



Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds

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When approached by humans, virtually all species flee, but we lack an understanding of the factors that influence flight response among species. Understanding this variation may allow us to understand how 'fear' structures communities, as well as to predict which species are likely to coexist with humans. I used flight initiation distance (FID) as a comparative metric of wariness and examined the relative importance of life history and natural history traits in explaining variation in FID in 150 species of birds. In a series of comparative analyses, I used independent contrasts to control for phylogenetic similarity and regressed continuous life history traits against flight initiation distance. Body size had a large and significant effect in explaining variation in flightiness: larger species initiated flight at greater distances than smaller species. After controlling for variation explained by body size, there was a nonsignificant positive relation between the age of first reproduction and FID. There were no relations between FID and clutch size, number of days spent feeding young, longevity, or habitat density. I used concentrated changes tests to look for evidence of coevolution between flightiness and dichotomous traits. Flightiness evolved multiple times and some clades were flightier than others. Flightiness was more likely to evolve in omnivorous/carnivorous species and in cooperatively breeding species. These results suggest that body size and age of first reproduction are important in explaining variation in disturbance tolerance in birds, and that species that capture live prey and those that are highly social are relatively wary. The results suggest a novel mechanism of how anthropogenic disturbance may contribute to extinction.

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While it is generally accepted that individuals may vary predictably along a 'shy–bold continuum' (Wilson et al. 1994), or have specific behavioural phenotypes (Gosling 2001; Sih et al. 2004a, b), we have a limited understanding of what explains differences between species in wariness or fearfulness. Despite an extensive literature on intraspecific variation in predation and antipredator behaviour (Lima & Dill 1990), relatively few studies have addressed the question of the evolution of interspecific differences (Greenberg 1983, 1990; Lima 1990, 1993; Beauchamp 1998, 2004; Swaddle & Lockwood 1998; Blumstein 2003; Blumstein et al. 2004a, 2005). Yet it is these interspecific differences that ultimately influence a species' distribution and abundance, as well as its vulnerability to environmental change. Identifying the factors or traits responsible for species-specific differences is the first step towards developing predictive models of fear in animals that will allow

us to understand how animals respond to anthropogenic disturbance (Blumstein & Fernández-Juricic 2004).

Several lines of evidence suggest that life history theory (Stearns 1977; Sibley 2002) may provide some explanatory value (Lima 1993). For example, it is well known that variation in reproductive value may influence defensive behaviour (Montgomerie & Weatherhead 1988) and the degree of risk that animals are willing to accept (Koops & Abrahams 1998). Additionally, fecundity and survival influence parental risk taking (Ghalambor & Martin 2001), and the timing of life history events may influence risk-taking behaviour directly or indirectly (Grand 1999). Thus, differences between species in wariness or risk tolerance might be explained by specific life history traits or where they fall along a life history continuum.

Natural history variation influences morphological antipredator adaptations (e.g. Lima 1993), and could also influence wariness. For instance, in those species where cover is obstructive, individuals in obstructive cover are warier than those in open areas (e.g. Blumstein & Daniel 2002). Thus, differences between species in wariness or risk tolerance could be associated with the

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relative density of cover in which the species is found. Animals that must subdue their foods might be more attentive than those who rely on vegetation, because predators must detect movement of their prey and be able to track moving prey; thus, carnivores and omnivores could conceivably be more wary.

I used a comparative empirical approach (Blumstein & Fernández-Juricic 2004) and examined relations between flight initiation distance, and several life history and natural history traits. I used birds as a model system because they have a wide range of life history traits and are found in a variety of habitat types (Bennett & Owens 2002). I used flight initiation distance as a comparative metric of wariness. Flight initiation distance (FID) is the distance that an individual approached by a predator initiates flight (Blumstein 2003), and this trait, while variable, reflects species-specific differences (Blumstein et al. 2003). Animals respond to approaching humans as they would predators (Frid & Dill 2002); thus, humans can be used as a standardized fearful stimulus. By walking towards focal subjects in a standardized way, I could estimate FID for many species. The decision to flee is one of several components of escape (Morse 1980; Ydenberg & Dill 1986; Lima & Dill 1990), and an individual's response may be subjected to trade-offs (Dill 1987; Blumstein & Bouskila 1996). Recent analyses suggest that FID is correlated with other aspects of escape (alert distance: Blumstein et al. 2005; scanning rate: Fernández-Juricic & Schroeder 2003), and thus FID promises to be a reasonable comparative metric of overall wariness. In the present study, I developed predictions of how several life history and natural history traits may influence FID.

Body size influences vulnerability (Werner 1984) as well as a species' extinction risk (Gaston & Blackburn 1995; Cardillo & Bromham 2001; Cardillo 2003; but see Crooks et al. 2001; Johnson 2002). Larger-bodied species should be less vulnerable to contemporary predation risk. However, body size is a correlate of endangerment (Gaston & Blackburn 1995) and a predictor of extinction in some taxa (Bennett & Owens 2002; Cardillo 2003). The mechanisms of increased vulnerability are generally unknown (Gaston & Blackburn 1995; but see Van Valkenburgh et al. 2004).

Previous work has identified significant positive relations between body size and both flight initiation distance (Blumstein et al. 2004a) and alert distance (Blumstein et al. 2005). However, body size may be correlated with another factor that is ultimately responsible for wariness. For instance, large-bodied species might be better able to detect approaching threats because they have larger eyes. A previous analysis rejected this suggestion and found that, after explaining significant variation in alert distance accounted for by body size, eye size had no effect on alert distance (Blumstein et al. 2004a). Because alert distance and FID are highly correlated, and based on this previous analyses with a smaller data set, I expected a positive and significant relation between body size and FID. Analyses of other life history and natural history traits would control for body size variation statistically when trying to identify other possible correlates of flightiness.

In birds (Newton 1998; Bennett & Owens 2002) and mammals (Wootton 1987), there is a positive relation between body size and age of first reproduction. Species that initiate reproduction later in life might be expected to be more cautious to ensure that they survive to reproduce. I thus predicted a positive relation between age at first reproduction and FID.

