |
| (B) Contrasts | | | | | | | |
| Log (flight distance) | 1.46 | 1 | 12.94 | 0.0007 | -1.33 (0.37) | 0.42 (0.19, 0.60) | 14.44 |
| Log (body mass) | 0.63 | 1 | 5.57 | 0.022 | 3.95 (1.68) | 0.29 (0.05, 0.50) | 2.28 |
| Log (body mass) squared | 0.73 | 1 | 6.51 | 0.013 | -1.25 (0.49) | 0.32 (0.08, 0.52) | 3.35 |
| Sexual dichromatism | 0.37 | 1 | 3.26 | 0.076 | 0.34 (0.19) | 0.23 (-0.01, 0.68) | 1.28 |
| Error | 6.65 | 59 | | | | | |

Pearson's correlation coefficient *r* is given as a standardized estimate of effect size. The best fit model for species (A) had the statistics $F = 18.34$, $df = 4,59$, $r^2 = 0.55$, $P < 0.0001$, AIC = 109.20, Cp = 5 (Mallow's Cp criterion for model selection), whereas the model for contrasts (B) had the statistics $F = 6.70$, $df = 4,59$, $r^2 = 0.10$, $P = 0.0002$, AIC = -133.68, Cp = 4. An alternative model for contrasts that only included flight distance, body mass, and body mass squared had the statistics $F = 6.70$, $df = 3,58$, $r^2 = 0.10$, $P = 0.0002$, AIC = -132.29, Cp = 5.26. Mallow's Cp criterion for the latter model indicated that this model was worse than the model presented in the table. Delta AIC is the change in AIC relative to the best fit model. CI, confidence interval.

**Figure 3**

Relative risk taking of singing individuals compared with other individuals in relation to song post exposure (% individuals singing from the top of the vegetation) for different species of birds. Analysis of species-specific data: $F = 8.55$, $df = 1,32$, $r^2 = 0.21$, $P = 0.0063$, slope (SE) = 0.39 (0.14); analysis of contrasts: $F = 10.61$, $df = 1,32$, $r^2 = 0.25$, $P = 0.0027$, slope (SE) = 0.29 (0.09). The line is the linear regression line for species-specific data.

obtained by Blumstein (2006) were very similar to our estimates for a sample of species, and estimates obtained by an independent observer in one of our study areas were also very similar to our estimates. This provides extensive evidence for the reliability of such behavioral estimates under field conditions. Previous studies have also shown a high degree of repeatability among observers and biologically relevant correlations (Blumstein 2006). We analyzed individual flight distances and showed that there were consistent differences between singing individuals and individuals involved in other activities. In addition, there was a significant effect of species showing species specificity for flight distances (see Blumstein et al. [2003] for a similar result). This implies that flight distances are a property of species, justifying the analysis of mean species-specific values in the comparative analyses. We used an index of the difference in mean flight distance between singing individuals and individuals engaged in other activities as

a measure of the relative risk taken by singing individuals. This index showed considerable interspecific variation, although the mean index was significantly larger than zero, implying that singing individuals on average took smaller risks than nonsinging individuals.

Although animals respond to approaching humans as they would to a predator (Frid and Dill 2002), it remains an untested, albeit likely, assumption that a shorter flight distance equates with an elevated risk of predation. Here, we exploited the unique situation of relative risk of predation for all breeding species having been estimated for our Danish study site (Møller and Nielsen 2006). We showed an intermediate to strong (sensu Cohen 1988) negative relationship between susceptibility of different prey species to predation by the sparrowhawk and mean flight distance, and the slope of this logarithmic relationship implies that predation risk increased by more than a factor 25 across the range of mean flight distances recorded (Table 2, Figure 2). This relationship implies that species with shorter flight distances indeed ran an elevated risk of predation. This effect was independent of additional factors that have previously been shown to affect susceptibility to predation by sparrowhawks in this population (Møller and Nielsen 2006). For example, we found an additional effect of body mass and body mass squared, showing that sparrowhawks preferred prey of intermediate body size. Therefore, we can conclude that field estimates of risk taking based on flight distances reflect risk of being eaten by a common avian predator.

The index of relative risk taken by singing individuals was strongly positively related to song post exposure (Figure 3), with species using exposed song posts taking relatively smaller risks when singing. Møller et al. (2005) showed that song post exposure varied in a systematic way with risk of predation by the sparrowhawk, with species with the most exposed song posts in the vegetation suffering the greatest risks of predation. In addition, species in grassland habitats had greater song post exposure than species breeding in bushes, which in turn had greater exposure than species inhabiting forests. Because different causal scenarios investigated with path analyses revealed that song post exposure subsequently affected the index of prey susceptibility (Møller et al. 2005), we suggest here that the current findings concerning risk taking by

Table 3

Models of the relationship between relative flight distance (difference in flight distance between singing and nonsinging individuals) in relation to song post exposure, habitat, and sexual dichromatism

| Variable | Sum of squares | df | <i>F</i> | <i>P</i> | Slope (SE) | Pearson <i>r</i> (95% CI) |
|----------------------|----------------|----|----------|----------|--------------|---------------------------|
| (A) Species | | | | | | |
| Song post exposure | 5.95 | 1 | 8.47 | 0.0067 | 0.50 (0.17) | 0.47 (0.16, 0.69) |
| Habitat | 0.69 | 1 | 0.98 | 0.33 | 0.04 (0.04) | 0.18 (−0.16, 0.48) |
| Sexual dichromatism | 0.09 | 1 | 0.12 | 0.73 | 0.02 (0.05) | 0.06 (−0.28, 0.38) |
| Error | 21.07 | 30 | | | | |
| (B) Contrasts | | | | | | |
| Song post exposure | 1.16 | 1 | 7.81 | 0.0090 | 0.30 (0.11) | 0.45 (0.14, 0.68) |
| Habitat | 0.004 | 1 | 0.03 | 0.86 | −0.01 (0.04) | 0.03 (−0.30, 0.36) |
| Sexual dichromatism | 0.04 | 1 | 0.30 | 0.59 | 0.02 (0.04) | 0.10 (−0.25, 0.42) |
| Error | 4.46 | 30 | | | | |

