

# Flight distance and population trends in European breeding birds

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Flight distance reflects the risk that individual animals are willing to take when approached by a potential predator, as shown by a negative relationship between susceptibility to predation and flight distance. Species with long flight distances should more often suffer from disruption of their activities by potential predators, including humans, than species with short distances, resulting in declining reproductive success and hence declining population size of such species if disturbance happens more often. Long flight distances thus suggest that individuals need large amounts of space for their body size, resulting in the prediction that species with long flight distances should have a higher frequency of declining populations than species with short flight distances, when human impact on natural habitats increases. Bird species with long flight distances had declining population trends across Europe in a comparative study of 56 species, even when controlling statistically for other factors associated with population declines, with effect sizes ranging from 0.36 to 0.58 (Pearson's  $r$ ). These findings suggest that standardized measures of flight distance provide reliable information about the population consequences of risk-taking behavior by individuals and the susceptibility of different species to increased levels of disturbance. *Key words:* bird census, birds, population consequences, risk taking. [*Behav Ecol* 19:1095–1102 (2008)]

Why are some species abundant and widespread while others are rare and locally distributed? These are central questions in ecology since the beginning of ecological research (e.g., Andrewartha and Birch 1954; Lack 1954; Begon et al. 1972; Krebs 1972; Ricklefs 1975). Body size is an important correlate of both range size and population size (Gaston 2002). However, given that body size correlates with numerous aspects of living organisms including physiology, life history, behavior, and ecology (e.g., Alexander 1971; Peters 1983; Reiss 1989; Roff 2001), such correlation between body size and range size and population size, respectively, are almost impossible to interpret. Therefore, the question remains. How can we identify factors that predict ecological success in terms of range size and population size?

Disruption of the activity of animals can have severe effects on different fitness components. Such disturbance effects can act through physiology, behavior, reproduction and survival, and nonlethal effects of predation risk. First, the most common effect of disturbance on physiology is the corticosterone response that can be elicited by a wide variety of different factors (Wingfield and Ramenofsky 1999). These include proximity of humans, but the response can also be induced by the proximity of predators (Scheuerlein et al. 2001; Fletcher and Boonstra 2006; Ylönen et al. 2006). The corticosterone response affects a wide variety of activities that in combination has the consequence of reducing the damaging effect of the stressor (Wingfield and Ramenofsky 1999). Exposure to potential predators including humans cannot only affect adult birds but also be transferred to their eggs with detrimental consequences for offspring development and growth (Saino

et al. 2005). In addition, exposure to the proximity of a predator can reduce the efficiency of the immune system, with subsequent increases in the prevalence and intensity of parasite infections (Navarro et al. 2004). A second example of disturbance effects with physiological consequences is increases in metabolism when animals are exposed to human proximity (Belanger and Bédard 1990; Nimon et al. 1995, 1996; Feret et al. 2003). Third, disturbance can also have dramatic effects on the behavior of animals by significant reductions in foraging activity and efficiency (Madsen 1998a; Feret et al. 2003; Bechet et al. 2004), and such effects can potentially affect the energy budget and thus future behavior and reproduction (Feret et al. 2003; Bechet et al. 2004). Fourth, physiological and behavioral consequences of disturbance can have significant effects on reproduction and survival of animals, with effects on long-term trends in population size (Wilson et al. 1991; Woehler et al. 1994; Giese 1996; Cogley and Shears 1999; Arroyo and Razin 2006). In particular, human activities can have dramatic indirect effects on animal behavior most notably through hunting (Madsen 1998a, 1998b; Feret et al. 2003; Tamisier et al. 2003; Bregnballe et al. 2004; Thiollay 2005; Arroyo and Razin 2006) but also through supposedly benign activities like tourism (Madsen 1998a; Arroyo and Razin 2006), sports fishing, sailing, windsurfing, and many others (Rodgers and Smith 1995; Madsen 1998a). Any animal that flees at a long distance when approached by an unarmed human will be at a selective disadvantage, and frequent flight when approached by hunters may also potentially have negative effects on condition and hence reproduction and survival. Finally, nonlethal effects of predation risk can have profound effects on fitness of individuals but also at the population and community levels (e.g., Abrams 1991; Lima 1998). These observations raise the broader question whether interspecific differences in flight distance will affect population trends.