Parents that invest relatively more in a few offspring might tolerate less risk than those who invest little in many offspring because their direct fitness is associated with offspring survival. This can be tested in two ways, by focusing on clutch size and by examining how the duration that young are fed explained variation in FID. I predicted that greater FIDs would be found in species with small clutches and in species that fed their young longer.

Longevity should be associated with risk taking and thus overall wariness. Species that live longer might be expected to be more cautious to ensure that they realize this potential. Natural data on longevity are difficult to collect and are often unreliable (Gaillard et al. 1994; Promislow 1994). Nevertheless, in cases where some estimate of life span was available, I predicted a positive relation between longevity and FID.

Individuals in locations with compromised visibility increase their vigilance (Leger et al. 1983; Arnez & Leger 1997; Boinski et al. 2003; Blumstein et al. 2004b). It is likely that species also differ based on their habitats. Dense vegetation makes it difficult for individuals to detect predators. Thus, I predicted that species typically found in dense habitats would be warier than those found in more open habitats so as not to be surprised at a close distance by an unseen predator.

Motion detection is essential to feed on fast-moving prey (Fleishman et al. 1995), and visual systems vary in their velocity detection thresholds (Hodos 1993). Species that must capture moving prey have more acute visual systems (Garamszegi et al. 2002), and raptors and some *Anolis* lizards have evolved bifoveal vision to help them detect small prey (Fite & Lister 1981). Assuming that food detection abilities can be used in other contexts (e.g. predator detection), I expected that diet should be associated with flightiness. Specifically, I expected that carnivores and omnivores (i.e. species that eat moving prey) would have greater detection abilities and therefore would be more flighty than herbivores.

Sociality involves many traits (Cahan et al. 2002). Among them is allocating time to monitor conspecifics (Roberts 1988). Thus, more social species may be generally more vigilant because they must monitor both conspecifics and predators, and this wariness might make species more responsive to approaching humans. I therefore expected that social system should influence wariness. In birds, I examined this hypothesis by comparing cooperative breeders (Cockburn 1998) with noncooperative breeders, because I thought that the social relationships and bonds seen in cooperatively breeding species would select for vigilance to monitor conspecifics.

METHODS

Estimating FID

Methods follow those reported in Blumstein (2003) and Blumstein et al. (2004a, 2005). Assistants and I focused on birds (from Australia, Europe and North America) that were foraging or engaged in 'relaxed behaviours', such as preening or roosting. Highly vigilant and obviously alarmed birds were not approached, nor were nesting individuals or endangered species. To estimate FID, a subject was identified and then approached at a steady pace of ~0.5 m/s. Observers noted the distance that they started walking towards birds (starting distance), and the distance at which the focal bird moved away (FID_{horizontal}), either on foot or by flight in response to the approach. This distance typically was obvious, with the exception of some species that actively move while foraging (practically, this was mostly a problem with shorebirds). When birds were already moving, observers focused on obvious departures from the focal subject's typical movement (e.g. a double-step or movement in another direction) to score flight initiation. This problem applied only to the relatively rare situation in which the bird walked away instead of flying away. Finally, observers noted the height the bird was off the ground (if it was off the ground). Distances were measured in paces and converted to metres. From the horizontal FID measurement and the perching height in the tree measurement, we calculated the 'direct'

FID $\left(\text{FID}_{\text{direct}} = \sqrt{\left(\text{FID}_{\text{horizontal}}^2 + \text{perching height}^2 \right)} \right)$, and

used this FID_{direct} measurement in subsequent analyses. I paid particular attention to ensure that all observers collected data consistently. New observers were trained until their observations were identical to those of a trained observer. All observers were also trained to discard an experimental approach if there was any doubt about any of the variables collected.

Subjects were not marked; however, observers attempted to avoid resampling individuals by flushing on birds in different geographical locations and not resampling the same location repeatedly. A modest degree of resampling subjects has been shown to not influence the results of studies like this (Runyan & Blumstein 2004). Birds were studied in both 'pristine' environments, with few if any visitors, and in areas with human activity. Analyses excluded observations on individuals in highly visited city parks, and individuals that approached humans for hand-outs rather than fleeing. To my knowledge, none of the species included in our analyses were actively hunted at the locations where we studied them.

From a database of over 350 species, I selected 150 species (representing 107 genera and 40 families) for which I had at least 10 observations and calculated a species' average FID (Appendix).

Comparative Analyses

Maximum body mass was tabulated from Dunning (1993), and when a species was not reported there, I

obtained means from species accounts published in *The Birds of North America* and the *Handbook of Australian, New Zealand, and Antarctic Birds*. A few remaining masses came from Geffen & Yom-Tov (2000) and Clement (2000).

Life history and natural history traits were primarily taken from species accounts published in *The Birds of North America* and the *Handbook of Australian, New Zealand, and Antarctic Birds* and a review of the evolution of cooperative breeding (Cockburn 2003). Other resources were used to fill in missing species as well as for European species. All told, I was able to obtain data on habitat type, diet, clutch size, and whether a species was a cooperative breeder for 150 species, the number of days a chick was fed for 86 species, age at first reproduction for 69 species and longevity for 38 species. Habitat openness was scored as 0 = completely open habitat (beaches, open deserts), 1 = partially closed habitat (e.g. shrub lands, farmland, parks, mixed habitats, dry or open woodlands) or 2 = closed habitats (dense forest, humid forest, rainforest). Other categorical traits were made dichotomous for analysis: diet was scored as carnivorous/omnivorous (species that were described as eating living prey more than 'rarely') or not; mating system was scored as cooperative breeding or not. Continuous variables were log₁₀-transformed for analysis to normalize distributions. The distance that a human begins walking towards a bird (i.e. the starting distance) explains significant and substantial variation in FID, probably because it is highly correlated with alert distance (Blumstein et al. 2005) and because individuals that detect approaching threats at a greater distance also initiate flight at a greater distance, so that they can escape while the cost of flight is relatively low. Therefore, the starting distance must be incorporated into subsequent analyses (Blumstein 2003). This relation logically should be forced through the origin, because a person beginning to approach a bird at 0 m could only elicit a 0 m FID.

