



The value of a mouthful: Flight initiation distance as an opportunity cost

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ABSTRACT

Flight initiation distance of animals when approached by a potential predator reflects the risk that an individual is willing to take when the individual has to gauge the value of staying put relative to the cost of flight. I predicted that this cost–benefit balance would depend on the opportunity cost of fleeing. This opportunity cost can be estimated as the difference in flight initiation distance (FID) between an individual engaged in eating rather than just loafing. I estimated FID of 55 species of birds when approached by a human whilst eating or loafing. There was highly significant variation in difference in FID between these two situations amongst species. Species eating mobile food that is difficult to catch showed little difference in FID between the two situations, whilst species eating immobile food such as seeds had longer FID when eating than when loafing. This difference was fully attributed to differences in relative eye size, because species that had longer FIDs when foraging rather than loafing had small eyes, whilst species with long FIDs when loafing rather than foraging had large eyes. Species with long FIDs, when foraging compared to loafing, had low adult annual survival rates and vice versa. This effect was independent of whether mobile or immobile food was consumed. These findings suggest that individuals of different species adjust their FID to the probability of adult survival and also that differences in visual acuity among species as reflected by eye size linked to differences in food mobility affect the opportunity cost of risk taking.

KEYWORDS

eye size – flight initiation distance – mobile prey – opportunity cost – risk taking – survival rate

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INTRODUCTION

All animals require food for maintenance and reproduction, but food is acquired at a risk of predation (e.g. Godin & Smith 1988). A delay in foraging has negative effects on nutritional state (Van der Veen & Sivars 2000) and starvation (Sih 1997). Thus animals face a trade-off with hungry individuals taking more or greater risks because the benefits of risk taking increase with increasing level of hunger (Damsgard & Dill 1998). Such differences in risk-taking behaviour may arise from different categories of individuals behaving differently. Previous studies have shown consistent individual differences in risk-taking behaviour (Godin & Dugatkin 1996; Coleman & Wilson 1998; Elliot & Thrash 2002). Such differences in risk taking may be caused by age, reproductive state and parasite prevalence (e.g. Koivula et al. 1994; Candolin 1998; Kavaliers & Choleris 2001).

Flight initiation distance (FID) reflects risk taking (Ydenberg & Dill 1986; Cooper & Frederick 2007, 2010; Møller et al. 2008), and thus it should depend on the relative value

of the current activity, which is basically an opportunity cost (Møller & Garamszegi 2012; Cooper & Blumstein 2014). Risk taking should be adjusted to the probability of survival, with individuals of species with low prospects of survival taking greater risks. However, survival rate is not the only factor affecting risk-taking behaviour but may also depend on the kind of food being consumed. Mobile food may easily escape when a predator distracts a potential prey individual, whilst there is no such risk for individuals consuming immobile food such as seeds. Thus, the trade-off between vigilance and feeding may depend on whether food can readily be recovered. Furthermore, species may differ in visual acuity, affecting the ability of individuals to detect and respond to potential risk and also to detect food. Some species have relatively large eyes that may provide individuals with more information about risks in the immediate neighbourhood (e.g. Garamszegi et al. 2002; Møller & Erritzøe 2010, 2014).

The cost of flight is basically an opportunity cost because flight interferes with other activities. This general opportunity cost has, to the best of my knowledge, not been quantified. Here I adopted a simple natural experiment to quantify the magnitude of this opportunity cost and its ecological correlates. Risk taking was estimated under two different conditions, whilst individuals were eating and whilst loafing. Because the value of food will depend on survival rate and a number of additional factors, as described earlier, it is difficult to disentangle the underlying relationship between risk taking and survival without accounting for these confounding effects. However, these confounding effects can potentially be lumped as residual effects because all individuals, if sampled randomly, will have the same probability of being a male, a juvenile, an infected individual or any other property that affects FID. If there is a difference in FID of individuals depending on their current behaviour, then this difference will not depend on residual effects after accounting for feeding and loafing because these residual effects will cancel out when investigating the difference in risk-taking behaviour between behavioural contexts. Therefore, the difference in risk-taking behaviour caused by current activity should be readily quantifiable, because the residual effects owing to sex, age, habitat and other variables cancel out when considering only the differences in risk-taking behaviour. This approach has previously been used to investigate differences in FID between displaying and non-displaying males (Møller *et al.* 2008) and differences in FID between urban and rural populations of the same species of birds (Møller 2008b).