An important requirement by all living organisms is the amount of space needed for successful survival and

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reproduction. Flight distance from a potential predator like a human being will mirror the risks that an individual is willing to take during its daily routine (Blumstein 2006), reflecting the trade-off between the benefits acquired by current activity and the costs of fleeing during the approach of a potential predator. Therefore, analysis of interspecific differences in risk taking as reflected by flight distance will provide important information about the extent to which individuals of different species perceive their environment. Such differences in flight distance will affect the susceptibility of different species to perturbations of the environment and the general disturbance regime caused by other species including human beings. Thus, interspecific differences in flight distance may thereby ultimately influence the distribution and abundance of different species (Blumstein and Fernández-Juricic 2004; Blumstein 2006) because species with long flight distances when approached by a potential predator or a human being will spend less time foraging and more time fleeing than a less wary species. This should result in interspecific differences in costs associated with flight and therefore ultimately differences in energy budget, with potential consequences for survival, reproduction, and population size.

If flight distance reflects “space requirement,” but also the amount of disturbance tolerated, then species with long flight distance should have greater requirements and hence declining populations in a world where human proximity and hence human disturbance is increasing. Thus, species with long flight distances should generally suffer from declining populations because increases in human population sizes and range of outdoor activities should cause disturbance, with consequences for foraging, net energy balance, and hence for survival of reproduction. Therefore, population trends of European birds should be negatively related to flight distance. Previous studies have indicated that agricultural habitats (Fuller et al. 1995; Chamberlain et al. 2000; Donald et al. 2001; Green et al. 2005), habitat loss and fragmentation (Fahrig 2003; Berthold and Fiedler 2005), migration (Hjort and Lindholm 1978; Baillie and Peach 1992; Bauer and Heine 1992; Berthold 2000; Lemoine and Böhning-Gaese 2003), northern distribution and climate change (Parmesan et al. 2000; Walther et al. 2002; Root et al. 2003, 2005; Julliard et al. 2004; Møller et al. 2004), brain mass (Shultz et al. 2005), and body mass (Bennett and Owens 2002) predicted population trends of common breeding birds. Therefore, I used these variables in addition to flight distance as additional predictors in analyses of population trends of breeding birds.

## MATERIALS AND METHODS

### Data

#### *Flight distance*

During March to August 2006–2007, I estimated flight distances for breeding birds, using a standardized technique developed by Blumstein (2006). All estimates were collected blindly with respect to the hypothesis being tested, preventing any conscious or unconscious bias. These recordings were made in Île-de-France and Bretagne, France, and Northern Jutland, Denmark. In brief, when an individual bird had been located while resting, foraging, preening, or singing, I moved at a normal walking speed toward the individual while recording the number of steps (which approximately equals the number of meters). Focal individuals were entirely chosen based on when an individual was first recorded. 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, I also recorded date and time of day 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. I avoided pseudoreplication by only recording individuals of a given sex and species at a given site. I avoided flight response of an individual to my approach affecting the flight response of the next individual chosen by subsequently locating an individual with binoculars ensuring that this individual was unaware of my presence as reflected by its behavior. I recorded a total of 2298 flight distances for 99 species.

Flight distance was consistent for the same species in different studies, as shown by a comparison of the data from the present study and that of Blumstein (2006) (Møller et al. 2008). Furthermore, flight distances estimated by an independent observer were very similar to my estimates (Møller et al. 2008). In addition, flight distances estimated in Denmark were very similar to distances in France (Møller et al. 2008). Finally, flight distances in summer and winter were strongly positively correlated (Møller et al. 2008). This provides evidence for reliability of the estimates.

Coloniality was defined as breeding pairs using territories that only contained nest sites while all other species were considered to be solitarily breeding (following Cramp and Simmons [1977–1994]). There was no significant effect of coloniality on flight distance (partial effect of coloniality in a model with log-transformed flight distance as the dependent variable and coloniality and log-transformed body mass as predictor variables; partial effect of coloniality:  $F = 0.02$ , degrees of freedom [df] = 1,96,  $P = 0.92$ ), suggesting that breeding sociality was not a confounding variable. Therefore, coloniality was not used in subsequent analyses.