Values of related species are not phylogenetically independent (i.e. species may resemble each other because of shared ancestry), but differences between them are, so I calculated phylogenetically independent contrasts for continuous variables (Felsenstein 2004). I used the Sibley & Ahlquist (1990) phylogeny and the Sibley & Monroe (1990) taxonomy. Unresolved congeners not specifically included in the Sibley & Ahlquist phylogeny were initially scored as polytomies. Polytomies were later resolved randomly using MacClade 4.03 (Maddison & Maddison 2001). I assumed a punctuational model of evolution, calculated contrasts using Compare 4.5 (Martins 2003) and, as required by the method, forced the regression of contrasts through the origin (Felsenstein 2004).

To study the effect of body size on FID, I regressed contrasts of log body size and contrasts of log starting distance against contrasts of log FID_{direct}. The data included species with a range of mean FID_{direct} ($\bar{X} \pm \text{SD}$: 16.8 ± 12.7 m; range 3.4–65.5 m), masses (30 ± 1053 g; range 5–8700 g) and starting distances (33.0 ± 22.4 m; range 8.0–103.8 m).

To study the effect of age at first reproduction, the duration that young were fed, longevity, clutch size and habitat openness, I fitted linear models of these contrasts and interpreted the effect of each variable after explaining

variation accounted for by contrasts of log body mass and contrasts of log starting distance.

For categorical traits, I used the concentrated changes test (Maddison 1990). To transform FID into a categorical variable, I regressed log body mass and starting distance against log FID and saved these residuals. Species with positive residuals were then categorized as 'flighty' and those with negative residuals were categorized as 'not flighty'. I also defined 'very flighty' species as those with standardized residuals of at least 0.5. The concentrated changes tests determined whether the evolutionary gain of flightiness (or 'very flightiness') was more likely to occur in species that were carnivorous or omnivorous or that were cooperative breeders.

I used MacClade 4.03 (Maddison & Maddison 2001) to calculate the concentrated changes test and reconstructed character evolution in three ways: (1) assuming strict parsimony; (2) using an ACCTRAN algorithm, which accelerates changes; and (3) using a DELTRAN algorithm, which delays changes. This resulted in three analyses for each independent variable. In all cases I used 10 000 simulations to calculate the reported *P* values. (The analyses of 'very flighty' species involved more independent origins than those for 'flighty' species, and MacClade required much longer to run those simulations. Thus, for the analyses of very flighty species, *P* values are estimated from 1000 simulations.) I also set 'either character' as ancestral (because in some cases it was not possible to hypothesize the ancestral condition). *P* values were calculated for the likelihood that there were at least the observed number of evolutionary gains and losses of sociality.

Analyses were conducted using SPSS 11 for the Macintosh, and linear models were fitted using the GLM univariate method. I interpret two-sided *P* values of less than 0.05 as significant. Residuals from general linear models were visually scrutinized and did not deviate substantially from normal. I report partial eta-squared value as a measure of effect size (Cohen 1988) and interpret variables with very small effect sizes as unimportant in explaining variation in FID.

RESULTS

In general, larger species flushed at significantly greater distances than smaller ones (Fig. 1a). After explaining variation in FID accounted for by log starting distance (partial eta-squared = 0.530, $B = 0.765$, $P < 0.001$), log body mass explained significant variation in FID (partial eta-squared = 0.044, $B = 0.063$, $P = 0.010$).

Species that first reproduced at greater ages tended to be more flighty (Fig. 1b). After accounting for significant variation explained by log starting distance (partial eta-squared = 0.534, $B = 0.601$, $P < 0.001$) and log body mass (partial eta-squared = 0.061, $B = 0.061$, $P = 0.044$), there was a modest, but nonsignificant effect of age at first reproduction in explaining variation in flight initiation distance (partial eta-squared = 0.043, $B = 0.038$, $P = 0.091$).

There was no effect of clutch size on flightiness, although the coefficient was negative (Fig. 1c). After accounting for significant variation explained by log starting

distance (partial eta-squared = 0.534, $B = 0.766$, $P < 0.001$) and log body mass (partial eta-squared = 0.046, $B = 0.064$, $P = 0.009$), there was no effect of log clutch size in explaining variation in flight initiation distance (partial eta-squared = 0.012, $B = -0.053$, $P = 0.194$).

There was no effect of the number of days that young were fed on flightiness (Fig. 1d). After accounting for significant variation explained by log starting distance (partial eta-squared = 0.365, $B = 0.612$, $P < 0.001$) and log body mass (partial eta-squared = 0.073, $B = 0.081$, $P = 0.013$), there was no effect of the log number of days that young were fed in explaining variation in flight initiation distance (partial eta-squared = 0.004, $B = 0.014$, $P = 0.547$).

There was no effect of longevity on flightiness (Fig. 1e). After accounting for significant variation explained by log starting distance (partial eta-squared = 0.365, $B = 0.578$, $P < 0.001$) and nonsignificant variation explained by log body mass (partial eta-squared = 0.040, $B = 0.073$, $P = 0.239$), there was no effect of log longevity in explaining variation in flight initiation distance (partial eta-squared = 0.004, $B = 0.050$, $P = 0.703$).

There was no effect of habitat openness on flightiness (Fig. 1f). After accounting for significant variation explained by log starting distance (partial eta-squared = 0.476, $B = 0.594$, $P < 0.001$) and log body mass (partial eta-squared = 0.060, $B = 0.073$, $P = 0.003$), there was no effect of habitat openness in explaining variation in flight initiation distance (partial eta-squared = 0.001, $B = 0.088$, $P = 0.671$).

Flightiness evolved multiple times, and some clades were flightier than others (see [Supplementary Information, Fig. S1](#)). The concentrated changes tests found strong evidence that flightiness and diet, and flightiness and sociality did not evolve independently. ACCTRAN ($P < 0.0001$), DELTRAN ($P < 0.0001$) and parsimonious trait reconstructions ($P < 0.0001$) suggested that carnivorous or omnivorous species were more likely to be flighty. Similarly, ACCTRAN ($P < 0.0001$), DELTRAN ($P < 0.0001$) and parsimonious trait reconstructions ($P < 0.0001$) suggested that cooperative breeding species were more likely to be flighty. When I focused on the 49 very flighty species, I found identical results (i.e. all *P* values < 0.0001).