The aim of the present study is to quantify the opportunity cost of fleeing for individuals involved in eating or loafing, respectively, assuming that individuals engaged in eating would differ in risk-taking behaviour from those engaged in loafing. I predicted that (1) species would differ in risk-taking behaviour dependent on current activity (i.e. eating or loafing) and (2) species eating mobile prey should differ in flight response in these two situations from species eating immobile food. Two different scenarios might apply. Individuals of species eating mobile prey might be distracted from vigilance, causing them to be less vigilant and, hence, have shorter FIDs when eating than when loafing. Alternatively, species feeding on mobile prey may have evolved greater visual acuity when foraging, and this increase in acuity could also be beneficial during predator avoidance. If that was the case, we should expect such species to have longer FIDs than species feeding on immobile food items. (3) Because information about risk and the environment is perceived through the eyes (and other sense organs), species with relatively larger eyes should be able to glean more information from the environment and, hence, adjust their flight behaviour accordingly (Møller & Erritzøe 2010, 2014). Thus, I predicted a negative relationship between difference in FID between foraging and loafing and relative eye size adjusted for body size. (4) Finally, I predicted that the relative risk taken whilst eating and loafing should depend on adult survival rate, species with high survival rates take relatively smaller risks when foraging.

1. MATERIALS AND METHODS

1.1. Study sites

Weekly during February to September 2008, I estimated FIDs for birds, using a standardised technique developed by Blumstein (2006). All estimates were collected blindly with respect to the hypothesis being tested, because the present study was not envisaged when the data were collected, preventing any conscious or unconscious bias. These recordings were made in Ile-de-France, France, and Northern Jutland, Denmark. I obtained data on 931 FIDs for individuals involved in eating and loafing for 55 species of birds.

1.2. Flight initiation distance

In brief, when an individual bird had been located with a pair of binoculars, I moved at a normal walking speed towards the individual whilst recording the number of steps (which approximately equals the number of meters (Møller *et al.* 2008)). The distance at which the individual took flight was recorded as the FID, whilst the starting distance was the distance from where the observer started walking up to the position of the bird. If the individual was positioned in the vegetation, the height above ground was recorded to the nearest meter. All individuals eating whilst being approached, as judged from food being present in the beak or on the substrate where the individual was pecking, were scored as eating, whilst individuals resting were assigned to a second category of 'loafing' individuals. Whilst recording these FIDs, I also recorded the date and time of day and the sex of the individual if external characteristics allowed sexing with binoculars. FID was estimated as the square root of the sum of the squared horizontal distance and the squared height above ground level (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 shorter FIDs than adults (A. P. Møller unpublished data). If there was doubt about age, an individual was not recorded. I avoided pseudo-replication by only recording individuals of a given sex and species at a given site.

FID was consistent for the same species in different studies, as shown by a comparison of data from previous studies (Møller *et al.* 2008a-c) and those of Blumstein (2006). Furthermore, FIDs estimated by an independent observer were also very similar to my estimates (Møller *et al.* 2008a-c). In addition, FIDs estimated in Denmark were very similar to distances in France (Møller *et al.* 2008c). Finally, FIDs in summer and winter were strongly positively correlated (Møller *et al.* 2008c). This provides evidence of reliability of estimates.

1.3. Confounding variables

Starting distance. The starting distance used when approaching an individual bird scored for FID is the distance at which the bird is initially seen and then approached. Previous studies have shown that starting distance is strongly positively cor-

related with FID (e.g. Blumstein 2006). I avoided this problem of collinearity by searching habitats for birds with a pair of binoculars when choosing an individual for estimating FID. In this way, I assured that almost all individuals were approached from a distance of at least 30 m, thereby keeping starting distances relatively constant across species.

Urban habitat type. Birds from urban habitats on an average have shorter FIDs compared to conspecifics from rural areas (Møller 2008). Therefore, all habitats in which FIDs were estimated were scored as either urban, when habitats consisted of continuous plots with houses, or areas with multi-storey buildings (see Møller 2008). All other habitats were scored as rural habitats.

Food mobility. Food was classified according to whether food items were able to escape through movement (food scored as mobile) or whether they were unable to do so (food scored as immobile). Thus, species feeding on live animals were all scored as feeding on mobile food, using information reported by Cramp and Perrins (1977–1994).