#### *Population trends*

I obtained estimates of European population trends for the period 1990–2005, based on national breeding bird censuses (Voricek 2003). There were only information available on population trends for 56 of the 99 species for which I had estimates of flight distances, and obviously, any conclusions about flight distance and population trends are restricted to this sample of species. The estimate of population trend is the proportional additive change in population size from an initial index value of one, with the European index being based on national indices weighted by the relative size of different national populations (<http://www.ebcc.info/index.php?ID=148>).

#### *Migration distance*

I determined the global northernmost and southernmost latitude of the breeding and the wintering distributions, respectively, to the nearest tenth of a degree of all species, based on information on breeding and wintering ranges shown on maps in Cramp and Simmons (1977–1994). Migration distance was simply calculated as the mean of the 2 latitudes during breeding minus the mean of the 2 latitudes during winter.

#### *Brain mass*

Information on brain mass was obtained from Mlikovsky (1990), Garamszegi et al. (2002), and Iwaniuk and Nelson (2003).

*Farmland habitat*

I extracted information on farmland habitat (coded as 0 or 1) from Cramp and Perrins (1977–1994). Coding for habitat was identical to scores for the 48 species that were investigated for population trends across Europe by Voricek (2003).

*Northern distribution limit*

Information on northern distribution limit was recorded from the maps of the worldwide breeding distribution of all species, as reported by Cramp and Perrins (1977–1994).

*Hunting*

Species were classified as hunted or not hunted based on knowledge about the local conditions in the areas where flight distances were estimated.

*Body mass*

Larger species have longer flight distances than small species (Blumstein 2006). Therefore, I used body mass of all species as additional predictor variables based on my own field measurements or in the absence of data as reported by Cramp and Perrins (1977–1994). All data are reported in the Supplementary material (Appendix B).

**Statistical analyses**

Flight distance, starting distance, brain mass, and body mass were  $\log_{10}$  transformed before analyses.

I tested whether flight distance is a species-specific attribute in a nested analysis of variance with flight distance as the response variable and species and starting distance as predictor variables.

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.

I controlled for similarity in phenotype among species due to common phylogenetic descent by calculating standardized independent linear contrasts (Felsenstein 1985), using the software CAIC (Purvis and Rambaut 1995). All branches of the phylogenies were assigned uneven branch lengths, assuming a gradual evolution model as implemented in the software, although a second set of analyses based on similar branch length produced qualitatively similar results to those reported here. I 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) I 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.

I used farmland habitat as a continuous variable in the analyses despite the fact that it was defined as a dichotomous variable because intermediate states of this variable are biologically

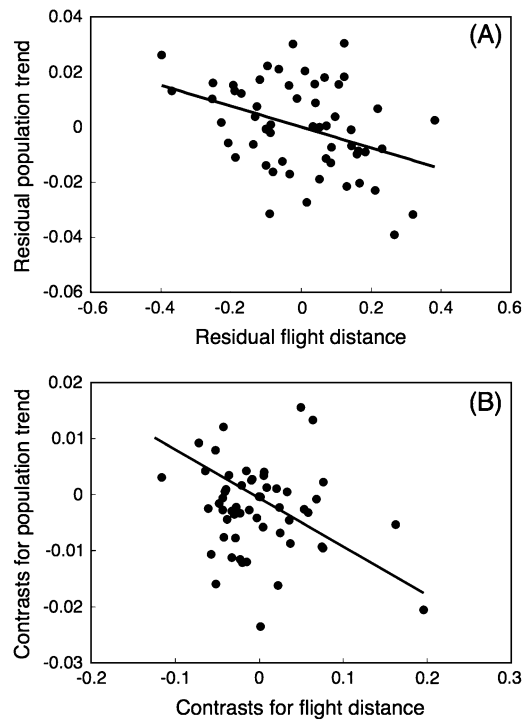
meaningful. Using variables as continuous variables in statistical analyses is similar to using a dichotomous variable as a dummy variable in standard regression analyses (Sokal and Rohlf 1995). Because analysis of standardized contrasts is only able to handle one dichotomous variable at a time (Purvis and Rambaut 1995), using these variables as continuous variables also allowed simultaneous statistical control of all potentially confounding variables.