DISCUSSION

Taken together, fearfulness coevolved with some life history traits, but others had no effect. Body size and age of first reproduction are positively although not significantly associated with flightiness in birds. Species that eat live food, and those that are highly social, are more flighty than herbivores or noncooperative breeders. I found no effect of the number of days that young were fed, longevity, clutch size or habitat openness on flightiness in a series of analyses that controlled for variation that might be explained by body size. Body size consistently explained 4–7% of the variation in FID. While a modest effect, the effect size of other life history traits was typically much smaller. Body size, thus, seems to

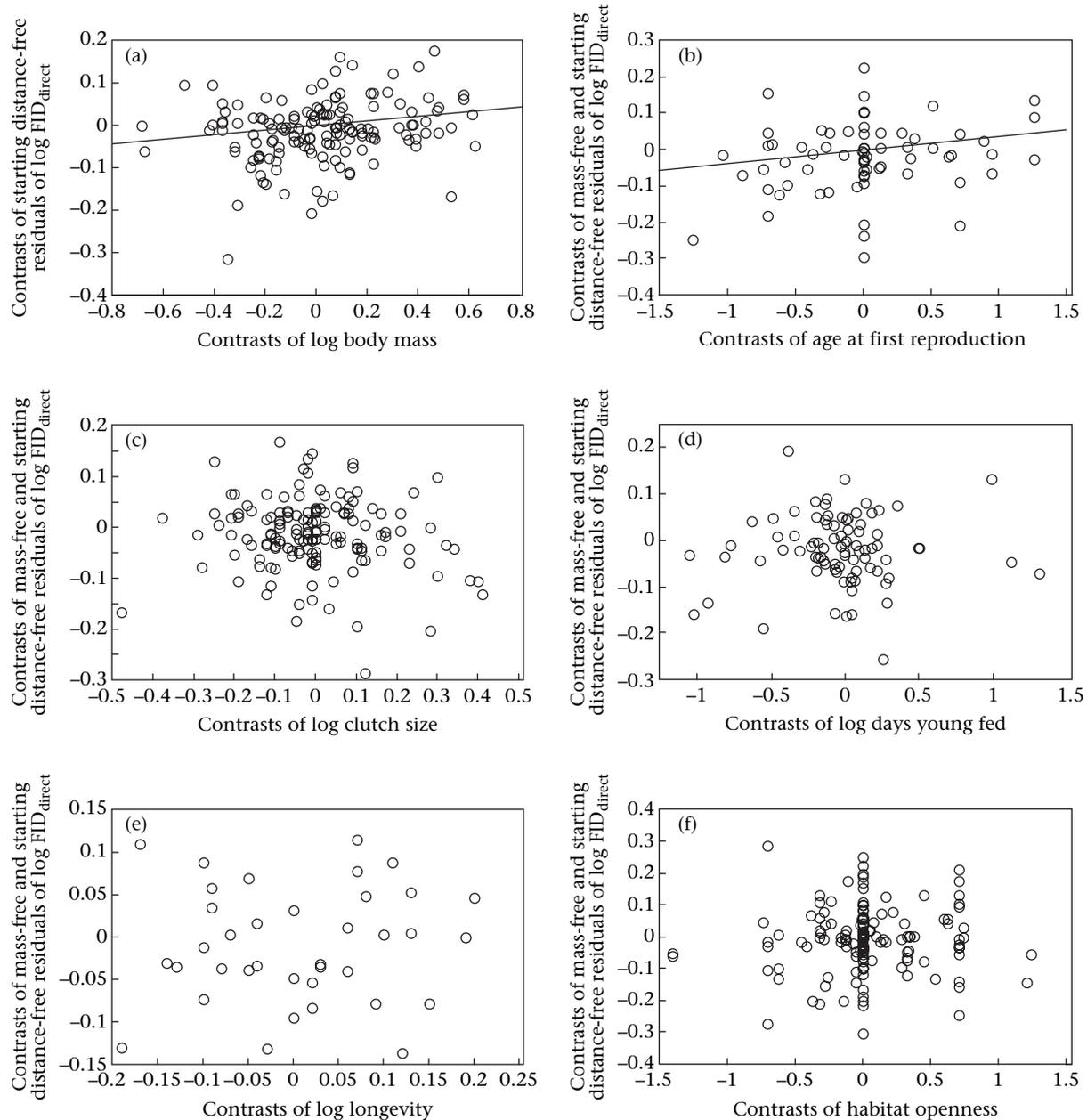


Figure 1. Effects of life history and natural history variation on flightiness in birds. Regressions of phylogenetically independent contrasts of life history traits and habitat openness on the phylogenetically independent contrasts of (a) starting distance-free residuals or (b–f) mass-free and starting distance-free residuals of log flight initiation distance (direct). Regression lines illustrate relations where $P < 0.01$.

be one of the major measured determinants of flightiness in birds.

There are a variety of reasons why body size might affect disturbance tolerance. Large size may be associated with greater vulnerability if predators are able to detect larger species at a distance. If large-bodied species are less agile than smaller-bodied species (Marden 1987; Witter et al. 1994), the benefit of escape might be greater in large-bodied species. Thus, for any given risk, large-bodied species may flush earlier. If large-bodied species have a lower cost of flight than small-bodied species, then we might expect that they would flush at greater distances (e.g. Ydenberg & Dill 1986). It is conceivable that small-bodied

species must allocate proportionally more time to foraging than larger species because of their relatively greater energy requirements (Bennett & Harvey 1987). If so, then the small species, even though disturbed, would tolerate a greater risk before flight.

