

Predator–prey interactions, flight initiation distance and brain size

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Abstract

Prey avoid being eaten by assessing the risk posed by approaching predators and responding accordingly. Such an assessment may result in prey–predator communication and signalling, which entail further monitoring of the predator by prey. An early antipredator response may provide potential prey with a selective advantage, although this benefit comes at the cost of disturbance in terms of lost foraging opportunities and increased energy expenditure. Therefore, it may pay prey to assess approaching predators and determine the likelihood of attack before fleeing. Given that many approaching potential predators are detected visually, we hypothesized that species with relatively large eyes would be able to detect an approaching predator from afar. Furthermore, we hypothesized that monitoring of predators by potential prey relies on evaluation through information processing by the brain. Therefore, species with relatively larger brains for their body size should be better able to monitor the intentions of a predator, delay flight for longer and hence have shorter flight initiation distances than species with smaller brains. Indeed, flight initiation distances increased with relative eye size and decreased with relative brain size in a comparative study of 107 species of birds. In addition, flight initiation distance increased independently with size of the cerebellum, which plays a key role in motor control. These results are consistent with cognitive monitoring as an antipredator behaviour that does not result in the fastest possible, but rather the least expensive escape flights. Therefore, antipredator behaviour may have coevolved with the size of sense organs, brains and compartments of the brain involved in responses to risk of predation.

Introduction

Predators affect their prey in a sequence of events that start by avoiding being found by the predator, followed by predator detection, warning and prey–predator signalling, eventually followed by defences that prey adopt to escape an attack and attempts to escape from certain death following capture by a predator (Endler, 1991; Ruxton *et al.*, 2004). At each of these sequential stages, individual prey may adopt a range of different kinds of behaviour that may evolve in response to

differences in the impact of predators and their diversity. Signalling by prey and their predators may evolve to allow assessment of reliable indicators of condition of prey and intent of predators (Caro, 1986a,b). Caro (2005) provided an exhaustive review of the diversity of such defences in birds and mammals. While this diversity of responses may suggest positive covariation between different kinds of antipredator behaviour, behaviour at early stages of the sequence of events involving a predator and its prey may interact antagonistically with behaviour at later stages (e.g. Hochberg, 1997). For example, antipredator behaviour that reduces the risk of detection may interfere with other antipredator behaviours such as flight, but it could still be favoured because such an early antipredator behaviour reduces the risk of a later close encounter with a predator. Such antagonistic defences may help explain

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how a diversity of antipredator defences is maintained when superficially all prey may benefit from the maximum level of defence.

Potential prey may evolve ways of probing the likelihood of attack by predators. This implies assessment and monitoring of predators, which in turn results in time use, information gathering by sense organs and information processing by the brain. If individuals and by implication species differ in their ability to assess the behaviour of predators, individuals with relatively larger brains for their body size should be better able to assess the risk of predation because a relatively larger brain is a proxy for greater cognitive ability and behavioural flexibility (e.g. Jerison, 1973; Striedter, 2005). Assessment should allow such individuals to avoid or delay flight and hence reduce energy costs of flight from an approaching predator. Information about potential predators and their activities is gathered by sense organs such as eyes and ears (Møller & Erritzøe, 2010). Large eyes capture more information from the environment, and the brain processes such information. Indeed, Møller & Erritzøe (2010) showed that flight initiation distance to an approaching predator increased with relative eye size in different species of birds, although there was no evidence suggesting that eye size had evolved in response to habitats or food items varying in difficulty of detection and capture. Bird species with larger eyes have a larger brain involved in processing the larger amount of information (Hughes, 1977; Garamszegi *et al.*, 2002; Land & Nilsson, 2002), and that is even the case when considering that nocturnal species have larger eyes, but not larger brains, than diurnal species (Garamszegi *et al.*, 2002). However, additional factors such as eye shape, retinal topology and ganglion cell density are linked to visual ability and processing of visual information (Martin, 1985, 2007; Zeigler & Bischof, 1993; Land & Nilsson, 2002). Whether flight initiation distance covaries with relative brain mass remains to be determined. Here, we extend these arguments for the relationship between monitoring of potential predators, antipredator behaviour and the evolution of brain size to specific parts of the brain involved in different aspects of monitoring of and response to potential predators. Specifically, the cerebellum plays a significant role in motor control, and therefore, its relative size should be correlated with antipredator behaviour, while that should not be the case for other compartments of the brain. A larger cerebellum would imply greater movement-related functions including coordination, precision and timing of activities involved in antipredator behaviour (e.g. Jerison, 1973; Striedter, 2005). Such a function by the cerebellum would be consistent with a significantly higher basal metabolic rate in bird species with longer flight initiation distances, because neural tissue has a metabolic rate that is 20-fold greater than that of other tissue (Møller, 2009). Although many comparative studies