Relative brain size was expressed as the residuals of a linear regression where the slope was obtained from a log–log phylogenetically corrected regression of brain size on body mass of a large set of 567 bird species for which we were able to retrieve information on both phenotypic traits (Mlikovsky 1990; Garamszegi et al. 2002; Iwaniuk and Nelson 2003) and to code the phylogeny (details not shown). The slope of this regression (based on phylogenetically independent contrasts) was  $\log(\text{brain mass}) = 0.581$  (standard error [SE] = 0.010)  $\log(\text{body mass})$  ( $F = 35.20$ ,  $df = 1,494$ ,  $P < 0.0001$ ; contrasts with standardized residuals  $>|1.96|$  were excluded from the regression analysis). The same procedure was adopted for contrast analyses. In this case, we first calculated contrasts of  $\log(\text{brain size})$  on  $\log(\text{body mass})$  for the set of species included in this study and then calculated the residuals of these contrasts from the above-mentioned phylogenetically corrected regression equation.

The composite phylogeny used in the comparative analyses was based on Sibley and Ahlquist (1990), combined with information from other sources (Sheldon et al. 1992, 2005; Suhonen et al. 1994; Blondel et al. 1996; Slikas et al. 1996; Badyaev 1997; Cibois and Pasquet 1999; Helbig and Seibold 1999; Voelker 1999; Barker et al. 2001, 2004; Yuri and Mindell 2002; Thomas et al. 2004; Voelker and Spellman 2004) (Figure 1 in the Supplementary material). Because information for the composite phylogeny 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 to those found when making the calculations using the taxonomy of Sibley and Monroe (1990).

Most statistical approaches assume 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 variables (Sokal and Rohlf 1995). I weighted each observation by sample size in order to use all data in an unbiased fashion, thereby giving each datum a weight that reflects its degree of precision due to sampling effort (Draper and Smith 1981; Neter et al. 1996). The results were qualitatively similar if I used log-transformed sample size as a weighting factor or if I used unweighted analyses. Comparative analyses may be confounded by sample size if sampling effort is important and if sample size varies considerably among taxa. In order to weight regressions by sample size in the analysis of contrasts, I calculated weights for each contrast by calculating the mean sample size for the taxa immediately subtended by that node (Møller and Nielsen 2007). Population trend was neither significantly related to sample size or log-transformed sample size for flight distance (sample size:  $F = 0.06$ ,  $df = 1,54$ ,  $P = 0.81$ ; log-transformed sample size:  $F = 0.79$ ,  $df = 1,54$ ,  $P = 0.38$ ) nor log-transformed flight distance strongly related to sample size or log-transformed sample size for flight distance (sample size:  $F = 1.32$ ,  $df = 1,54$ ,  $P = 0.26$ ; log-transformed sample size:  $F = 4.53$ ,  $df = 1,54$ ,  $P = 0.04$ ).

Regressions of standardized linear contrasts were forced through the origin because the comparative analyses assume



**Figure 1**  
Population trend for European birds in relation to mean flight distance (meters) of adult individuals of different bird species (A) and (B) standardized linear contrasts. The lines are the regression lines weighted by sample size. Population trend and flight distance was adjusted for effects of body mass.

that there has been no evolutionary change in a character when the predictor variable has not changed (Purvis and Rambaut 1997).

## RESULTS

### Intra- and interspecific variation in flight distance

There was significant variation in flight distance among species ( $F = 22.13$ ,  $df = 98,1939$ ,  $r^2 = 0.51$ ,  $P < 0.0001$ ), with more variation among than within species (Sums of squares [among species] = 139.12, Sums of squares [within species] = 135.47). This provides evidence of flight distances being a species-specific attribute. Mean flight for different species ranged from 3.28 to 200 m, with a mean weighted by sample size of 10.39 m (SE = 1.06; after back-transformation from the  $\log_{10}$ -transformed data),  $N = 99$  species. Inspection of the phylogenetic distribution of flight distance revealed that long flight distances were the ancestral state (Figure 1 in Appendix A). Species that were subject to hunting did not have significantly shorter flight distances for their body size than other species (model that included log-transformed body mass:  $F = 0.001$ ,  $df = 1,53$ ,  $r^2 = 0.00$ ,  $P = 0.93$ ).