Life history traits are expected to be correlated with each other, and finding any significant life history trait suggests that life history variation, in general, may affect fearfulness. The expected relation between age at first reproduction and flightiness was based on 69 species, but estimates of longevity were based on only 30 species. Age at maturity is perhaps a better metric of longevity (Gaillard et al. 1994; Promislow 1994), and unless there is social

suppression of reproduction (Wasser & Barash 1983), age at first reproduction should be correlated with age at maturity. Thus, the finding that age at first reproduction has a modest effect on flightiness is consistent with the hypothesis that life history influences fearfulness. In contrast, the lack of significant relations between flightiness and other measures of parental investment (clutch size, days spent feeding) was unexpected, given Ghaleb & Martin's (2001) experimental results that illustrated a risk-taking survival trade-off. Specifically, they found that birds took greater risks to care for offspring when their own mortality rates were higher (and thus residual reproductive value was lower). Perhaps my findings highlight the relatively small effect of life history traits on species-typical behaviour.

The finding that both diet and sociality coevolved with flightiness suggests that these traits affect the evolutionary origin of wariness. I suspect they do so via 'carry-over effects' from selection on other traits. Animals that eat living prey should be more attentive to movement, and social species should be more attentive to detecting conspecifics. Thus, selection on these traits may alone be a sufficient explanation for why these species are flightier.

Of course there are other factors that may also influence flightiness. For instance, the remarkably versatile corvids (Fig. S1) are relatively flighty. Corvids also have relatively large brains and have high rates of feeding innovations, characteristics associated with species richness (Nicolakakis et al. 2003). Costs of lost foraging opportunities brought about by wariness might be counterbalanced by rapidly habituating to nonthreatening situations.

These results demonstrate that we can predict species-specific variation in antipredator behaviour with knowledge of life history and natural history traits. Body size, age at first reproduction, diet and sociality greatly influence how species will respond to approaching threats. These results also allow us to predict which species will be vulnerable to human disturbance and offer the intriguing suggestion that there might be another mechanism underlying anthropogenic extinctions.

As previously discussed, body size is often correlated with extinction probability. Previous hypotheses have focused on the observation that larger species are the target of human hunters (Owens & Bennett 2000; but see Wroe et al. 2004) and the inevitable metabolic cost and smaller population sizes associated with large body size (e.g. Van Valkenburgh et al. 2004). I suggest that another mechanism might be associated with vulnerability, and that this mechanism might explain some of the extinctions associated with Pleistocene human range expansions (Barnosky et al. 2004).

If large-bodied species are more easily disturbed, then they will spend more time escaping possible threats. A simulation model examining the cost of human disturbance found large reductions in the number of food items captured following disturbance (Blumstein et al. 2005). Animals typically select foraging locations to reduce encounters with potentially disturbing humans (Sibbald et al. 2001; also see Gill et al. 1996), and increased human disturbance may lead to a loss of species (Fernández-Juricic 2002; Rodríguez-Prieto & Fernández-Juricic 2005). In

stressful conditions, this increased energy expenditure associated with escaping humans might prove fatal in two ways. First, by avoiding risky areas that contain disturbances, individuals may forage in suboptimal or insufficient areas and simply starve. Second, repeated disturbance could erode individual condition. The large literature on state-dependent foraging (Clark 1994) provides ample evidence that species in poor condition often take greater risks (e.g. Bachman 1993; Krause et al. 1998). Taking greater risks around a novel predator (humans) might ultimately lead to greater mortality.

These scenarios assume that individuals do not habituate to ongoing disturbance. However, habituation is not ubiquitous. Studies of chaparral birds in coastal southern California (unpublished data) suggest that some species habituated to increased disturbance while others sensitized. More research is required to explain species differences in the propensity to habituate or sensitize. However, studies of individually identified yellow-bellied marmots, *Marmota flaviventris*, in Colorado, have demonstrated that some individuals habituated to repeated human exposure, while others either had no response or sensitized (Runyan & Blumstein 2004). Thus, some species, unable to habituate, could be forced from preferred foraging areas and might suffer greater condition-related mortality than undisturbed species. Large-bodied species, because they need absolutely more food, might be particularly vulnerable to disturbance while foraging.

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SUPPLEMENTARY INFORMATION

Supplementary information associated with this article can be found, in the online version, at [doi:10.1016/j.anbehav.2005.05.010](https://doi.org/10.1016/j.anbehav.2005.05.010).

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Appendix

Table A1. Mean \pm SD distance (in metres) that experimental approaches were initiated (starting distance), the mean \pm SD direct distance between the observer and the bird when it initiated flight (FID_{direct}), and sample sizes from which these estimates were derived