Eye size. Eye size was recorded as the smallest and the largest diameter of the eye (to the nearest 0.1 mm with a caliper). Eye size was subsequently estimated as the volume of a spheroid, using the two diameters above (Garamszegi et al. 2002). This procedure provides reliable estimates as revealed by highly consistent estimates amongst species (Garamszegi et al. 2002). Here I used estimates reported by Garamszegi et al. (2002).

Adult survival rate. Adult survival rate was recorded from Cramp and Perrins (1977–1994). If more than a single estimate was reported in that source, I used the one with the largest sample size.

Body mass. Body mass was recorded for the breeding season, as reported by Cramp and Perrins (1977–1994). If more than a single estimate was reported in that source, I used the one with the largest sample size. The data set is reported in Appendix 1.

1.4. Statistical analyses

All analyses were made with JMP (SAS 2012). I calculated least-square mean (LSM) FIDs for eating and loafing individuals of each species by inclusion of activity (eating or loafing), habitat (urban or rural), species and activity by species interaction as factors in a model with \log_{10} -transformed FID as the dependent variable. This procedure allowed me to estimate mean FID after statistically controlling for any confounding effects of habitat (urban or rural). FID, eye size and body mass were \log_{10} -transformed, whilst survival rate was square-root arcsine-transformed to normalise variables.

1.5. Comparative analyses

Analyses of comparative data based on single species may provide misleading conclusions if sister taxa are more similar with respect to the variables under investigation than randomly chosen species. Therefore, I analysed statistically independent, standardised linear contrasts (Felsenstein 1985), which

controls for similarity in phenotype amongst species because of common descent. The contrasts were calculated using the software of Purvis and Rambaut (1995), implemented in the software CAIC. All regressions were forced through the origin (Felsenstein 1985), because the dependent variable is not assumed to have changed, when the predictor variable has not evolved. Standardisation of contrast values was checked by examination of absolute values of standardised contrasts versus their standard deviations (Garland 1992; Garland et al. 1992). Plotting the resulting contrasts against the variances of the corresponding nodes revealed that these transformations made the variables suitable for regression analyses. To further test for the robustness of the conclusions, I used the ranks of the contrasts of predictor variables in the regression models (Møller & Birkhead 1994), and these analyses all produced statistically similar conclusions.

The comparative analyses relied on a composite phylogeny created by using information from Hackett et al. (2008) and Sibley and Ahlquist (1990), supplemented with information from another source to resolve relationships between species (Jönsson & Fjeldså 2006).

2. RESULTS

The difference in standardised FID between eating and loafing situations for 55 different species of birds was on an average -0.022 (SE = 0.024), median = -0.003 and range -0.398 to $+0.339$, with a distribution that did not differ significantly from normality (Shapiro–Wilk W test, $W = 0.96$, $P = 0.15$). A mixed model revealed a significant effect of species, with a non-significant effect of activity and a significant interaction between activity and species (Table 1). The latter effect implies that species differed in the effect of activity on FID. Finally, there was a significant effect of habitat (rural or urban).

The linear regression of FID when loafing against FID when eating was highly significant (Fig. 1; $F_{1,53} = 96.53$, $r^2 = 0.65$, $P < 0.0001$; reduced major axis slope 0.805 (SE = 0.066)). The reduced major axis slope was significantly smaller than one ($t_{53} = 2.95$, $P < 0.001$), implying that species with long FIDs when loafing had relatively shorter FIDs than expected when eating.

The difference in FID between eating and loafing individuals was related to whether food items were mobile or immobile (Fig. 2; $F_{1,53} = 8.74$, $r^2 = 0.14$, $P = 0.0046$), with the mean difference being smaller for species eating mobile compared to immobile food. Whilst the value for species eating immobile food differed significantly from zero ($t_{13} = -3.00$, $P < 0.001$), there was no significant difference for species eating mobile food ($t_{41} = 0.76$, $P = 0.45$).

Species that had relatively longer FID when eating than loafing had relatively larger eyes than species that had relatively longer FID when loafing (Fig. 3; partial $F_{1,51}$ (after controlling statistically for body mass) = 7.83, $r^2 = 0.13$, $P = 0.0072$, slope (SE) = -0.385 (0.138)). This effect was statistically independent of whether food was mobile (partial $F_{1,50} = 2.12$, $r^2 = 0.04$, $P = 0.15$).