Mean flight distance for species increased significantly with body mass (linear regression based on  $\log_{10}$ -transformed variables, weighted by sample size:  $F = 65.99$ ,  $df = 1,97$ ,  $r^2 = 0.40$ ,  $P < 0.0001$ , slope [SE] = 0.27 [0.03]). This relationship was much weaker in a phylogenetic regression ( $F = 4.49$ ,  $df = 1,97$ ,  $r^2 = 0.04$ ,  $P = 0.037$ , slope [SE] = 0.20 [0.10]), implying that body mass was an important confounding variable in the comparative analyses.

**Table 1**  
Full models of European population trends in relation to flight distance and confounding variables in birds

Variable	Sum of squares	df	F	P	Slope (SE)
<b>Species</b>					
Flight distance	0.060	1	11.77	0.0012	-0.053 (0.015)
Starting distance	0.002	1	0.49	0.49	
Migration distance	0.000	1	0.00	0.97	
N latitude	0.005	1	0.91	0.35	
Farmland	0.008	1	1.71	0.20	
Residual brain mass	0.023	1	4.54	0.039	0.021 (0.010)
Error	0.245	48			
<b>Contrasts</b>					
Flight distance	0.007	1	6.96	0.011	-0.040 (0.015)
Starting distance	0.000	1	0.41	0.52	
Migration distance	0.002	1	1.80	0.19	
N latitude	0.003	1	3.57	0.065	
Farmland	0.002	1	2.42	0.13	
Residual brain mass	0.000	1	0.24	0.63	
Error	0.045	48			

The models were weighted by sample size and had the statistics (A)  $F = 4.72$ ,  $df = 6,48$ ,  $r^2 = 0.37$ ,  $P = 0.0007$ , and (B)  $F = 3.00$ ,  $df = 6,48$ ,  $r^2 = 0.06$ ,  $P = 0.011$ .

### Population trends and flight distance

The population trends of 56 species of birds across Europe ranged from -0.0419 to 0.0283, with a mean of -0.0033 (SE = 0.0016), showing no evidence of a general decline (1-sample  $t$ -test,  $t = -1.51$ ,  $df = 55$ ,  $P = 0.14$ ). Population trend was explained by flight distance (partial regression:  $F = 26.19$ ,  $df = 1,53$ ,  $r^2 = 0.33$ ,  $P < 0.0001$ , slope [SE] = -0.054 [0.011], effect size estimated as Pearson's  $r = 0.58$ ) and body mass (partial regression:  $F = 8.95$ ,  $df = 1,53$ ,  $r^2 = 0.14$ ,  $P = 0.0042$ , slope [SE] = 0.014 [0.005], effect size = 0.38), with species with long flight distances and smaller species having population declines more frequently than predicted by chance (Figure 1A). An analysis of contrasts only confirmed the effect of flight distance, with an effect size of 0.40 (Figure 1B;  $F = 10.12$ ,  $df = 1,53$ ,  $r^2 = 0.16$ ,  $P = 0.0025$ , slope [SE] = -0.039 [0.012], effect size = 0.40), whereas the effect of body mass did not reach statistical significance ( $F = 0.70$ ,  $df = 1,53$ ,  $r^2 = 0.01$ ,  $P = 0.41$ , effect size = 0.11).

A full model that included flight distance and all potentially confounding variables showed a significant effect of flight distance and residual brain mass (Table 1; effect size for flight distance = 0.44; effect size for residual brain mass = 0.29). In an analysis of contrasts, only flight distance was retained as a significant predictor (Table 1; effect size = 0.36).

## DISCUSSION

Flight distance of adult birds when approached by a human being varied significantly among species, with mean distance explaining interspecific variation in population trends in Europe, with a large effect size of 0.36–0.58 depending on the analysis. In general, bird species with long flight distances for their body mass had declining populations compared with species with short flight distances, and this effect was independent of a range of factors previously suggested to account for interspecific variation in population trends.