Family	Latin name	Common name	Starting distance	FID _{direct}	N
Megapodiidae	<i>Alectura lathami</i>	Australian brush turkey	26.6 \pm 20.3	12.0 \pm 13.0	11
Anatidae	<i>Cygnus atratus</i>	Black swan	95.9 \pm 47.3	50.4 \pm 35.8	19
Anatidae	<i>Chenonetta jubata</i>	Australian wood duck	39.7 \pm 31.8	25.5 \pm 24.9	44
Anatidae	<i>Anas superciliosa</i>	Pacific black duck	57.1 \pm 36.6	38.9 \pm 29.0	50
Anatidae	<i>Anas gracilis</i>	Grey teal	64.3 \pm 35.2	41.6 \pm 22.8	23
Anatidae	<i>Anas castanea</i>	Chestnut teal	62.4 \pm 30.6	46.5 \pm 21.4	55
Picidae	<i>Picus viridis</i>	Eurasian green woodpecker	27.7 \pm 6.1	8.6 \pm 4.1	24
Coraciidae	<i>Eurystomus orientalis</i>	Dollarbird	41.9 \pm 33.1	25.9 \pm 22.5	23
Halcyonidae	<i>Dacelo novaeguineae</i>	Laughing kookaburra	26.4 \pm 17.4	13.8 \pm 12.3	54
Halcyonidae	<i>Todiramphus sanctus</i>	Sacred kingfisher	41.9 \pm 38.3	20.9 \pm 6.8	16
Cuculidae	<i>Cacomantis flabelliformis</i>	Fan-tailed cuckoo	18.4 \pm 8.3	10.6 \pm 5.7	19
Psittacidae	<i>Trichoglossus haematodus</i>	Rainbow lorikeet	21.8 \pm 11.4	10.0 \pm 8.1	11
Cacatuidae	<i>Cacatua roseicapilla</i>	Galah	29.6 \pm 17.0	8.9 \pm 5.6	64
Cacatuidae	<i>Cacatua galerita</i>	Sulphur-crested cockatoo	28.0 \pm 17.3	15.3 \pm 14.9	41
Psittacidae	<i>Platycercus elegans</i>	Crimson rosella	19.7 \pm 12.3	9.1 \pm 6.4	83
Psittacidae	<i>Platycercus eximius</i>	Eastern rosella	24.8 \pm 17.3	13.9 \pm 8.8	31
Columbidae	<i>Streptopelia chinensis</i>	Spotted turtle-dove	24.9 \pm 13.7	12.9 \pm 9.0	52
Columbidae	<i>Macropygia amboinensis</i>	Brown cuckoo-dove	20.9 \pm 10.0	8.1 \pm 4.8	11
Columbidae	<i>Ocyphaps lophotes</i>	Crested pigeon	27.4 \pm 13.4	12.7 \pm 9.2	31
Columbidae	<i>Geopelia humeralis</i>	Bar-shouldered dove	66.3 \pm 35.8	22.1 \pm 14.8	93
Columbidae	<i>Leucosarcia melanoleuca</i>	Wonga pigeon	28.4 \pm 16.7	18.5 \pm 10.9	22
Columbidae	<i>Zenaida macroura</i>	Mourning dove	23.3 \pm 13.9	15.2 \pm 12.1	15
Rallidae	<i>Porphyrio porphyrio</i>	Purple swamphen	52.8 \pm 31.0	34.5 \pm 21.8	68
Rallidae	<i>Gallinula tenebrosa</i>	Dusky moorhen	23.9 \pm 11.6	14.8 \pm 10.7	37
Rallidae	<i>Fulica atra</i>	Eurasian coot	24.9 \pm 17.6	19.2 \pm 15.8	10
Scolopacidae	<i>Limosa fedoa</i>	Marbled godwit	44.3 \pm 23.5	17.7 \pm 8.6	36
Scolopacidae	<i>Numenius phaeopus</i>	Whimbrel	77.1 \pm 66.1	37.7 \pm 30.4	28
Scolopacidae	<i>Numenius americanus</i>	Long-billed curlew	48.4 \pm 26.8	25.7 \pm 9.7	18
Scolopacidae	<i>Numenius madagascariensis</i>	Eastern curlew	103.8 \pm 53.1	65.5 \pm 41.6	42
Scolopacidae	<i>Tringa (Heteroscelus) brevipes</i>	Grey-tailed tattler	38.9 \pm 25.7	17.3 \pm 8.6	45
Scolopacidae	<i>Catoptrophorus semipalmatus</i>	Willet	44.8 \pm 21.7	20.8 \pm 10.2	93
Scolopacidae	<i>Arenaria interpres</i>	Ruddy turnstone	28.6 \pm 10.0	13.8 \pm 6.4	51
Scolopacidae	<i>Limnodromus griseus</i>	Short-billed dowitcher	29.8 \pm 15.0	12.7 \pm 6.2	11
Scolopacidae	<i>Calidris mauri</i>	Western sandpiper	31.7 \pm 18.7	15.6 \pm 9.3	22
Scolopacidae	<i>Calidris ruficollis</i>	Red-necked stint	31.2 \pm 11.0	16.4 \pm 8.7	61
Scolopacidae	<i>Calidris minutilla</i>	Least sandpiper	23.2 \pm 17.1	9.2 \pm 5.7	33
Scolopacidae	<i>Calidris acuminata</i>	Sharp-tailed sandpiper	26.5 \pm 12.9	14.8 \pm 8.7	28
Burhinidae	<i>Burhinus grallarius</i>	Bush stone-curlew	41.6 \pm 29.3	25.9 \pm 20.7	13
Haematopodidae	<i>Haematopus longirostris</i>	Pied oystercatcher	95.9 \pm 54.8	38.5 \pm 18.0	23
Haematopodidae	<i>Haematopus fuliginosus</i>	Sooty oystercatcher	58.2 \pm 25.8	30.5 \pm 15.8	59
Recurvirostridae	<i>Himantopus himantopus</i>	Black-winged stilt	56.9 \pm 22.2	38.3 \pm 21.1	63
Recurvirostridae	<i>Himantopus mexicanus</i>	Black-necked stilt	47.6 \pm 26.7	22.3 \pm 12.9	52
Charadriidae	<i>Pluvialis fulva</i>	Pacific golden plover	35.4 \pm 21.6	21.9 \pm 12.1	21
Charadriidae	<i>Pluvialis squatarola</i>	Black-bellied plover	63.9 \pm 29.8	36.0 \pm 18.7	41
Charadriidae	<i>Charadrius ruficapillus</i>	Red-capped plover	36.9 \pm 16.6	22.0 \pm 7.7	16
Charadriidae	<i>Euseyornis melanops</i>	Black-fronted dotterel	38.6 \pm 14.2	22.7 \pm 9.3	46
Charadriidae	<i>Vanellus miles</i>	Masked lapwing	92.2 \pm 48.4	46.8 \pm 30.5	37
Laridae	<i>Larus delawarensis</i>	Ring-billed gull	54.9 \pm 22.4	22.0 \pm 13.1	15
Laridae	<i>Larus dominicanus</i>	Kelp gull	62.8 \pm 34.7	24.4 \pm 11.4	14
Laridae	<i>Larus occidentalis</i>	Western gull	37.2 \pm 25.9	17.4 \pm 10.8	26
Laridae	<i>Larus novaehollandiae</i>	Silver gull	63.1 \pm 36.0	16.8 \pm 12.1	136
Laridae	<i>Sterna caspia</i>	Caspian tern	54.5 \pm 15.4	35.0 \pm 10.4	12
Laridae	<i>Sterna bergii</i>	Crested tern	71.0 \pm 36.2	17.3 \pm 10.7	37
Laridae	<i>Sterna albifrons</i>	Little tern	48.2 \pm 26.6	21.5 \pm 7.9	18
Accipitridae	<i>Elanus axillaris</i>	Black-shouldered kite	73.2 \pm 35.2	23.1 \pm 14.9	10
Podicipedidae	<i>Tachybaptus novaehollandiae</i>	Australasian grebe	30.3 \pm 15.7	23.4 \pm 14.1	19
Anhingiidae	<i>Anhinga melanogaster</i>	Darter	45.3 \pm 21.1	24.0 \pm 14.9	20
Phalacrocoracidae	<i>Phalacrocorax melanoleucos</i>	Little pied cormorant	56.5 \pm 32.6	19.8 \pm 14.3	58
Phalacrocoracidae	<i>Phalacrocorax varius</i>	Pied cormorant	72.5 \pm 27.9	31.3 \pm 18.0	25
Phalacrocoracidae	<i>Phalacrocorax sulcirostris</i>	Little black cormorant	58.3 \pm 33.0	24.0 \pm 15.3	38
Phalacrocoracidae	<i>Phalacrocorax carbo</i>	Great cormorant	56.4 \pm 24.8	32.3 \pm 20.6	34
Ardeidae	<i>Egretta novaehollandiae</i>	White-faced heron	78.9 \pm 46.5	31.2 \pm 20.1	33
Ardeidae	<i>Egretta garzetta</i>	Little egret	88.9 \pm 35.8	52.4 \pm 23.0	10
Ardeidae	<i>Egretta thula</i>	Snowy egret	47.9 \pm 34.0	18.6 \pm 15.7	47
Ardeidae	<i>Ardea herodias</i>	Great blue heron	73.9 \pm 46.3	36.6 \pm 23.1	46