have investigated the relationship between relative brain size and ecology (e.g. Dunbar, 1993; Lefebvre *et al.*, 2002; Emery *et al.*, 2007), only few studies have investigated how the evolution of compartmentalization of the brain is linked to ecology (e.g. Iwaniuk, 2004; Kiecker & Lumsden, 2005). Here, we provide such an analysis.

Flight initiation distance is a behavioural measure of the distance at which potential prey take flight when approached by a predator (Hediger, 1934; Blumstein, 2006). Prey optimize this distance because the advantages of flight and avoidance of predation are traded against the high energy costs of short escape flights and the opportunity costs of lost foraging events (Ydenberg & Dill, 1986). Thus, prey should optimize flight initiation distance relative to their future expectation of survival and reproduction, that is, residual reproductive value. Consistent with this expectation of optimization, relative flight initiation distance (flight initiation distance in a model that includes \log_{10} -transformed body mass as an additional predictor) is significantly negatively related to predation risk with shorter flight initiation distances in species with higher predation risk, higher rates of parasitism and a fast life history (low survival prospects, many clutches per year and larger clutch sizes) (Møller, 2008a,c, 2010a,b,c; Møller & Garamszegi, 2012). Finally, relative flight initiation distance is a significant predictor of population trends of bird species across the European continent, suggesting that individuals belonging to risk-sensitive species take flight at long distances with negative consequences for energy expenditure and hence fecundity, survival and population growth (Møller, 2008b).

The objective of this study was to test the prediction that larger relative brain size for a given body size allows for safer and more precise monitoring of predator behaviour, hence reducing the number of costly escape flights. In addition, we predicted that a larger relative size of the cerebellum adjusted for body size would allow for earlier escape from a potential predator through cognitive aspects of monitoring. Organs and behaviour show allometry, with larger species having larger organs and longer flight distances. Hence, brain and cerebellum size, and escape flight distance were adjusted for body size because it is the relative size of brains and flight distance that reflect whether individuals of a species have values that are smaller or larger than expected. We used flight initiation distance as a proxy of 'fearfulness' (Hediger, 1934; Blumstein, 2006) because a longer flight initiation distance implies a more risk-averse response by an individual. The ultimate test of the functional value of such an antipredator behaviour is the link to probability of survival (Shultz & Dunbar, 2006). Empirical tests have shown that mammals with relatively smaller brains run higher risks of predation (Shultz & Dunbar, 2006), and bird species with shorter flight initiation distances