This study was based on extensive field data on flight distance of adult birds during the breeding season, and I tested the reliability of flight distance estimates in several ways. First, my mean estimates were very similar to 2 independent data sets

of mean flight distances obtained by an independent observer in one of my study areas (E. Flensted-Jensen) and obtained elsewhere in Europe by Blumstein (2006). The degree of consistency was very high, implying that flight distance estimates can be reliably estimated as described here. These findings also imply that estimates are repeatable across relatively large geographic scales. The present study was based on the assumption that flight distance from a human approaching an individual bird reflected natural behavior performed in response to a potential risk of predation. Elsewhere, I have tested this assumption by showing that mean flight distance of different species of passerine birds is strongly negatively correlated with risk of predation by the European sparrow hawk *Accipiter nisus* (Møller et al. 2008). Therefore, mean flight distance as reported here is reflecting not only the response to an approaching human but also the accepted risk to predation by one of the most common predators in the Western Palearctic. The significant increase in flight distance of birds with increasing body mass may arise from large bird species needing longer distances for takeoff and climb rates decreasing with increasing body mass (Hedenström and Ålerstam 1992; Møller 2008).

Ornithological societies have been conducting bird censuses for more than 40 years, with population trends now being available for the entire European continent (Voricek 2003). The ecological and environmental factors responsible for interspecific differences in population trends have been the subject of close scrutiny during the last decade. Previous studies have indicated that agricultural habitats (Fuller et al. 1995; Chamberlain et al. 2000; Donald et al. 2001; Green et al. 2005), habitat loss and fragmentation (Fahrig 2003; Berthold and Fiedler 2005), migration (Hjort and Lindholm 1978; Baillie and Peach 1992; Bauer and Heine 1992; Berthold 2000; Lemoine and Böhning-Gaese 2003; Sanderson et al. 2006), northern distribution limits and therefore climate change (Parmesan et al. 2000; Walther et al. 2002; Root et al. 2003, 2005; Julliard et al. 2004; Møller et al. 2004), brain mass (Shultz et al. 2005), and body mass (Bennett and Owens 2002) predicted population trends of common breeding birds through effects of environmental change on these variables. I analyzed these factors but also flight distance as predictors of European population trends. Only flight distance was retained as a significant predictor in both species-specific and comparative analyses (Table 1). This finding suggests that mean flight distance and, by inference, the risk that the average individual of different species is willing to take when approached by a potential predator, as shown by relationships between flight distance and risk of predation by sparrow hawk, malarial infection, and innate immune response (Møller et al. 2008), provides the best known predictor of population trends. Whereas many other studies have suggested that other factors account for population trends, I was unable to provide any significant evidence consistent with those previous claims. Here I hypothesize that the population declines of species with long flight distances have come about by increasing levels of disturbance by humans and perhaps their domestic animals (such as dogs and cats) during the last decades.

Because flight distance was defined as the distance when an individual bird took flight when approached by a human, previous experience with humans could have played a role as a mechanism underlying interspecific differences in population trends. If that were the case, this would still raise the question why species that suffered from declining populations did not become habituated to humans. Three pieces of evidence suggests that habituation is not the underlying cause of interspecific differences in flight distance. First, flight distance is significantly negatively related to risk of predation by the European sparrow hawk (Møller et al. 2008), suggesting that

risk taking as reflected by flight distance relates directly to risk of mortality. Furthermore, singing males had shorter flight distances when prevalence of malaria was high and when levels of innate immunity were high (Møller et al. 2008). These findings suggest that short flight distances are associated with considerable risks and that species with reduced survival prospects as reflected by parasitism and immunity take greater risks than the average species. Second, the difference in flight distance between urban and rural populations of the same species is positively related to time since urbanization (Møller 2008). Third, individuals are consistent in flight distance when tested repeatedly (Møller AP, unpublished data), suggesting that habituation is not causing flight distance to decrease rapidly with increasing exposure to humans.