(continued)

Table A1. (continued)

Family	Latin name	Common name	Starting distance	FID _{direct}	N
Ardeidae	<i>Ardea alba</i>	Great egret	73.4±45.6	39.9±24.8	79
Threskiornithidae	<i>Threskiornis molucca</i>	Australian white ibis	83.6±50.1	32.8±20.4	48
Threskiornithidae	<i>Threskiornis spinicollis</i>	Straw-necked ibis	61.7±32.5	42.4±25.2	10
Threskiornithidae	<i>Platalea regia</i>	Royal spoonbill	85.7±39.9	44.4±24.9	24
Pelecanidae	<i>Pelecanus conspicillatus</i>	Australian pelican	77.4±54.5	32.6±25.4	39
Climacteridae	<i>Cormobates leucophaeus</i>	White-throated treecreeper	12.1±4.5	5.8±2.9	17
Climacteridae	<i>Climacteris picumnus</i>	Brown treecreeper	11.1±5.3	5.1±3.1	13
Menuridae	<i>Menura novaehollandiae</i>	Superb lyrebird	19.4±15.1	10.5±8.6	26
Ptilonorhynchidae	<i>Ailuroedus crassirostris</i>	Green catbird	15.3±5.0	9.7±4.1	16
Ptilonorhynchidae	<i>Ptilonorhynchus violaceus</i>	Satin bowerbird	16.4±6.8	9.5±5.1	22
Maluridae	<i>Malurus cyaneus</i>	Superb fairy-wren	13.0±5.9	6.5±3.4	93
Maluridae	<i>Malurus lamberti</i>	Variiegated fairy-wren	9.2±6.0	4.5±3.4	38
Maluridae	<i>Stipiturus malachurus</i>	Southern emu-wren	9.9±3.8	7.0±3.3	13
Meliphagidae	<i>Lichmera indistincta</i>	Brown honeyeater	18.1±8.9	9.8±5.6	16
Meliphagidae	<i>Meliphaga lewinii</i>	Lewin's honeyeater	16.0±12.7	8.2±6.0	32
Meliphagidae	<i>Lichenostomus chrysops</i>	Yellow-faced honeyeater	9.5±5.1	5.8±3.6	29
Meliphagidae	<i>Lichenostomus penicillatus</i>	White-plumed honeyeater	16.1±7.8	9.8±5.6	23
Meliphagidae	<i>Philemon corniculatus</i>	Noisy friarbird	20.5±8.4	11.1±5.3	55
Meliphagidae	<i>Phylidonyris novaehollandiae</i>	New Holland honeyeater	13.4±9.0	7.9±6.0	47
Meliphagidae	<i>Phylidonyris melanops</i>	Tawny-crowned honeyeater	19.5±10.4	9.8±6.7	11
Meliphagidae	<i>Acanthorhynchus tenuirostris</i>	Eastern spinebill	9.7±4.3	5.8±2.6	39
Meliphagidae	<i>Manorina melanophrys</i>	Bell miner	9.6±6.6	5.0±3.0	44
Meliphagidae	<i>Manorina melanocephala</i>	Noisy miner	21.1±23.7	7.5±14.9	37
Meliphagidae	<i>Anthochaera chrysoptera</i>	Little wattlebird	15.8±10.2	7.3±3.0	40
Meliphagidae	<i>Anthochaera carunculata</i>	Red wattlebird	14.3±8.6	8.7±6.4	15
Meliphagidae	<i>Epthianura albifrons</i>	White-fronted chat	35.5±14.7	22.6±7.8	23
Pardalotidae	<i>Sericornis citreogularis</i>	Yellow-throated scrubwren	11.7±6.6	5.6±4.3	51
Pardalotidae	<i>Sericornis frontalis</i>	White-browed scrubwren	9.1±4.6	4.2±2.5	41
Pardalotidae	<i>Sericornis magnirostris</i>	Large-billed scrubwren	8.0±2.1	4.4±4.4	17
Pardalotidae	<i>Acanthiza pusilla</i>	Brown thornbill	9.5±4.4	6.7±9.9	28
Pardalotidae	<i>Acanthiza reguloides</i>	Buff-rumped thornbill	9.5±4.1	4.3±1.8	14
Pardalotidae	<i>Acanthiza nana</i>	Yellow thornbill	11.3±6.4	6.3±2.4	17
Pardalotidae	<i>Gerygone mouki</i>	Brown gerygone	8.6±3.7	4.2±1.9	32
Petroicidae	<i>Eopsaltria australis</i>	Eastern yellow robin	16.2±8.3	9.9±5.6	77
Cinlosomatidae	<i>Psophodes olivaceus</i>	Eastern whipbird	11.3±5.1	5.9±3.3	50
Corcoracidae	<i>Corcorax melanorhamphos</i>	White-winged chough	23.7±10.6	16.2±7.3	14
Pachycephalidae	<i>Pachycephala pectoralis</i>	Golden whistler	14.7±6.4	7.9±3.9	18
Pachycephalidae	<i>Colluricincla harmonica</i>	Grey shrike-thrush	21.4±13.8	12.8±11.4	15