experience greater risks of death due to predation (Møller *et al.*, 2008). Therefore, we predicted that (i) relative flight initiation distance adjusted for body size should increase with relative eye size adjusted for body size if earlier visual detection resulted in earlier monitoring of the predator and hence earlier escape, whereas it should decrease with relative brain size if a relatively larger brain implies safer and more precise monitoring of the risk of predation by a potential predator, and in addition; (ii) relative flight initiation distance adjusted for body size should be longer in species with a relatively large cerebellum for a given body size if motor control by the cerebellum in addition to monitoring of the whereabouts of a potential predator was an important component of the relationship between antipredator behaviour and relative brain size. These hypothetical effects of brain size and cerebellum size rely on the greater physical abilities of escape first being taken into consideration. We did so by the inclusion of body size as an additional variable in the statistical models. Flight initiation distance may be confounded by effects of habitat because an individual in completely open grassland may be more exposed to predation than an individual situated in shrub or forest. Likewise, individuals belonging to a more social species may experience greater safety in numbers or benefit from more eyes looking out for potential predators. Finally, flight initiation distance may depend on whether prey are mobile or immobile, with the latter kind of prey increasing the visual abilities of predators. Although Møller & Erritzøe (2010) showed an absence of such effects, we still considered these potential confounding variables here. We tested these novel predictions using information on eye size, brain size, cerebellum size and flight initiation distance for 107 species of birds.

Materials and methods

Flight initiation distance

Regularly during February–September 2006–2008, A. P. Møller (APM) estimated flight initiation distances of birds, using a standardized technique in Ile-de-France, France, and Northern Jutland, Denmark. In brief, when an individual bird had been located with a pair of binoculars, APM moved at a normal walking speed towards the individual, while recording the number of steps (which approximately equals the number of metres (Møller, 2008a)). Flight initiation distance estimated as the number of steps is strongly positively correlated with the measured distance using a Nikon Forestry 550 Hypsometer for a sample of 50 flight initiation distances ($F_{1,48} = 12,241.13$, $r^2 = 0.996$, $P < 0.0001$, estimate (SE) = 1.0002 (0.0090); intercept (SE) = 0.0023 (0.0087), $t_{48} = 0.26$, $P = 0.79$). If more than a single individual was present, APM recorded the

flight initiation distance of the first observed individual. The distance at which the individual took flight was recorded as the flight initiation distance, and the starting distance was the distance from where the observer started walking towards the bird when first observed. If the individual was positioned in the vegetation, the height above ground was recorded to the nearest metre. While recording these flight initiation distances, APM also recorded date and time of the day. Flight initiation distance was estimated as the Euclidian distance, which equals the square root of the sum of the squared horizontal distance and the squared height above ground level (Blumstein, 2006).

All recordings were made during the breeding season, when most individuals are sedentary, thus preventing the same individual from being recorded in different sites. For example, flight initiation distances were recorded for pigeons and doves throughout February–September in France, whereas distances for late breeding warblers were recorded in May–June. Thus, flight initiation distances were only recorded during the actual breeding seasons of the different species. APM avoided pseudo-replication by only recording individuals of a given sex, age and species at a given site. Thus, if a male and a female were recorded at a given site, both were included in the data set, and one male recorded at a given site on two different days was recorded as a single observation. For the present study, APM recorded a total of 4347 flight initiation distances for 151 species, but this sample size was reduced to 107 species because information on eye size was unavailable for 44 species.

Flight initiation distance was consistent for the same species in different studies, as shown by a comparison of data from previous studies (data and analyses reported in Møller (2008a,b,c)) and those of Blumstein (2006). Furthermore, flight initiation distances estimated by an independent observer (E. Flensted-Jensen) were also very similar to the estimates (data and analyses) reported in Møller (2008a,b,c). In addition, flight initiation distances estimated in Denmark were similar to the distances in France (details on data and analyses are reported in Møller (2008c)). Finally, flight initiation distances in summer and winter were strongly positively correlated (data and analyses reported in Møller (2008c)). This provides evidence of reliability of flight initiation distance estimates across spatial and temporal scales.