The actual mechanisms, underlying the patterns reported here, were not the subject of this study but obviously need to be addressed explicitly. A potential mechanism links flight distance and disturbance to foraging efficiency and resource use (Madsen 1998a; Fernández-Juricic 2002; Feret et al. 2003; Bechet et al. 2004; Blumstein et al. 2005; Rodríguez-Prieto and Fernández-Juricic 2005), body condition (Feret et al. 2003; Bechet et al. 2004), and therefore to reproductive success (Wilson et al. 1991; Woehler et al. 1994; Giese 1996; Cogley and Shears 1999; Arroyo and Razin 2006). This mechanism implies that a high level of responsiveness to disturbance reduces resource use and foraging efficiency under a high and increasing disturbance regime, causing a reduction in body condition and subsequently reduced reproductive success. Such nonlethal effects of disturbance are important in ecology (e.g., Abrams 1991; Lima 1998). Alternatively, flight distance can be considered to represent the risk that an individual of a given species is willing to take when engaged in a given activity (Blumstein 2006). Therefore, individuals with large residual reproductive value should take small risks, providing a link between a fast life history and short flight distances. This potential mechanism may help explain the coexistence of species with short and long flight distances because such species would represent different life-history strategies.

In conclusion, I have described a novel measure of animal behavior that correlates with population trends in birds. This index of space use and disturbance tolerance may assess the susceptibility of different species to perturbations, be they hunting, tourism, or other human activities, but also as a means of assessing general risk aversiveness of different species.

## SUPPLEMENTARY MATERIAL

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

E. Flensted-Jensen kindly provided data on flight distances.

## APPENDIX A

Composite phylogenetic relationship between bird species with information on flight distance. The main sources were Sibley and Ahlquist (1990), combined with other sources listed in Materials and methods. Species with short (white branches) and long flight distances for a given body mass are shown.

## APPENDIX B

Information on mean flight distance (meters), sample size for flight distance, European population trend, body mass (grams), brain mass (grams), farmland breeding habitat, migration distance (degrees latitude), northernmost breeding distribution limit (degrees N latitude), and hunting (0—not hunted, 1—hunted) for bird species included in the present study. See Materials and methods for further information.