Pearson's correlation coefficient *r* is given as a standardized estimate of effect size. The model based on species-specific data had the statistics $F = 3.10$, $df = 3,30$, $r^2 = 0.24$, $P = 0.041$, $AIC = -8.26$, $C_p = 4$ (Mallow's C_p criterion for model selection), whereas the best fit model that only included song post exposure had the statistics $F = 8.55$, $df = 1,32$, $r^2 = 0.21$, $P = 0.0063$, $AIC = -11.12$, $C_p = 1.02$. The model based on contrasts had the statistics $F = 3.49$, $df = 3,30$, $r^2 = 0.26$, $P = 0.028$, $AIC = -60.05$, $C_p = 3$. The best fit model for contrasts that only included song post exposure had the statistics $F = 10.61$, $df = 1,32$, $r^2 = 0.25$, $P = 0.0027$, $AIC = -63.63$, $C_p = -0.62$. CI, confidence interval.

Table 4
Models of the relationship between relative flight distance (difference in flight distance between singing and nonsinging individuals) in relation to song post exposure, susceptibility to predation, and body mass

| Variable | Sum of squares | df | <i>F</i> | <i>P</i> | Slope (SE) | Pearson <i>r</i> (95% CI) |
|-----------------------------|----------------|----|----------|----------|--------------|---------------------------|
| (A) Species | | | | | | |
| Song post exposure | 6.23 | 1 | 10.02 | 0.0037 | 0.45 (0.14) | 0.51 (0.20, 0.73) |
| Susceptibility to predation | 0.14 | 1 | 0.23 | 0.64 | -0.02 (0.05) | 0.09 (-0.26, 0.42) |
| Body mass | 3.13 | 1 | 5.03 | 0.033 | 0.12 (0.05) | 0.39 (0.05, 0.64) |
| Error | 17.42 | 28 | | | | |
| (B) Contrasts | | | | | | |
| Song post exposure | 1.16 | 1 | 9.02 | 0.0056 | 0.29 (0.10) | 0.49 (0.18, 0.72) |
| Susceptibility to predation | 0.01 | 1 | 0.10 | 0.75 | -0.02 (0.05) | 0.06 (-0.29, 0.39) |
| Body mass | 0.33 | 1 | 2.59 | 0.12 | 0.13 (0.08) | 0.29 (-0.06, 0.58) |
| Error | 3.61 | 28 | | | | |

Pearson's correlation coefficient *r* is given as a standardized estimate of effect size. The model based on species-specific data had the statistics $F = 5.18$, $df = 3, 28$, $r^2 = 0.36$, $P = 0.0056$, $AIC = -11.45$, $Cp = 4$ (Mallow's Cp criterion for model selection), whereas the best fit model that only included song post exposure and body mass had the statistics $F = 7.19$, $df = 2, 31$, $r^2 = 0.32$, $P = 0.0027$, $AIC = -13.19$, $Cp = 2.30$. The model based for contrasts had the statistics $F = 5.23$, $df = 3, 28$, $r^2 = 0.16$, $P = 0.0054$, $AIC = -60.62$, $Cp = 3$, whereas alternative models that only included song post exposure had the statistics $F = 12.02$, $df = 1, 30$, $r^2 = 0.29$, $P = 0.0016$, $AIC = -61.27$, $Cp = 2.19$, included song post exposure and susceptibility to predation had the statistics $F = 6.21$, $df = 2, 29$, $r^2 = 0.30$, $P = 0.0057$, $AIC = -59.87$, $Cp = 3.59$, and included song post exposure and body mass had the statistics $F = 8.05$, $df = 2, 29$, $r^2 = 0.36$, $P = 0.0017$, $AIC = -62.51$, $Cp = 1.10$. Mallow's Cp criterion for the full model was closer to the number of parameters in the model, indicating that this model provided the best fit. CI, confidence interval.

singing individuals can be interpreted as a means of reducing the predation cost of exposed display. Individuals of species with exposed song posts were more wary and left their song post at a greater distance from an approaching human than did individuals of species with less exposed song posts. That was also the case after controlling for the effect of susceptibility to predation. Alternatively, longer flight distances by spe-

cies with more exposed song posts could simply arise from individuals being able to detect a potential danger earlier. We can dismiss that possibility for 2 different reasons. First, we detected species with exposed song posts and started walking toward such species at a similar distance as species with more concealed song posts. Second, given the increased risk of predation experienced by species with exposed song posts