The starting distance used when approaching an individual bird scored for flight initiation distance is the distance at which the bird is initially seen and then approached. Previous studies have shown that starting distance is strongly positively correlated with flight initiation distance (e.g. Blumstein, 2003, 2006; Cooper, 2005, 2008; Dumont *et al.*, 2012), thereby potentially causing a problem of collinearity that may not even be of biological significance (Dumont *et al.*, 2012). APM eliminated this potential problem of collinearity by

searching habitats for birds with a pair of binoculars when choosing an individual for estimating flight initiation distance. APM recorded flight initiation distance and starting distance for large-sized species (heavier than 150 g) by starting at distances of ca. 100 m. For smaller species, APM started to walk at normal speed while recording starting distance and flight initiation distance when at a distance of ca. 30 m. In this way, APM assured that almost all individuals were approached from a distance of at least 30 m, thereby keeping starting distances constant across species. \log_{10} -transformed flight initiation distance was negatively related to \log_{10} -transformed starting distance in a model that included species, age, habitat, country and \log_{10} -transformed body mass as factors ($F_{1,4188} = 37.97$, $P < 0.0001$), but only explained 1% of the variance. None of the results presented in this article changed statistically when including starting distance as an additional variable, and we thus excluded this variable from all subsequent analyses for simplicity.

Brain size and component parts

We used an extensive database on brain size of birds from Denmark (mainly the southern part) recorded by J. Erritzøe (JE) in a consistent way during 1960–2013. The fact that only one person recorded all weights eliminates any heterogeneity due to interobserver variability. This database consists of brain mass of 5558 individual birds, excluding any individuals with damaged heads. Previous analyses have shown a high degree of consistency between mean estimates derived from this database and other databases (Garamszegi *et al.*, 2002; Møller *et al.*, 2005).

We made an extensive search of the literature on the size of components of the brain in adult birds using studies by Portmann (1947), Ebinger & Löhmer (1984), Boire & Baron (1994), Iwaniuk (2004) and Kalisinska (2005) as sources. This provided a total sample of 64 species with information on the size of component parts of the brain. Any heterogeneity in these data due to measurement methods will only cause random noise and make detection of relationships conservative.

Eye size

JE measured by post-mortem examination of dead birds the smallest and the largest diameter of the eye (to the nearest 0.1 mm with a calliper) for 3454 birds, excluding any individuals with damaged heads. Although eye shape varies between species (Zeigler & Bischof, 1993), we assumed in the following that eyes had a spheroid shape and calculated their volume using the equation.

$$\text{Eye volume (cm}^3\text{)} = 2 \times 1.33 \pi a^2 \text{ (cm}^2\text{)} b \text{ (cm)},$$

where a is smallest and b is the largest radius of the eyes (Garamszegi *et al.*, 2002).

Body mass

JE recorded body mass of adult birds, or if information was missing, we used data from the breeding season published by Cramp & Perrins (1977–1994). Such estimates of body mass are highly repeatable among sources.

Habitats, sociality and predation risk

We quantified habitats using information from our own field studies of flight initiation distances relying on the height above the ground (see ‘Flight Initiation Distance’ above). A value of 0 implies that an individual was recorded on the ground, whereas larger values imply greater heights above ground level (Møller & Erritzøe, 2010).

We classified sociality in two different ways by relying on information recorded during our field study. Breeding sociality was classified as solitary (a score of 0) when pairs were reproducing in large all-purpose territories or colonial when more pairs were aggregated in small nesting territories (a score of 1). Sociality outside the breeding season was scored on a logarithmic scale from 1 over 2, 3, 4 to 5 for the maximum number of individuals recorded in a flock being 1, 10, 100, 1000, 10 000 or 100 000.

We classified food items as live (a score of 1) or immobile or sessile (a score of 0 for plants and seeds; Møller & Erritzøe, 2010) relying on the study of Cramp & Perrins (1977–1994).

Predation risk for a given species was recorded as the observed frequency of prey relative to the expected frequency based on the abundance of that species during the breeding season in the environment. This information was based on a 21-year study of European sparrowhawks by Nielsen (2004) in an area of 2417 km² in northern Denmark (Møller *et al.*, 2008). Prey remains of the European sparrowhawk were systematically collected near 940 nests during April–September 1977–1997, with only prey judged to be less than 1 month old being included. A total of 31 745 prey items of 64 species of birds were used, whereas 3178 other prey items were excluded because they were mammals, cage birds or migrants. All nest sites were visited a similar number of times during each breeding season, and sampling effort can therefore be considered to be similar across sites.