Species	Flight distance (m)	N	European population trend	Body mass (g)	Brain mass (g)	Farmland breeding habitat	Migration distance	Northernmost breeding distribution limit	Hunting
<i>Aegithalos caudatus</i>	4.17	4	0.0017	8.80	0.41	0	0.00	70.33	0
<i>Alauda arvensis</i>	13.92	29	-0.0133	36.40	0.97	1	13.02	71.16	0
<i>Anthus trivialis</i>	13.28	17	-0.0261	23.40	0.68	0	47.07	70.50	0
<i>Buteo buteo</i>	51.07	8	0.0000	806.50	7.90	0	29.57	67.33	0
<i>Carduelis cannabina</i>	13.90	28	-0.0419	18.95	0.67	1	4.11	66.00	0
<i>Carduelis carduelis</i>	7.66	4	0.0130	15.60	0.59	1	1.16	63.57	0
<i>Carduelis chloris</i>	7.10	34	-0.0052	27.65	0.89	0	1.34	70.31	0
<i>Carduelis flammea</i>	2.62	6	0.0237	13.05	0.59	0	9.46	76.00	0
<i>Carduelis spinus</i>	3.96	5	-0.0008	13.80	0.56	0	6.83	70.00	0
<i>Certhia brachydactyla</i>	7.61	8	0.0283	9.15	0.53	0	0.00	55.74	0
<i>Certhia familiaris</i>	4.55	3	-0.0028	9.15	0.55	0	0.00	70.33	0
<i>Columba palumbus</i>	10.99	66	0.0070	494.50	2.38	1	2.04	67.33	1
<i>Corvus corone</i>	29.30	56	0.0025	544.50	8.14	1	5.71	71.17	1
<i>Corvus monedula</i>	23.37	32	-0.0168	249.00	4.69	1	0.28	66.36	1
<i>Cuculus canorus</i>	21.03	12	-0.0115	120.50	2.24	0	49.38	70.47	0
<i>Dendrocopos major</i>	11.68	8	0.0166	89.65	2.51	0	0.00	68.67	0
<i>Emberiza citrinella</i>	12.51	64	-0.0118	26.75	0.82	1	4.72	70.44	0
<i>Emberiza schoeniclus</i>	12.79	59	-0.0107	18.80	0.68	1	10.52	71.18	0
<i>Erithacus rubecula</i>	5.43	26	0.0145	16.35	0.66	0	5.00	70.00	0
<i>Falco tinnunculus</i>	18.02	3	-0.0325	174.50	3.68	1	5.59	70.63	0
<i>Ficedula hypoleuca</i>	5.39	1	-0.0165	14.35	0.45	0	42.99	70.67	0
<i>Fringilla coelebs</i>	8.92	67	-0.0029	24.20	0.77	0	5.54	71.25	0
<i>Galerida cristata</i>	6.72	2	0.0095	44.65	1.08	1	0.00	57.59	0
<i>Garrulus glandarius</i>	10.81	13	0.0102	161.70	4.15	0	0.00	69.83	0
<i>Hippolais icterina</i>	8.05	13	-0.0098	13.30	0.54	0	71.33	70.00	0
<i>Hirundo rustica</i>	10.20	25	-0.0244	19.10	0.58	1	42.34	70.38	0
<i>Lanius collurio</i>	6.10	2	0.0089	30.70	1.00	0	64.72	66.33	0
<i>Lullula arborea</i>	5.00	2	0.0069	30.05		0	3.79	62.14	0
<i>Miliaria calandra</i>	12.59	19	-0.0033	47.65	1.17	1	6.41	59.26	0
<i>Motacilla alba</i>	11.88	30	-0.0120	20.75	0.58	1	18.12	71.17	0
<i>Motacilla flava</i>	9.70	9	0.0156	17.45	0.47	1	40.98	70.67	0
<i>Muscicapa striata</i>	8.50	6	-0.0156	15.50	0.53	0	64.40	70.50	0
<i>Parus ater</i>	5.09	5	-0.0145	9.25	0.51	0	0.00	67.33	0
<i>Parus caeruleus</i>	6.12	34	0.0080	11.75	0.65	0	0.00	67.33	0
<i>Parus major</i>	5.59	63	0.0047	18.50	0.85	0	0.00	70.67	0
<i>Parus palustris</i>	7.14	12	-0.0213	11.90	0.58	0	0.00	65.00	0
<i>Passer montanus</i>	4.91	34	-0.0087	21.70	0.79	1	3.62	70.10	0
<i>Phoenicurus phoenicurus</i>	9.03	8	0.0128	15.90	0.54	0	33.93	70.50	0
<i>Phylloscopus collybita</i>	6.71	16	0.0018	7.70	0.38	0	22.55	70.29	0
<i>Phylloscopus trochilus</i>	8.49	48	-0.0225	9.35	0.31	0	68.08	71.18	0
<i>Pica pica</i>	15.61	61	-0.0368	228.00	5.34	1	0.00	71.25	1
<i>Picus viridis</i>	17.12	9	0.0250	193.50	4.35	0	0.00	66.00	0
<i>Prunella modularis</i>	5.51	22	-0.0091	18.95	0.71	0	9.23	70.67	0
<i>Pyrrhula pyrrhula</i>	5.90	11	-0.0144	31.05	0.89	0	0.00	70.31	0
<i>Regulus regulus</i>	4.01	10	-0.0179	5.80	0.38	0	0.00	70.29	0
<i>Saxicola rubetra</i>	17.26	9	-0.0002	16.60	0.67	1	34.84	70.00	0
<i>Sitta europaea</i>	7.63	8	-0.0202	23.90	1.11	0	0.00	67.00	0
<i>Sturnus vulgaris</i>	14.66	62	-0.0044	80.50	1.70	1	2.63	71.25	0
<i>Sylvia atricapilla</i>	6.03	23	0.0194	18.85	0.67	0	19.64	70.10	0
<i>Sylvia borin</i>	6.18	34	-0.0019	19.05	0.62	0	63.25	70.31	0
<i>Sylvia communis</i>	7.95	55	0.0155	14.50	0.56	1	53.05	69.33	0
<i>Troglodytes troglodytes</i>	5.81	30	0.0184	8.90	0.50	0	1.34	69.33	0
<i>Turdus merula</i>	7.76	182	0.0116	95.85	1.92	0	3.98	71.17	0
<i>Turdus philomelos</i>	11.40	21	0.0110	70.50	1.59	0	14.65	70.33	0
<i>Turdus viscivorus</i>	20.84	8	-0.0057	117.80	2.21	0	4.36	69.00	0
<i>Vanellus vanellus</i>	39.47	51	-0.0370	218.50	2.16	1	12.08	70.16	1

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