The difference in FID between eating and loafing was predicted by adult survival rate (Fig. 4; $F_{1,41} = 4.22$, $r^2 = 0.09$, $P = 0.046$, slope (SE) = -0.354 (0.172)). This effect was independent of body mass ($F_{1,40} = 0.85$, $r^2 = 0.02$, $P = 0.36$) and whether food was mobile ($F_{1,40} = 0.59$, $r^2 = 0.01$, $P = 0.45$). Weighting models by sample size for FID estimates also revealed a significant effect of survival rate ($F_{1,541} = 6.11$, $r^2 = 0.13$, $P = 0.018$, slope (SE) = -0.386 (0.156)).

from a potential predator. Whilst individuals of bird species eating mobile prey may completely lose their meal whilst temporarily escaping from a potential predator, this risk is much lower or non-existent for species eating immobile food. These differences may have two possible consequences. First, mobile prey can escape and hence will be more difficult to recover following flight from a potential predator. If this hypothesis is correct, then species eating mobile prey should have relatively

Table 1. Mixed model of FID (\log_{10} -transformed) in relation to species (random factor), activity (eating or loafing), activity by species interaction and habitat (rural or urban).

Variable	df	F	P	Estimate (SE)
Intercept	64.66	646.18	< 0.0001	0.981 (0.039)
Activity	860.5	0.25	0.62	-0.006 (0.012)
Activity by species	850.4	1.90	0.0001	
Habitat	842.7	10.61	0.0012	-0.044 (0.014)

The random species effect had a variance component of 0.07 (95% CI = 0.039, 0.096) accounting for 59.34% of the variance. The model had adjusted $R^2 = 0.63$.

3. DISCUSSION

The main findings of this study of FID of birds when eating and loafing, respectively, were that species differed in flight behaviour between activities. Further analyses revealed that the difference in FID depended on whether a species consumed mobile prey, the relative size of eyes and adult survival rate.

FID reflects risk taking (Ydenberg & Dill 1986; Cooper & Frederick 2007, 2010; Møller et al. 2008) and thus should depend on the relative cost of giving up current activities such as eating (Cooper & Blumstein 2014). This opportunity cost is likely to be small relative to the cost of falling prey to a predator, although I am unaware of any quantifications of this cost. Although I did not find any main effect of activity (eating or loafing) on FID, there was a highly significant interaction between activity and species, implying that species differed in relative FID during eating and loafing, respectively. This suggests that species differ in susceptibility to predation risk (e.g. Møller et al. 2008). The risk that individuals of different species take during eating compared to loafing is related to their body size, diet, eye size and adult survival rate. The difference in FID between situations when individuals were eating and loafing was not the same across species. In fact, species with short FIDs during loafing had relatively long FIDs during eating and vice versa (Fig. 1).

Species differ in the risk that they run from losing their food when distracted during vigilance or actual escape

shorter FIDs than species eating immobile prey. That should be the case when eating rather than loafing. That was clearly not the case because it was species eating immobile prey that differed in relative FID between eating and loafing. The second hypothesis posits that species eating mobile prey may be better able to perceive risks than species eating immobile food. That should allow the former species to fly away when threatened by a potential predator, and that should be independent of current behaviour. Such an effect could be due to the relative size of eyes (Møller & Erritzøe 2010, 2014). Here I have shown a difference in relative FID between species eating mobile and immobile prey. Post-hoc analyses revealed that the difference in FID between eating and loafing situations did not deviate significantly from zero amongst species eating mobile food but did so for species eating immobile food. The latter species had longer FIDs when eating than when loafing, consistent with the second hypothesis.

Birds with larger eyes for their body size glean more information from the environment as shown by their relatively larger brain size (Garamszegi et al. 2002). Thus, species with relatively large eyes might be better able to discern risk caused by an approaching predator (Møller & Erritzøe 2010, 2014). Indeed, Møller and Erritzøe (2010) found in an analysis of birds that species with large eyes for their body size had relatively long FIDs. There was a significant negative relationship between difference in FID between activities and eye size independent of body mass. When entering prey mobility into