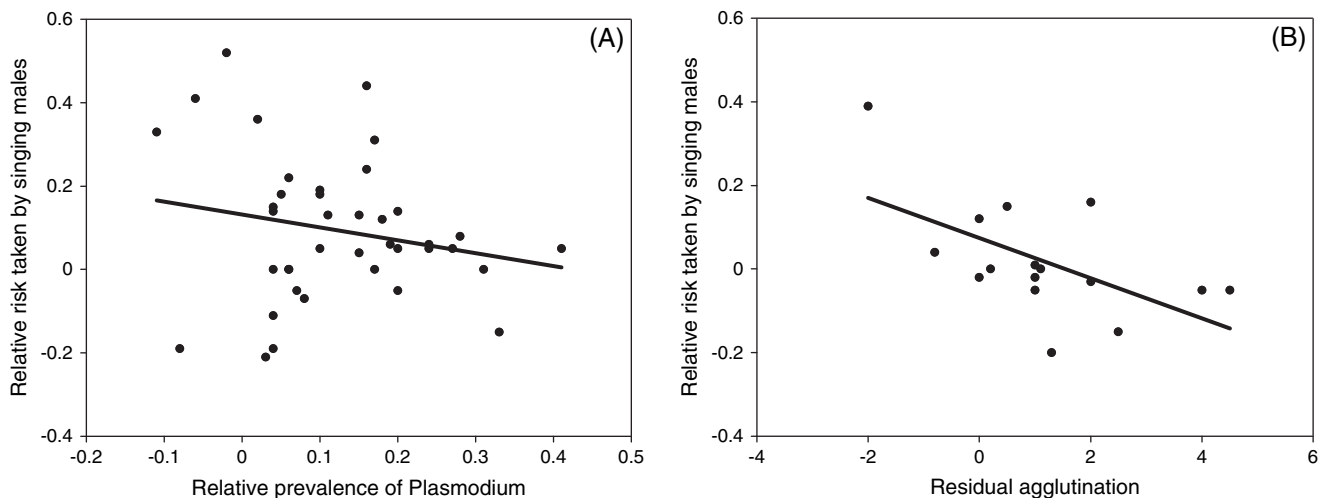


Figure 4

Relative risk taking of singing individuals compared with other individuals in relation to (A) prevalence of *Plasmodium* (% individuals infected with the blood parasite) and (B) abundance of NAbs in different species of birds. The relationships were adjusted for the effects of body mass by calculating residuals, whereas the statistics were based on using body mass as an additional independent variable. (A) A multiple regression with difference in flight distance between singing and nonsinging individuals as the dependent variable weighted by sample size with body mass as an additional variable using species-specific data: $F = 8.38$, $df = 2, 36$, $r^2 = 0.32$, $P = 0.0010$; partial regression for prevalence of *Plasmodium*: $F = 6.05$, $df = 1, 36$, $P = 0.019$, slope (SE) = -0.37 (0.15); contrasts: partial regression for prevalence of *Plasmodium*: $F = 4.82$, $df = 1, 33$, $P = 0.035$, slope (SE) = -0.43 (0.20); partial regression for other genera of blood parasites: $F < 1.19$, $df = 1, 33$, $P > 0.28$. The lines are the linear regression lines for species-specific data. (B) A multiple regression weighted by sample size with body mass as an additional variable: $F = 7.09$, $df = 2, 15$, $r^2 = 0.49$, $P = 0.0068$, partial regression for NAbs: $F = 11.75$, $df = 1, 15$, $P = 0.0037$, slope (SE) = -0.037 (0.011); contrasts: partial regression for NAbs: $F = 4.82$, $df = 1, 15$, $P = 0.035$, slope (SE) = -0.43 (0.20).

Table 5
Models of the relationship between relative flight distance (difference in flight distance between singing and nonsinging individuals) in relation to NABs, prevalence of *Plasmodium*, and body mass

| Variable | Sum of squares | df | F | P | Slope (SE) | Pearson <i>r</i> (95% CI) | Delta AIC |
|----------------------|----------------|----|-------|---------|----------------|---------------------------|-----------|
| (A) Species | | | | | | | |
| NABs | 2.80 | 1 | 11.37 | 0.0046 | −0.034 (0.010) | 0.67 (0.31, 0.86) | 8.70 |
| <i>Plasmodium</i> | 3.95 | 1 | 16.02 | 0.0013 | −0.593 (0.148) | 0.73 (0.41, 0.89) | 11.73 |
| Body mass | 10.94 | 1 | 44.34 | <0.0001 | 0.451 (0.068) | 0.87 (0.69, 0.95) | 23.69 |
| Error | 3.45 | 14 | | | | | |
| (B) Contrasts | | | | | | | |
| NABs | 0.03 | 1 | 3.58 | 0.08 | −0.025 (0.013) | 0.45 (−0.00, 0.75) | 1.86 |
| <i>Plasmodium</i> | 0.07 | 1 | 7.96 | 0.014 | −0.500 (0.177) | 0.60 (0.20, 0.83) | 5.65 |
| Body mass | 0.26 | 1 | 28.19 | 0.0001 | 0.444 (0.084) | 0.82 (0.58, 0.93) | 16.75 |
| Error | 0.13 | 14 | | | | | |

Pearson's correlation coefficient *r* is given as a standardized estimate of effect size. The best fit model based on species-specific data had the statistics $F = 16.67$, $df = 3, 14$, $r^2 = 0.78$, $P < 0.0001$, $AIC = -21.72$, $C_p = 4$ (Mallow's C_p criterion for model selection), whereas the best fit model based on contrasts had the statistics $F = 17.63$, $df = 3, 14$, $r^2 = 0.56$, $P < 0.0001$, $AIC = -77.07$, $C_p = 3$. An alternative model for contrasts that only included prevalence of *Plasmodium* and body mass had the statistics $F = 21.05$, $df = 2, 15$, $r^2 = 0.74$, $P < 0.0001$, $AIC = -75.21$, $C_p = 4.58$. Mallow's C_p criterion for the latter model indicated that this model was considerably worse than the model presented in the table. Delta AIC is the change in AIC relative to the best fit model. CI, confidence interval.

(Møller et al. 2005), we can infer that any individual that took flight at a long distance would simultaneously reduce the risk of falling prey to a predator.

Malaria is well known for its damaging effects on erythrocytes, thereby reducing metabolic efficiency and blood flow to the brain and the spleen (Atkinson and Van Riper 1991; Chen et al. 2001). Furthermore, malaria also induces immune responses, heat-shock proteins, and fever (Wakelin 1996; Merino et al. 1998; Chen et al. 2001). All these effects should render infected individuals more likely to fall prey to a predator, as has been shown (Møller and Nielsen 2006), thereby reducing the residual reproductive value of an infected individual. Therefore, malarial infection and infection with other virulent diseases should directly affect the risk-taking behavior during sexual display because an infected individual is less likely to be alive the next breeding season than an uninfected individual. Indeed, singing birds took relatively greater risks in species with high prevalence of *Plasmodium* infections compared with species with low prevalence (Figure 4A), whereas no similar relationship was found for 3 other genera of blood parasites. Indeed, infections with *Plasmodium* seem to have more severe consequences for hosts than infections with other blood parasites (Atkinson and Van Riper 1991). This effect is as predicted, supporting the hypothetical increase in risk taking when the fitness return of sexual display is reduced by an external cause of mortality.