We calculated the expected number of prey using published information on the breeding density of birds (Grell, 1998). Maps of the density of breeding birds were based on systematic point counts of breeding birds carried out by hundreds of amateurs, allowing estimates of the mean density of breeding prey species in the study areas of Nielsen (2004). Such point counts provide reliable estimates of breeding bird density (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 according to the abundance based on point counts multiplied by the total number of prey individuals. All data are reported in Tables S1 and S2 in the Supporting Information.

Statistical analyses

We \log_{10} -transformed FID, size of telencephalon, cerebellum, optic tectum, brain mass and body mass to obtain variables that did not deviate from normal distributions. We estimated relative size of the three brain components and the total brain by estimating phylogenetically corrected sizes, which is the relative size of characters adjusted for body size, after considering that allometry is also affected by the phylogenetic distribution of observations. Thus, this analysis takes into account the fact that allometric relationships are biased due to nonindependence of species-specific values, a problem that is not addressed in many studies of scaling of brains and brain components (Harvey & Pagel, 1991). To address this problem of biased estimates of scaling, we first estimated the phylogenetically corrected allometry coefficients for brain mass, telencephalon, optic tectum and cerebellum, respectively, against body mass (these were 0.58 for brain mass, 0.69 for telencephalon, 0.49 for optic tectum and 0.59 for cerebellum), and we then subtracted the estimated size of these characters based on the phylogenetically corrected allometric relationships from the observed \log_{10} -transformed size (see Møller (2009) for this procedure applied to basal metabolic rate, which constitutes a similar case of collinearity). This procedure reduced the strength of the correlations between variables (Pearson's $r = 0.59$ – 0.74 vs. 0.94 – 0.99 for the \log_{10} -transformed values). Indeed, variance inflation factors were all < 10 following this procedure (Kleinbaum *et al.*, 1998).

We related \log_{10} -transformed flight initiation distance to \log_{10} -transformed eye volume, \log_{10} -transformed brain mass and \log_{10} -transformed body mass in a model that included the three factors simultaneously, relying on type III sums of squares. In a second model, we related \log_{10} -transformed flight initiation distance to \log_{10} -transformed eye volume, \log_{10} -transformed brain mass and \log_{10} -transformed cerebellum size in a model that included the three factors simultaneously, relying on type III sums of squares.

Analyses of comparative data based on species may result in misleading conclusions if sister taxa are more similar than randomly chosen species. Therefore, we analysed statistically independent, standardized linear contrasts (Felsenstein, 1985), which controls for

similarity in phenotype among species due to common descent, using the software of Purvis & Rambaut (1995). 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. We explicitly tested the underlying assumptions of the comparative analyses by analysis of standardization of contrast values checking whether absolute values of standardized contrasts were related to their standard deviations (Garland *et al.*, 1992; Garland & Ives, 2000). Plotting the resulting contrasts against the variances of the corresponding nodes revealed that these transformations made the variables suitable for regression analyses. To reduce the consequent problem of heterogeneity of variance, (i) outliers (contrasts with Studentized residuals > 3) were excluded from subsequent analyses (Jones & Purvis, 1997) and (ii) analyses were repeated with the independent variable expressed in ranks (Møller & Birkhead, 1994). All these analyses produced statistically similar conclusions, and the presented analyses thus included these outliers.

The comparative analyses relied on composite phylogenies created using the study of Davis (2008). As the information for the composite phylogeny came from different studies using different methods, consistent estimates of branch lengths were unavailable. Therefore, branch lengths were transformed assuming a gradual model of evolution, with branch lengths being proportional to the number of species contained within a clade. The results based on these branch lengths were compared to those obtained using constant branch lengths (a punctuated model of evolution). Nowhere were the results qualitatively different. The phylogeny is reported in Fig. S1.