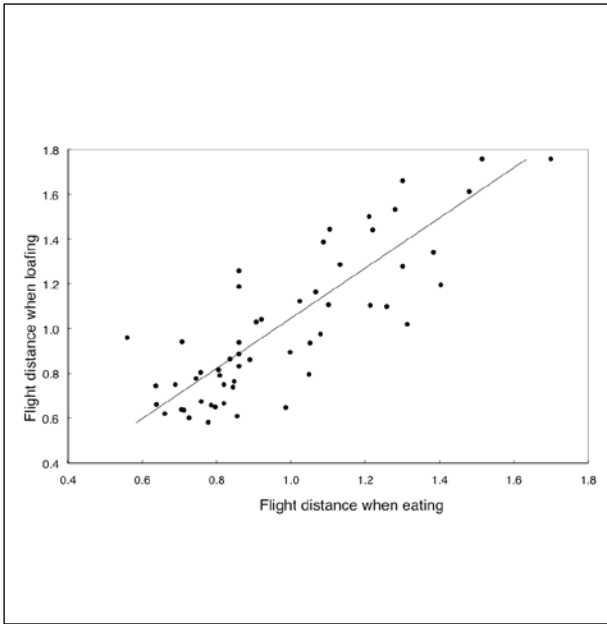


Figure 1. \log_{10} -transformed FID (m) when eating in relation to \log_{10} -transformed FID when loafing (m) for different species of birds. The line shows equality in FID in the two situations with $Y = X$.

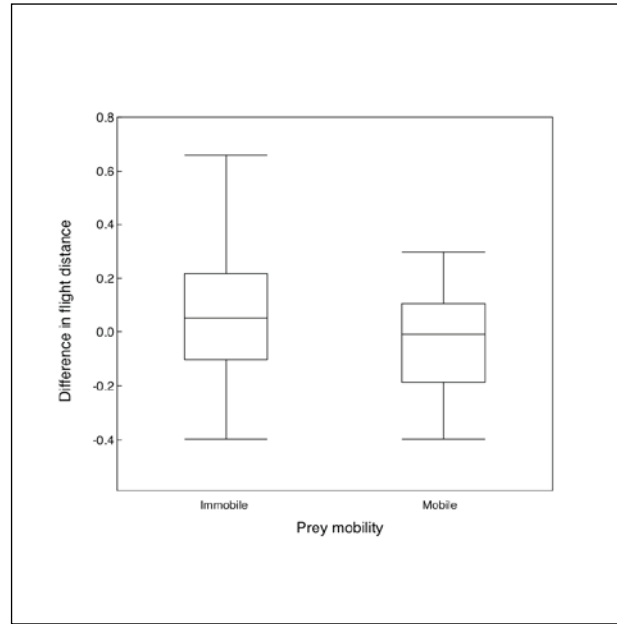


Figure 2. Difference in FID when eating and FID when loafing for different bird species eating mobile and immobile food. The box plots show medians, quartiles and 5- and 95-percentiles.

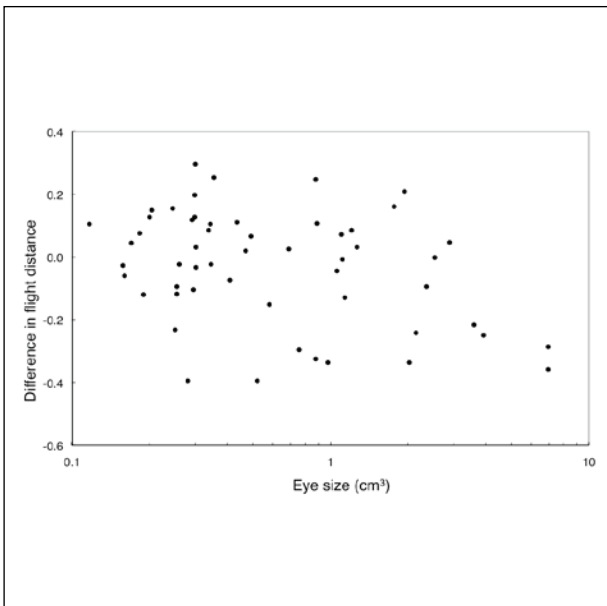


Figure 3. Difference in FID when eating and FID when loafing in relation to eye size (cm^3) for different bird species.