The flip side of disease is defense against disease. Selection should have caused individuals to increase investment in immune defense when the risk of fitness loss is the greatest, resulting in a greater reduction in residual reproductive value when the impact of parasitism and hence immunity is elevated. Here, we used a data set on interspecific variation in NAB levels to test the prediction that species with high levels of antibodies took relatively greater risks when singing. NABs constitute the innate first line of defense against pathogens including bacteria (Congdon et al. 1969; Carroll and Prodeus 1998), and this measure is therefore particularly suitable for many studies because it is relatively insensitive to external influences. Singing males took greater risks than individuals involved in other activities when individuals of that species

had high NAB levels (Figure 4B). This finding is as expected if a high level of NABs reflect a strong impact of parasites on a given host species because individuals of such a species would suffer from elevated risks of death due to parasitism.

The different findings concerning relative risk taken by singing individuals suggest that birds are able to trade the benefits of display against the costs of natural selection. The results also suggest that sick individuals either due to malaria or other infections adjust their behavior to take greater relative risks when singing, thereby potentially improving their success from display in the face of an elevated risk of predation. Indeed, Møller and Nielsen (2006) have shown that malarial infection dramatically increases the risk of sparrowhawk predation. This emphasizes the intricate feedback loops between signaling, predation, and parasitism. Signals may increase risks of predation, such risks can be partially mitigated by changes in behavior, disease affects the risk of predation, and the risk of mortality associated with disease in turn affects the risks taken during display. Our results have implication for the cost of bird song. Females may be expected to prefer males that can bear the cost of singing at exposed sites and taking high risk during singing. Therefore, risk-taking behavior can be a component of cost that can guarantee that song is a reliable signal of male quality. It would be interesting to see not only how individuals differing in disease status changed their display behavior but also their risk-taking behavior. In particular, it would be particularly rewarding to test how experimental infections or cures affected subsequent changes in display and risk taking.

In conclusion, we have shown that a simple index of risk taking as estimated from flight distance of birds during field conditions reliably reflects the risk of predation by sparrowhawks. Relative risk taking by singing individuals were independently related not only to exposure of song posts but also to health status of individuals as reflected by malarial infection and level of innate immune defense. These findings suggest that flight distance represents a fine-tuned behavior that individuals adopt to optimize their sexual display in an attempt to maximize the benefits and minimize the predation costs of song.

APPENDIX 1

Information on prey vulnerability to sparrowhawk predation, body mass (g), flight distance (m), starting distance (m), sample size for flight distance, and sexual dichromatism for species of birds analyzed for relative flight distance of singing males