We assessed relationships based on effect sizes according to the criteria listed by Cohen (1988) for small (Pearson's $r = 0.10$, explaining 1% of the variance), intermediate (9% of the variance) or large effects (25% of the variance). Effect sizes were based on partial effects after accounting for the effects of the other predictor variables in Tables 1–2. All analyses were conducted using JPM, version 10.0 (SAS, 2012).

Results

Flight initiation distance and eye and brain size

Flight initiation distance increased independently with three factors (Table 1). Species with larger eyes fled at longer distances (Fig. 1a), with an effect size that was intermediate (Table 1). In addition, species with larger brains fled at shorter distances (Fig. 1b), with an intermediate effect size (Table 1). Finally, large species fled at longer distances independently of eye size and brain size with an intermediate effect size (Table 1).

Table 1 Flight initiation distance (m) in relation to eye volume (cc), brain mass (g) and body mass (g) in birds according to analyses of contrasts. Effect size is Pearson’s product–moment correlation coefficient for the partial effects.

Variable	Sum of squares	d.f.	<i>F</i>	<i>P</i>	Estimate (SE)	Effect size
Eye volume	0.157	1	12.95	0.0005	0.595 (0.165)	0.33
Brain mass	0.070	1	5.77	0.018	−0.727 (0.303)	0.23
Body mass	0.051	1	4.19	0.043	0.387 (0.189)	0.20
Error	1.247	103				

The model had the statistics $F_{3,103} = 9.15$, $r^2 = 0.08$, $P < 0.0001$.

Table 2 Flight initiation distance (m) in relation to eye volume (cc), brain mass (g) and size of the cerebellum (g) in birds according to analyses of contrasts. Effect size is Pearson’s product–moment correlation coefficient for the partial effects.

Variable	Sum of squares	d.f.	<i>F</i>	<i>P</i>	Estimate (SE)	Effect size
Eye volume	0.115	1	10.84	0.0018	0.633 (0.192)	0.42
Brain mass	0.106	1	10.05	0.0026	−1.227 (0.387)	0.41
Cerebellum size	0.084	1	7.92	0.0069	1.082 (0.385)	0.37
Error	0.540	50				

The model had the statistics $F_{3,50} = 8.93$, $r^2 = 0.15$, $P < 0.0001$.

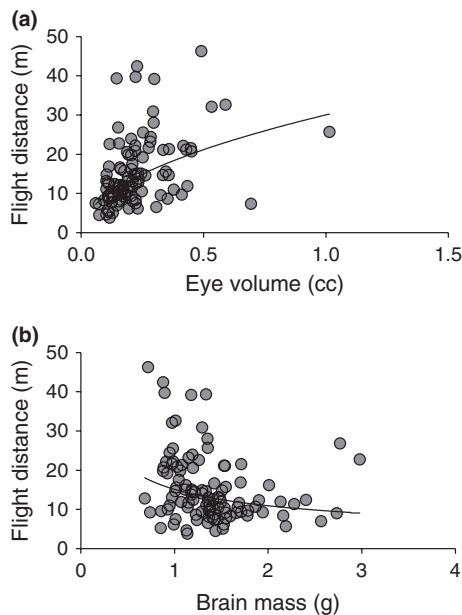


Fig. 1 Flight initiation distance (m) in relation to (a) eye size (volume in cc) and (b) brain mass (g) in different species of birds, after these variables were adjusted for the effects of body mass. The line is the double log relationship.

Several potentially confounding variables may have affected these conclusions. However, flight initiation distance was not significantly related to habitat ($F_{1,104} = 1.84$, $P = 0.18$), breeding sociality ($F_{1,104} = 0.03$, $P = 0.96$), flock size ($F_{1,104} = 1.44$, $P = 0.23$) or the capture of live prey ($F_{1,104} = 4.04$, $P = 0.06$), and they were thus not retained in the statistical models. The

107 species included in the present study only included a single nocturnal species (*Athene noctua*), but exclusion of that species did not affect any of the conclusions (results not shown).