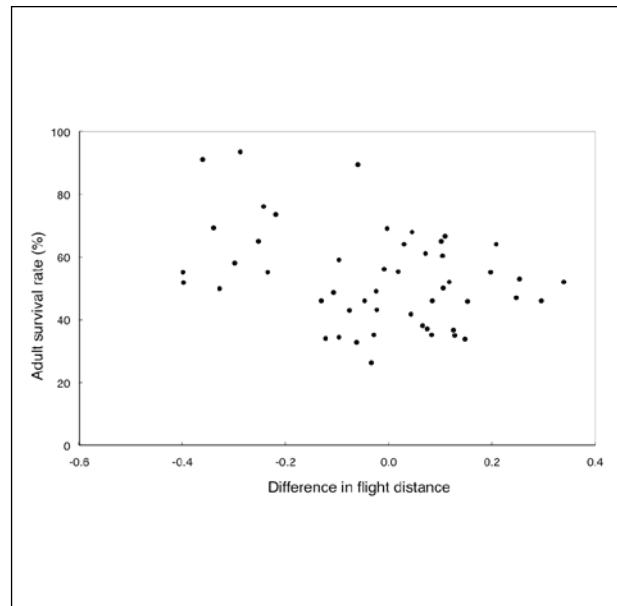


Figure 4. Difference in FID when eating and FID when loafing for different bird species in relation to adult survival rate.

the model that also contained eye size as a predictor variable, the effect of prey mobility was no longer statistically significant. This implies that the effect of prey mobility on difference in FID was mediated by eye size.

Survival probability should affect the risk that individuals are willing to take with species with high adult survival rates taking smaller risks when engaged in activities that could impair survival (Blumstein 2006). Møller and Garamszegi (2012)

have previously found support for this prediction using FIDs and adult survival rates of birds. Here, I have adopted a more powerful test by comparing behaviour in different situations (eating and loafing), finding a negative correlation between adult survival rate and difference in FID when individuals are eating or loafing. This effect was independent of the potentially confounding effects of body mass and prey mobility, suggesting

that the most obvious potentially confounding variables were unlikely to account for the result.

There are several potential implications of the findings reported here. First, relative FID provides a direct estimate of the opportunity cost of fleeing. Any temporal or spatial change in FID will have consequences for the trade-off between food acquisition and predator avoidance. Thus, individuals should have been selected to optimise this trade-off. Whilst the opportunity cost of flight may be small, this study has shown that it is still fully feasible to demonstrate its existence and also to relate this cost to ecology and life history. Second, comparison of behavioural responses between eating and loafing individuals, singing and non-singing individuals (Møller et al. 2008) or urban and rural individuals (Møller 2008b) may provide insights into life history trade-offs that are

otherwise difficult to investigate. As already stated in the Introduction, differences in behaviour between such activities may constitute a powerful research tool because many potentially confounding factors are automatically controlled because of residual variation cancelling out.

In conclusion, I have shown large differences in risk-taking behaviour of individuals amongst activities by birds reflecting the opportunity cost of flight. These differences depended on whether mobile prey were consumed, the relative size of eyes and adult survival rate. The fact that the difference in FID between eating and loafing is negatively correlated with adult survival rate provides crucial evidence for the assumption that risk-taking behaviour is adjusted to the life history costs and benefits of this behaviour.

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Appendix 1

Table A1. Summary statistics for flight distance of eating and loafing birds (least square means adjusting for habitat), mobility of food (0 – immobile food, 1 – mobile food), eye volume (cm³), adult survival rate (%), and body mass (g). See Materials and methods for further details.