| Species | Prey vulnerability | Body mass (g) | Flight distance (m) | Starting distance (m) | N | Sexual dichromatism |
|--------------------------------------|--------------------|---------------|---------------------|-----------------------|-----|---------------------|
| <i>Acrocephalus palustris</i> | -0.47 | 12.00 | 8.84 | 33.00 | 9 | 0 |
| <i>Aegithalos caudatus</i> | -0.68 | 8.80 | 4.17 | 7.75 | 4 | 0 |
| <i>Alauda arvensis</i> | -0.14 | 36.40 | 41.89 | 48.55 | 29 | 0 |
| <i>Anthus campestris</i> | -0.38 | 28.80 | 18.22 | 66.20 | 2 | 0 |
| <i>Anthus pratensis</i> | 0.18 | 19.25 | 16.94 | 26.94 | 31 | 0 |
| <i>Anthus trivialis</i> | 0.15 | 23.40 | 13.28 | 20.00 | 17 | 0 |
| <i>Apus apus</i> | -1.55 | 39.65 | 38.00 | 83.00 | 5 | 0 |
| <i>Carduelis cannabina</i> | 0.40 | 18.95 | 13.90 | 19.14 | 28 | 1 |
| <i>Carduelis carduelis</i> | -0.26 | 15.60 | 7.66 | 32.45 | 4 | 1 |
| <i>Carduelis chloris</i> | 0.17 | 27.65 | 7.10 | 18.71 | 34 | 1 |
| <i>Carduelis flammea</i> | -0.90 | 13.05 | 12.62 | 14.00 | 6 | 1 |
| <i>Carduelis spinus</i> | 1.49 | 13.80 | 3.96 | 37.41 | 5 | 1 |
| <i>Certhia familiaris</i> | 0.77 | 9.15 | 4.55 | 11.83 | 3 | 0 |
| <i>Coccothraustes coccothraustes</i> | 0.55 | 54.70 | 8.60 | 10.00 | 1 | 0 |
| <i>Columba palumbus</i> | -1.16 | 494.50 | 10.99 | 25.91 | 66 | 0 |
| <i>Corvus monedula</i> | -2.08 | 249.00 | 23.37 | 51.81 | 32 | 0 |
| <i>Cuculus canorus</i> | -1.23 | 120.50 | 21.03 | 38.33 | 12 | 0 |
| <i>Delichon urbica</i> | -0.53 | 19.55 | 6.35 | 25.00 | 27 | 0 |
| <i>Emberiza citrinella</i> | 0.06 | 26.75 | 12.51 | 19.86 | 64 | 1 |
| <i>Emberiza schoeniclus</i> | -0.19 | 18.80 | 12.79 | 23.10 | 59 | 1 |
| <i>Erithacus rubecula</i> | 0.18 | 16.35 | 5.43 | 15.23 | 26 | 0 |
| <i>Ficedula hypoleuca</i> | 0.64 | 14.35 | 5.39 | 30.00 | 1 | 1 |
| <i>Fringilla coelebs</i> | 0.06 | 24.20 | 8.92 | 15.84 | 67 | 1 |
| <i>Galerida cristata</i> | -0.08 | 44.65 | 6.72 | 42.61 | 2 | 0 |
| <i>Garrulus glandarius</i> | 0.45 | 161.70 | 10.81 | 18.92 | 13 | 0 |
| <i>Hippolais icterina</i> | -1.68 | 13.30 | 8.05 | 27.08 | 13 | 0 |
| <i>Hirundo rustica</i> | -0.11 | 19.10 | 10.20 | 21.92 | 25 | 1 |
| <i>Lanius collurio</i> | 1.11 | 30.70 | 6.10 | 38.91 | 2 | 1 |
| <i>Loxia curvirostra</i> | 1.37 | 40.60 | 4.60 | 42.12 | 12 | 1 |
| <i>Lullula arborea</i> | 0.22 | 30.05 | 5.00 | 17.24 | 2 | 0 |
| <i>Luscinia luscinia</i> | -2.42 | 25.00 | 15.89 | 33.50 | 4 | 0 |
| <i>Miliaria calandra</i> | -0.62 | 47.65 | 12.59 | 17.63 | 19 | 0 |
| <i>Motacilla alba</i> | 0.27 | 20.75 | 11.88 | 25.10 | 30 | 1 |
| <i>Motacilla cinerea</i> | 0.22 | 17.35 | 6.13 | 14.06 | 16 | 1 |
| <i>Motacilla flava</i> | 0.94 | 17.45 | 9.70 | 17.33 | 9 | 1 |
| <i>Muscicapa striata</i> | -0.11 | 15.50 | 8.50 | 28.00 | 6 | 0 |
| <i>Oenanthe oenanthe</i> | 0.72 | 23.95 | 14.67 | 21.33 | 6 | 1 |
| <i>Parus ater</i> | -0.44 | 9.25 | 5.09 | 9.80 | 5 | 0 |
| <i>Parus caeruleus</i> | 0.03 | 11.75 | 6.12 | 17.74 | 34 | 1 |
| <i>Parus cristatus</i> | -0.05 | 11.15 | 6.08 | 21.14 | 7 | 0 |
| <i>Parus major</i> | 0.32 | 18.50 | 5.59 | 15.97 | 63 | 1 |
| <i>Parus palustris</i> | -0.42 | 11.90 | 7.14 | 18.83 | 12 | 0 |
| <i>Passer domesticus</i> | 0.25 | 30.35 | 3.83 | 24.44 | 64 | 1 |
| <i>Passer montanus</i> | 0.51 | 21.70 | 4.91 | 20.18 | 34 | 0 |
| <i>Phoenicurus ochruros</i> | -0.08 | 16.00 | 7.00 | 62.16 | 3 | 1 |
| <i>Phoenicurus phoenicurus</i> | -0.47 | 15.90 | 9.03 | 30.50 | 8 | 1 |
| <i>Phylloscopus trochilus</i> | -0.59 | 9.35 | 8.49 | 19.56 | 48 | 0 |
| <i>Pica pica</i> | -1.68 | 228.00 | 15.61 | 30.61 | 61 | 0 |
| <i>Prunella modularis</i> | 0.33 | 18.95 | 5.51 | 12.32 | 22 | 0 |
| <i>Pyrrhula pyrrhula</i> | 0.26 | 31.05 | 5.90 | 30.82 | 11 | 1 |
| <i>Regulus regulus</i> | -0.34 | 5.80 | 4.01 | 17.20 | 10 | 1 |
| <i>Riparia riparia</i> | -0.33 | 13.15 | 23.81 | 30.00 | 7 | 0 |
| <i>Saxicola rubetra</i> | 0.20 | 16.60 | 17.26 | 26.89 | 9 | 1 |
| <i>Sitta europaea</i> | 1.22 | 23.90 | 7.63 | 23.13 | 8 | 1 |
| <i>Streptopelia decaocto</i> | -0.78 | 201.50 | 5.31 | 22.40 | 20 | 0 |
| <i>Sturnus vulgaris</i> | 0.04 | 80.50 | 14.66 | 22.11 | 62 | 1 |
| <i>Sylvia atricapilla</i> | -0.44 | 18.85 | 6.03 | 20.39 | 23 | 1 |
| <i>Sylvia borin</i> | -0.35 | 19.05 | 6.18 | 21.76 | 34 | 0 |
| <i>Sylvia communis</i> | -0.23 | 14.50 | 7.95 | 25.13 | 55 | 1 |
| <i>Sylvia curruca</i> | -0.07 | 12.40 | 4.70 | 19.33 | 15 | 0 |
| <i>Troglodytes troglodytes</i> | -0.99 | 8.90 | 5.81 | 18.47 | 30 | 0 |
| <i>Turdus merula</i> | 0.21 | 95.85 | 7.76 | 23.29 | 182 | 1 |
| <i>Turdus philomelos</i> | 0.90 | 70.50 | 11.40 | 25.24 | 21 | 0 |
| <i>Turdus viscivorus</i> | 0.10 | 117.80 | 20.84 | 37.63 | 8 | 0 |

See Methods for sources and methods.

APPENDIX 2

Information on bird species used for investigating relative flight distance of singing individuals: body mass (g); relative flight distance of singing males; sample size for flight distance; prevalence of *Plasmodium*, *Haemoproteus*, *Leucocytozoon*, and *Trypanosoma*; NAb abundance; adult T-cell response (mm); sexual dichromatism; song post exposure; and singing habitat