We related preference of particular prey species by the European sparrowhawk to body mass and body mass squared because predators generally prefer prey of an intermediate body size (Møller *et al.*, 2008). Adding \log_{10} -transformed flight initiation distance to this model showed a significant negative partial relationship [$F_{1,67} = 5.92$, $P = 0.018$, estimate (SE) = −0.808 (0.332)]. In contrast, adding eye volume to this model did not show a significant change in predation risk with a change in eye volume ($F_{1,67} = 2.28$, $P = 0.14$). Likewise, risk of predation was not significantly related to \log_{10} -transformed brain mass ($F_{1,67} = 0.87$, $P = 0.35$). Finally, risk of predation was not significantly related to \log_{10} -transformed cerebellum size ($F_{1,35} = 0.17$, $P = 0.68$). These findings suggest that with the exception of flight initiation distance, all other effects were indirect rather than direct effects on the risk of predation.

Flight initiation distance and component parts of the brain

Flight initiation distance increased with three factors (Table 2). Again, flight initiation distance increased with eye size and decreased with brain mass, with both effect sizes being large (Table 2). In addition, flight initiation distance increased with size of the cerebellum with an intermediate effect size (Fig. 2). In contrast, the effects of telencephalon and optic tectum on flight initiation distance were not statistically significant

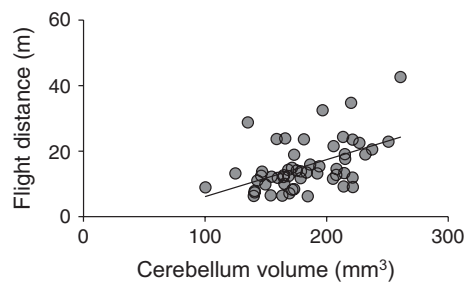


Fig. 2 Flight initiation distance (m) in relation to size of the cerebellum (g) in different species of birds, after adjusting for the effects of eye size and brain size. The line is the linear regression line.

(partial effect of telencephalon when added to the model in Table 2: $F_{1,47} = 1.95$, $r^2 = 0.04$, $P = 0.17$, effect size = 0.20; partial effect of optic tectum: $F_{1,47} = 0.45$, $r^2 = 0.01$, $P = 0.51$, effect size = 0.10). Partial effects for eye volume and brain mass in Tables 1–2 did not differ significantly from each other as shown by the estimates and their standard errors.

Discussion

The main findings of this study were that (i) relative flight initiation distance adjusted for body size increased with relative eye size adjusted for body size, but decreased with the relative size of the brain adjusted for body size and (ii) flight initiation distance increased with relative size of the cerebellum adjusted for body size, which is the part of the brain that is involved in motor control. These findings suggest that antipredator behaviour, eye size and brain size, in particular the size of the cerebellum, have coevolved to allow prey to adjust their antipredator behaviour to visual information and the processing of such visual information by the brain. These correlations are open to interpretation.

Prey respond in many different ways to predators, and this diversity of behaviour reflects the complexity of the task of avoiding and evading predation (Endler, 1991; Ruxton *et al.*, 2004; Caro, 2005). Indeed, different antipredator behaviours may be antagonistic because a focus on one kind of behaviour with a certain fitness value may render individual prey unable or less able to adopt another kind of antipredator behaviour at later stages of the interaction between predator and prey (e.g. Endler, 1991). Behaviour at later stages in the interaction will generally provide lower fitness benefits than earlier events. For example, rapid flight from a predator may prevent closer scrutiny of the risk of attack or monitoring of the whereabouts of the predator, suggesting that immediate flight from a potential predator may not always be the best option. Here, we have presented data suggesting that birds with relatively large eyes for their body size have longer