Species	Flight distance when eating	Flight distance when loafing	Mobility of food	Eye volume (cm ³)	Adult survival rate (%)	Body mass (g)
<i>Alauda arvensis</i>	1.21	1.10	1	0.44	66.50	36.40
<i>Anas crecca</i>	1.48	1.61	0	1.14	46.00	286.50
<i>Anas platyrhynchos</i>	0.99	0.65	0	2.02	52.00	1119.00
<i>Anthus pratensis</i>	1.08	0.98	1	0.34	65.00	19.25
<i>Anthus trivialis</i>	0.86	0.94	1	0.41	42.85	23.40
<i>Carduelis cannabina</i>	0.91	1.03	0	0.19	34.00	18.95
<i>Carduelis carduelis</i>	0.84	0.86	0	0.16	35.00	15.60
<i>Carduelis chloris</i>	0.86	0.89	0	0.26	43.00	27.65
<i>Charadrius hiaticula</i>	1.09	1.39	1	0.76	58.00	63.25
<i>Columba palumbus</i>	1.40	1.20	0	1.93	64.00	494.50
<i>Corvus corone</i>	1.22	1.44	1	3.58	73.60	544.50
<i>Dendrocopos major</i>	1.10	1.44	1	0.98	69.20	89.65
<i>Emberiza citrinella</i>	1.05	0.80	0	0.35	53.00	26.75
<i>Emberiza schoeniclus</i>	0.56	0.96	0	0.28	51.70	18.80
<i>Erithacus rubecula</i>	0.70	0.64	1	0.49	38.00	16.35
<i>Falco tinnunculus</i>	1.28	1.53	1	3.91	65.00	174.50
<i>Fringilla coelebs</i>	0.86	0.83	0	0.30	64.00	24.20
<i>Galerida cristata</i>	1.13	1.29	1	0.58	.	44.65
<i>Gallinula chloropus</i>	0.89	0.86	1	1.27	.	348.50
<i>Garrulus glandarius</i>	1.03	1.12	0	2.35	59.00	161.70
<i>Hippolais icterina</i>	0.78	0.66	1	0.30	34.80	13.30
<i>Lanius collurio</i>	0.84	0.74	1	0.88	50.00	30.70
<i>Larus argentatus</i>	1.21	1.50	1	6.94	93.50	895.00
<i>Larus fuscus</i>	1.30	1.66	1	6.94	91.00	817.50
<i>Larus ridibundus</i>	1.51	1.76	1	2.14	76.00	280.50
<i>Motacilla alba</i>	1.05	0.94	1	0.29	52.00	20.75
<i>Motacilla cinerea</i>	0.92	1.04	1	0.25	.	17.35
<i>Motacilla flava</i>	1.07	1.16	1	0.25	34.25	17.45
<i>Oenanthe oenanthe</i>	0.86	1.26	1	0.52	55.00	23.95
<i>Parus ater</i>	0.80	0.65	1	0.20	33.80	9.25
<i>Parus caeruleus</i>	0.66	0.62	1	0.17	41.60	11.75
<i>Parus major</i>	0.64	0.74	1	0.29	48.60	18.50
<i>Passer domesticus</i>	0.78	0.58	0	0.30	55.00	30.35
<i>Phalacrocorax carbo</i>	1.70	1.76	1	.	89.50	2254.00
<i>Phoenicurus ochruros</i>	0.81	0.79	1	0.47	55.30	16.00
<i>Phylloscopus collybita</i>	0.73	0.60	1	0.20	36.70	7.70
<i>Phylloscopus trochilus</i>	0.69	0.75	1	0.16	32.70	9.35
<i>Pica pica</i>	1.10	1.11	1	2.53	69.00	228.00
<i>Picus viridis</i>	1.26	1.10	1	1.76	.	193.50
<i>Prunella modularis</i>	0.64	0.66	1	0.34	49.00	18.95
<i>Saxicola rubetra</i>	1.31	1.02	1	0.30	46.00	16.60
<i>Serinus serinus</i>	1.00	0.89	0	0.12	60.30	11.95
<i>Streptopelia decaocto</i>	0.82	0.75	0	1.10	61.00	201.50

continued Table A1. Summary statistics for flight distance of eating and loafing birds (least square means adjusting for habitat), mobility of food (0 – immobile food, 1 – mobile food), eye volume (cm³), adult survival rate (%), and body mass (g). See Materials and methods for further details.

<i>Sturnus unicolor</i>	0.86	1.19	1	0.88	49.90	90.60
<i>Sturnus vulgaris</i>	0.86	0.61	1	0.88	47.00	80.50
<i>Sylvia atricapilla</i>	0.76	0.67	1	0.34	46.00	18.85
<i>Sylvia communis</i>	0.74	0.78	1	0.30	26.10	14.50
<i>Sylvia curruca</i>	0.82	0.67	1	0.24	45.80	12.40
<i>Sylvia melanocephala</i>	0.71	0.94	1	0.25	55.00	13.45
<i>Troglodytes troglodytes</i>	0.71	0.64	1	0.18	37.00	8.90
<i>Turdus merula</i>	0.81	0.81	1	1.11	56.00	95.85
<i>Turdus philomelos</i>	0.76	0.80	1	1.06	46.00	70.50
<i>Turdus pilaris</i>	0.85	0.76	1	1.20	35.00	92.10
<i>Upupa epops</i>	1.30	1.28	1	0.69	.	67.05
<i>Vanellus vanellus</i>	1.38	1.34	1	2.89	67.80	218.50

Figure A1. Phylogenetic relationship among the 55 species of birds in this study. See Materials and methods for sources.