| Species | Body mass (g) | Relative flight distance of singing males | N | Prevalence of <i>Plasmodium</i> | Prevalence of <i>Haemoproteus</i> | Prevalence of <i>Leucocytozoon</i> | Prevalence of <i>Trypanosoma</i> | NAb abundance | Sexual dichromatism | Song post exposure | Habitat |
|-----------------------------------|---------------|---|-----|---------------------------------|-----------------------------------|------------------------------------|----------------------------------|---------------|---------------------|--------------------|---------|
| <i>Acrocephalus schoenobaenus</i> | 11.9 | 0.13 | 31 | 0.00 | 0.13 | 0.01 | 0.01 | 1.00 | 0 | 33 | 1 |
| <i>Aegithalos caudatus</i> | 8.8 | 0.08 | 4 | 0.00 | 0.00 | 0.00 | 0.00 | — | 0 | — | 2 |
| <i>Alauda arvensis</i> | 36.4 | 0.51 | 29 | 0.00 | 0.09 | 0.00 | 0.00 | — | 0 | 100 | 0 |
| <i>Anthus spinoletta</i> | 21.5 | -0.22 | 21 | 0.00 | 0.00 | 0.08 | 0.00 | — | 0 | — | 0 |
| <i>Anthus trivialis</i> | 23.4 | 0.32 | 17 | 0.00 | 0.10 | 0.12 | 0.02 | — | 0 | 100 | 1 |
| <i>Carduelis chloris</i> | 27.6 | 0.05 | 34 | 0.07 | 0.37 | 0.00 | 0.00 | 0.00 | 1 | 55 | 2 |
| <i>Certhia brachydactyla</i> | 9.1 | -0.15 | 8 | — | — | — | — | — | 0 | 33 | 2 |
| <i>Columba palumbus</i> | 494.5 | 0.15 | 66 | 0.14 | 0.25 | 0.13 | 0.07 | — | 0 | 60 | 2 |
| <i>Cuculus canorus</i> | 120.5 | -0.10 | 12 | 0.00 | 0.00 | 0.00 | 0.00 | — | 0 | 40 | 2 |
| <i>Emberiza citrinella</i> | 26.8 | 0.09 | 64 | 0.03 | 0.62 | 0.05 | 0.01 | 2.25 | 1 | 72 | 1 |
| <i>Emberiza schoeniclus</i> | 18.8 | 0.09 | 59 | 0.00 | 0.01 | 0.09 | 0.02 | — | 1 | 63 | 0 |
| <i>Erethacus rubecula</i> | 16.4 | 0.00 | 26 | 0.01 | 0.07 | 0.04 | 0.01 | — | 0 | 52 | 2 |
| <i>Fringilla coelebs</i> | 24.2 | 0.17 | 67 | 0.00 | 0.29 | 0.14 | 0.07 | 1.00 | 1 | 46 | 2 |
| <i>Garrulus glandarius</i> | 161.7 | 0.11 | 13 | 0.03 | 0.06 | 0.84 | 0.09 | — | 0 | — | 2 |
| <i>Hippolais icterina</i> | 13.3 | -0.23 | 13 | 0.07 | 0.07 | 0.00 | 0.00 | 0.67 | 0 | 30 | 2 |
| <i>Hirundo rustica</i> | 19.1 | 0.11 | 25 | 0.00 | 0.02 | 0.01 | 0.04 | 0.00 | 1 | — | 0 |
| <i>Miliaria calandra</i> | 47.7 | 0.20 | 19 | 0.20 | 0.10 | 0.00 | 0.00 | — | 0 | 96 | 0 |
| <i>Motacilla flava</i> | 17.4 | 0.09 | 9 | 0.02 | 0.03 | 0.10 | 0.04 | — | 1 | 100 | 0 |
| <i>Muscicapa striata</i> | 15.5 | -0.10 | 6 | 0.00 | 0.20 | 0.26 | 0.14 | — | 0 | 35 | 2 |
| <i>Parus ater</i> | 9.2 | -0.06 | 5 | 0.01 | 0.02 | 0.10 | 0.02 | 0.00 | 0 | 33 | 2 |
| <i>Parus caeruleus</i> | 11.8 | -0.08 | 34 | 0.01 | 0.09 | 0.16 | 0.04 | 0.00 | 1 | 58 | 2 |
| <i>Parus major</i> | 18.5 | 0.00 | 63 | 0.04 | 0.46 | 0.03 | 0.01 | 1.00 | 1 | 61 | 2 |
| <i>Passer domesticus</i> | 30.4 | 0.02 | 64 | 0.07 | 0.15 | 0.00 | 0.00 | 0.50 | 1 | 85 | 0 |
| <i>Passer montanus</i> | 21.7 | -0.01 | 34 | 0.13 | 0.12 | 0.00 | 0.00 | 1.20 | 0 | 90 | 1 |
| <i>Phoenicurus phoenicurus</i> | 15.9 | 0.07 | 8 | 0.01 | 0.02 | 0.20 | 0.23 | 4.00 | 1 | 36 | 2 |
| <i>Phylloscopus collybita</i> | 7.7 | -0.08 | 16 | 0.00 | 0.05 | 0.04 | 0.04 | — | 0 | — | 2 |
| <i>Phylloscopus trochilus</i> | 9.3 | 0.21 | 48 | 0.01 | 0.09 | 0.04 | 0.02 | — | 0 | 66 | 2 |
| <i>Pica pica</i> | 228.0 | 0.47 | 61 | 0.00 | 0.07 | 0.45 | 0.12 | — | 0 | — | 2 |
| <i>Prunella modularis</i> | 19.0 | -0.16 | 22 | 0.00 | 0.06 | 0.06 | 0.01 | 2.33 | 0 | 82 | 2 |
| <i>Regulus regulus</i> | 5.8 | -0.01 | 10 | 0.00 | 0.00 | 0.03 | 0.01 | — | 1 | 40 | 2 |
| <i>Saxicola rubetra</i> | 16.6 | 0.13 | 9 | 0.00 | 0.29 | 0.13 | 0.16 | — | 1 | 85 | 0 |
| <i>Sitta europaea</i> | 23.9 | -0.23 | 8 | 0.00 | 0.30 | 0.10 | 0.10 | — | 1 | 90 | 2 |
| <i>Sturnus vulgaris</i> | 80.5 | 0.46 | 62 | 0.00 | 0.01 | 0.01 | 0.00 | 0.00 | 1 | 80 | 2 |
| <i>Sylvia atricapilla</i> | 18.9 | -0.05 | 23 | 0.00 | 0.34 | 0.01 | 0.00 | 4.50 | 1 | 21 | 2 |
| <i>Sylvia borin</i> | 19.0 | -0.01 | 34 | 0.01 | 0.28 | 0.04 | 0.01 | 5.40 | 0 | 44 | 2 |
| <i>Sylvia communis</i> | 14.5 | -0.07 | 55 | 0.00 | 0.16 | 0.01 | 0.00 | 3.50 | 1 | 62 | 1 |
| <i>Sylvia curruca</i> | 12.4 | 0.09 | 15 | 0.03 | 0.06 | 0.00 | 0.00 | — | 0 | 100 | 1 |
| <i>Troglodytes troglodytes</i> | 8.9 | -0.17 | 30 | 0.00 | 0.01 | 0.01 | 0.01 | — | 0 | 26 | 2 |
| <i>Turdus merula</i> | 95.8 | 0.07 | 182 | 0.13 | 0.09 | 0.11 | 0.02 | 4.75 | 1 | 48 | 2 |
| <i>Turdus philomelos</i> | 70.5 | 0.14 | 21 | 0.02 | 0.12 | 0.30 | 0.04 | — | 0 | 66 | 2 |

See Methods for sources.