flight initiation distances (Møller & Erritzøe, 2010), a reduction in risk of predation (Møller *et al.*, 2008) and a relatively large brain involved in assessment and monitoring of predators. Early flight may not always be the energetically least expensive antipredator behaviour because individuals with long flight initiation distances experience greater cumulative energy costs than individuals with short flight initiation distances for a given rate of encounters with potential predators. Individual prey may vary in behavioural responses to predators, causing unpredictability for the predator (Domenici *et al.*, 2011a,b). Once an escape has been initiated, some escape trajectories may allow further assessment of the threat. Here, we provide extensive evidence based on a large number of bird species suggesting continued assessment and monitoring of predators well before flight initiation. Although potential prey detect predators at long distances when prey have large eyes for their body size (Møller & Erritzøe, 2010; this study), flight initiation distance is reduced in prey species with larger brains. Apparently, assessment allows the avoidance of, or delay in, flight response and hence fewer flights and thus lower energy expenditure. In addition, we found an additional effect of body mass, with larger species taking flight at longer distances probably due to longer take-off distances being required for large species for simple mechanical, aerodynamic (Pennycuik, 1989; Norberg, 1990) and physiological reasons (Møller *et al.*, 2013).

The brain is involved in processing information gleaned by the eyes (Hughes, 1977; Garamszegi *et al.*, 2002; Møller & Erritzøe, 2010), and birds with relatively large eyes also have relatively large brains that have evolved to process information gleaned from larger sense organs (Møller & Erritzøe, 2010). Previous studies have shown that nocturnal species have relatively larger eyes than diurnal species (Hughes, 1977; Garamszegi *et al.*, 2002; Land & Nilsson, 2002). The present study only included one nocturnal species (*Athene noctua*), but exclusion of that species did not affect any of the conclusions. However, specific parts of the brain are likely to play a key role in this task. Here, we have shown that flight initiation distance is positively related to the relative size of the cerebellum with a large effect size. Because relatively longer flight distances for a given body size are associated with a reduced risk of predation (Møller *et al.*, 2008), this positive relationship between flight initiation distance and size of the cerebellum is as predicted because a relatively larger cerebellum should provide greater motor control, implying greater movement-related functions including coordination, precision and timing of antipredator behaviour (Striedter, 2005). In contrast, we found small and nonsignificant effect sizes for the relationships between flight initiation distance and relative size of the optic tectum and the telencephalon. Hence, the association between flight initiation distance and

component parts of the brain was specific to the cerebellum, and we found no evidence of an evolutionary increase in one part of the brain being accompanied by an oppositely directed evolutionary trend in other parts of the brain.

Predator–prey interactions are traditionally studied in terms of functional and numerical responses (Crawley, 1992), evolutionary escalation in offence and defence (Vermeij, 1987) and evolution of antagonistic behaviour in predators and prey (Endler, 1991). Here, we have integrated this approach by showing that antipredator behaviour reflects assessment and monitoring of predators by prey as linked to brain morphology and cognition. In addition, Møller *et al.* (2013) have recently shown physiological and morphological adaptations to escape from predators in many of the same species that we have studied here. The congruence of these findings suggests that there is further scope for integration of these different levels of research. However, two sorely missing aspects are individual-based information on escape behaviour and how this relates to risk of predation, and individual-based information on how variation in predator behaviour towards prey affects survival and reproduction. It will be a future challenge to address these problems under field conditions.

In conclusion, the distance at which animals take flight from a potential predator is a question not only of detection of a predator, as indicated by longer flight initiation distances in species of birds with relatively larger eyes, or a question of motor control, as suggested by longer flight initiation distances in species with a relatively larger cerebellum, but also of assessment and monitoring of the threat of predation, as reflected by flight initiation distances being shorter in species with relatively large brains for their body size.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Electronic Supplementary Material.

Table S1 Electronic Supplementary Material.

Table S2 Electronic Supplementary Material.

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