SUPPLEMENTARY MATERIAL

Supplementary Figure 1 can be found at <http://www.beheco.oxfordjournals.org/>.

E. Flensted-Jensen kindly provided his flight distance data that allowed the cross-validation.

REFERENCES

- Abbas AK, Lichtman AH, Pober JS. 1994. Cellular and molecular immunology. Philadelphia (PA): Saunders.
- Atkinson C, Van Riper C 3rd. 1991. Pathogenicity and epizootiology of avian haematocyst: *Plasmodium*, *Leucocytozoon* and *Haemoproteus*. In: Loye JE, Zuk M, editors. Bird-parasite interactions. Oxford: Oxford University Press. p. 19–48.
- Bachman GC. 1993. The effect of body condition on the trade-off between vigilance and foraging in Belding's ground squirrels. Anim Behav. 46:233–244.
- Badyaev AV. 1997. Altitudinal variation in sexual dimorphism: a new pattern and alternative hypotheses. Behav Ecol. 8:675–690.
- Barker FK, Barrowclough GF, Groth JG. 2001. A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. Proc R Soc Lond B Biol Sci. 269:295–308.
- Barker FK, Cibois A, Schikler P, Feinstein J, Cracraft J. 2004. Phylogeny and diversification of the largest avian radiation. Proc Natl Acad Sci USA. 101:11040–11045.

- Belperron AA, Bockenstedt LK. 2001. Natural antibody affects survival of the spirochete *Borrelia burgdorferi* within feeding ticks. *Infect Immun.* 69:6456–6462.
- Blondel J, Catzeflis F, Perret P. 1996. Molecular phylogeny and the historical biogeography of the warblers of the genus *Sylvia* (Aves). *J Evol Biol.* 9:871–891.
- 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.
- Blumstein DT, Anthony LL, Harcourt RG, Ross G. 2003. Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? *Biol Conserv.* 110:97–100.
- Blumstein DT, Bouskila A. 1996. Assessment and decision making in animals: a mechanistic model underlying behavioral flexibility can prevent ambiguity. *Oikos.* 77:569–576.
- Burnham KP, Anderson DR. 1998. Model selection and inference. New York: Springer.
- Caro T. 2005. Antipredator defenses in birds and mammals. Chicago (IL): Chicago University Press.
- Carroll MC, Prodeus AP. 1998. Linkages of innate and adaptive immunity. *Curr Opin Immunol.* 10:36–40.
- Catchpole CK, Slater PJB. 1995. Bird song: biological themes and variations. Cambridge: Cambridge University Press.
- Chen M, Shi L, Sullivan D Jr. 2001. *Haemoproteus* and *Schistosoma* synthesize heme polymers similar to *Plasmodium* hemozoin and β -hematin. *Mol Biochem Parasitol.* 113:1–8.
- Clark CW. 1994. Antipredator behavior and the asset-protection principle. *Behav Ecol.* 5:159–170.
- Cohen J. 1988. Statistical power analysis for the behavioral sciences. 2nd ed. Hillsdale (NJ): Lawrence Erlbaum.
- Congdon LL, Farmer JN, Longenecker BM, Breitenbach RP. 1969. Natural and acquired antibodies to *Plasmodium lophurae* in intact and bursaless chickens. II. Immunofluorescent studies. *J Parasitol.* 55:817–824.
- Curio E. 1976. The ethology of predation. Berlin (Germany): Springer.
- Dill LM. 1987. Animal decision making and its ecological consequences; the future of aquatic ecology and behavior. *Can J Zool.* 65:803–811.
- Dunning JB Jr. 1993. CRC handbook of avian body masses. Boca Raton (FL): CRC Press.
- Felsenstein J. 1985. Phylogenies and the comparative method. *Am Nat.* 125:1–15.
- Fisher RA. 1930. The genetical theory of natural selection. Oxford: Clarendon Press.
- Freckleton RP, Harvey PH, Pagel M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *Am Nat.* 160:712–726.
- Frid A, Dill LM. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conserv Ecol.* 6:11.
- Garamszegi LZ. 2006. Comparing effect sizes across variables: generalization without the need for Bonferroni correction. *Behav Ecol.* 17:682–687.
- Garland T Jr, Harvey PH, Ives AR. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst Biol.* 41:18–32.
- Ghalambor CK, Martin TE. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. *Science.* 292:494–497.
- Götmark F, Post P. 1996. Prey selection by sparrowhawks, *Accipiter nisus*: relative predation risk for breeding passerine birds in relation to their size, ecology and behaviour. *Philos Trans R Soc Lond B Biol Sci.* 351:1559–1577.
- Green R. 1979. Sampling design and statistical methods for environmental biologists. New York: Wiley.
- Grell MB. 1998. Fuglenes Danmark. Copenhagen (Denmark): Gad.
- Helbig AJ, Seibold I. 1999. Molecular phylogeny of Palearctic-African *Acrocephalus* and *Hippolais* (Aves: Sylviidae). *Mol Phylogenet Evol.* 11:246–260.
- Huhta E, Rytönen S, Solonen T. 2003. Plumage brightness of prey increases predation risk: an among-species comparison. *Ecology.* 84:1793–1799.
- Jennions MD, Møller AP, Petrie M. 2001. Sexually selected traits and adult survival: a meta-analysis of the phenotypic relationship. *Q Rev Biol.* 76:3–36.
- JMP. 2000. JMP. Cary (NC): SAS Institute Inc.
- Johnstone RA. 1995. Sexual selection, honest advertisement and the handicap principle—reviewing the evidence. *Biol Rev Camb Philos Soc.* 70:1–65.
- Jones KE, Purvis A. 1997. An optimum body size for mammals? Comparative evidence from bats. *Funct Ecol.* 11:751–756.
- Krause J, Loader SP, McDermott J, Ruxton GD. 1998. Refuge use by fish as a function of body length-related metabolic expenditure and predation risks. *Proc R Soc Lond B Biol Sci.* 265:2373–2379.
- Matson KD, Ricklefs RE, Klasing KC. 2005. A hemolysis-hemagglutination assay for characterizing constitutive innate humoral immunity in wild and domestic birds. *Dev Comp Immunol.* 29:275–286.
- Merino S, Martínez J, Barbosa A, Møller AP, de Lope F, Pérez J, Rodríguez-Caabeiro F. 1998. Increase in heat-shock protein from blood cells in response of nestling house martins (*Delichon urbica*) to parasitism: an experimental approach. *Oecologia.* 116:343–347.
- Møller AP, Birkhead TR. 1994. The evolution of plumage brightness in birds is related to extra-pair paternity. *Evolution.* 48:1089–1100.
- Møller AP, Christie P, Lux E. 1999. Parasite-mediated sexual selection: effects of parasites and host immune function. *Q Rev Biol.* 74:3–20.
- Møller AP, Erritzøe J. 2000. Predation against birds with low immunocompetence. *Oecologia.* 122:500–504.
- Møller AP, Haussay C. 2007. Fitness consequences of variation in natural antibodies and complement in the barn swallow *Hirundo rustica*. *Funct Ecol.* 21:363–371.
- Møller AP, Jennions MD. 2002. How much variance can be explained by ecologists and evolutionary biologists? *Oecologia.* 132:492–500.
- Møller AP, Nielsen JT. 2006. Prey vulnerability in relation to sexual coloration of prey. *Behav Ecol Sociobiol.* 60:227–233.
- Møller AP, Nielsen JT. 2007. Malaria and risk of predation: a comparative study of birds. *Ecology.* 88:871–881.
- Møller AP, Nielsen JT, Garamszegi LZ. 2005. Song post exposure, song features and predation risk. *Behav Ecol.* 17:155–163.
- Mullarney T, Svensson L, Zetterström D, Grant PJ. 2000. The complete guide to the birds of Europe. London: Harper Collins.
- Nakagawa S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behav Ecol.* 15:1044–1045.
- Ochsenbein AF, Fehr T, Lutz C, Suter M, Brombacher F, Hengartner H, Zinkernagel RM. 1999. Control of early viral and bacterial distribution and disease by natural antibodies. *Science.* 286:2156–2159.
- Pagel M. 1997. Inferring evolutionary processes from phylogenies. *Zool Scr.* 26:331–348.
- Purvis A, Rambaut A. 1995. Comparative analysis by independent contrasts (CAIC). *Comput Appl Biosci.* 11:247–251.
- Read AF. 1987. Comparative evidence supports the Hamilton and Zuk hypothesis on parasites and sexual selection. *Nature.* 328:68–70.
- Reid RR, Prodeus AP, Kahn W, Hsu T, Rosen FS, Carroll MC. 1997. Endotoxin shock in antibody-deficient mice: unravelling the role of natural antibody and complement in clearance of lipopolysaccharide. *J Immunol.* 159:970–975.
- Rosenthal R. 1994. Parametric measures of effect size. In: Cooper H, Hedges LV, editors. The handbook of research synthesis. New York: Russell Sage. p. 231–244.
- Scherrer B. 1972. Etude sur le poste de chant. *Jean-le-Blanc.* 11:2–46.
- Scheuerlein A, Ricklefs RE. 2004. Prevalence of blood parasites in European passeriform birds. *Proc R Soc Lond B Biol Sci.* 271:1363–1370.
- Sheldon FH, Slikas B, Kinnarney M, Gill FB, Zhao E, Silverin B. 1992. DNA-DNA hybridization evidence of phylogenetic relationships among major lineages of *Parus*. *Auk.* 109:173–185.
- Sibley CG, Ahlquist JE. 1990. Phylogeny and classification of birds, a study in molecular evolution. New Haven (CT): Yale University Press.
- Sibley CG, Monroe BL Jr. 1990. Distribution and taxonomy of birds of the World. New Haven (CT): Yale University Press.
- Slikas B, Sheldon FH, Gill FB. 1996. Phylogeny of titmice (Paridae): I. Estimate of relationships among subgenera based on DNA-DNA hybridization. *J Avian Biol.* 27:70–82.
- Sokal RR, Rohlf FJ. 1995. Biometry. 3rd ed. New York: Freeman.
- Svensson L. 1984. Identification guide to European passerines. Stockholm (Sweden): L. Svensson.

- Temple SA. 1986. Do predators always capture substandard individuals disproportionately from prey populations? *Ecology*. 68: 669–674.
- Voelker G, Spellman GM. 2004. Nuclear and mitochondrial DNA evidence of polyphyly in the avian superfamily Muscicapidae. *Mol Phylogenet Evol*. 30:386–394.
- Wakelin D. 1996. *Immunity to parasites: how parasitic infections are controlled*. Cambridge: Cambridge University Press.
- Ward S, Lampe HM, Slater PJB. 2004. Singing is not energetically demanding for pied flycatchers, *Ficedula hypoleuca*. *Behav Ecol*. 15:477–484.
- Whiteman NK, Matson KD, Bollmer JL, Parker PG. 2006. Disease ecology in the Galapagos hawk (*Buteo galapagoensis*): host genetic diversity, parasite load and natural antibodies. *Proc R Soc Lond B Biol Sci*. 273:797–804.
- Zuk M, Kolluru GR. 1998. Exploitation of sexual signals by predators and parasitoids. *Q Rev Biol*. 73:415–438.