Corvidae	<i>Aphelocoma californica</i>	Western scrub-jay	23.9±13.0	15.0±8.9	27
Corvidae	<i>Corvus monedula</i>	Eurasian jackdaw	42.6±8.3	24.6±14.3	14
Corvidae	<i>Corvus coronoides</i>	Australian raven	42.0±27.7	25.8±22.2	63
Artamidae	<i>Cracticus torquatus</i>	Grey butcherbird	33.4±21.1	19.3±13.3	10
Dicruridae	<i>Gymnorhina tibicen</i>	Australian magpie	24.4±13.0	10.9±8.7	91
Artamidae	<i>Strepera graculina</i>	Pied currawong	26.0±17.9	15.1±11.6	26
Oriolidae	<i>Oriolus sagittatus</i>	Olive-backed oriole	17.0±10.7	11.3±5.9	33
Camppephagidae	<i>Rocina novaehollandiae</i>	Black-faced cuckoo-shrike	36.9±22.3	21.1±13.2	20
Dicruridae	<i>Rhipidura leucophrys</i>	Willie wagtail	20.4±13.9	11.8±9.7	46
Dicruridae	<i>Rhipidura fuliginosa</i>	Grey fantail	12.8±6.5	6.8±4.3	37
Dicruridae	<i>Rhipidura rufifrons</i>	Rufous fantail	12.5±4.0	6.4±2.0	11
Artamidae	<i>Grallina cyanoleuca</i>	Magpie-lark	35.7±17.7	19.0±10.5	97
Muscicapidae	<i>Zoothera lunulata</i>	Bassian thrush	15.4±6.6	8.9±3.1	31
Turdidae	<i>Turdus migratorius</i>	American robin	22.6±12.3	11.2±7.4	13
Muscicapidae	<i>Erithacus rubecula</i>	European robin	29.2±5.5	11.1±4.3	16
Sturnidae	<i>Sturnus vulgaris</i>	Common starling	26.4±13.7	13.6±9.0	32
Sturnidae	<i>Sturnus unicolor</i>	Spotless starling	29.8±6.7	13.2±6.2	14
Sturnidae	<i>Acridotheres tristis</i>	Common myna	22.8±13.6	11.6±9.4	40
Certhiidae	<i>Certhia brachydactyla</i>	Short-toed treecreeper	22.3±2.6	7.2±2.4	15
Paridae	<i>Parus ater</i>	Coal tit	10.2±1.8	3.4±1.0	14
Paridae	<i>Parus major</i>	Great tit	18.5±5.1	6.3±2.1	15
Paridae	<i>Parus caeruleus</i>	European blue tit	18.3±6.1	6.9±1.9	14
Aegithalidae	<i>Psaltriparus minimus</i>	Bush-tit	12.9±8.6	6.9±4.2	26
Hirundinidae	<i>Hirundo neoxena</i>	Welcome swallow	25.4±18.2	11.0±5.6	32
Regulidae	<i>Regulus calendula</i>	Ruby-crowned kinglet	10.2±4.0	4.7±2.1	10
Pycnonotidae	<i>Pycnonotus jocosus</i>	Red-whiskered bulbul	23.8±16.8	18.4±13.2	25
Sylviidae	<i>Cisticola exilis</i>	Golden-headed cisticola	9.0±4.7	5.4±3.0	41
Zosteropidae	<i>Zosterops lateralis</i>	Silvereye	11.0±6.2	6.1±3.8	34
Sylviidae	<i>Acrocephalus stentoreus</i>	Clamorous reed-warbler	15.5±9.4	11.5±9.4	20
Sylviidae	<i>Phylloscopus collybita</i>	Eurasian chiffchaff	24.7±5.3	6.0±1.5	15

Table A1. (continued)

Family	Latin name	Common name	Starting distance	FID _{direct}	N
Timaliidae	<i>Chamaea fasciata</i>	Wrentit	9.0±4.7	5.0±3.4	10
Fringillidae	<i>Passer domesticus</i>	House sparrow	21.6±11.6	13.2±8.6	18
Fringillidae	<i>Passer montanus</i>	Eurasian tree-sparrow	20.3±7.6	8.0±3.0	15
Passeridae	<i>Motacilla alba</i>	White wagtail	28.9±3.6	7.7±1.8	16
Motacillidae	<i>Anthus novaeseelandiae</i>	Richard's pipit	23.0±11.7	12.4±5.2	63
Passeridae-Estrildinae	<i>Neochmia temporalis</i>	Red-browed finch	13.8±8.7	7.5±5.1	51
Passeridae	<i>Lonchura punctulata</i>	Nutmeg mannikin	19.6±9.1	11.0±6.3	43
Passeridae	<i>Lonchura castaneothorax</i>	Chestnut-breasted mannikin	21.2±5.5	14.4±4.5	10
Fringillidae	<i>Fringilla coelebs</i>	Chaffinch	28.3±6.2	7.7±2.1	15
Fringillidae	<i>Carduelis chloris</i>	European greenfinch	22.7±2.2	6.9±1.6	15
Fringillidae	<i>Carduelis carduelis</i>	European goldfinch	25.7±4.9	9.2±2.5	18
Emberizidae	<i>Melospiza melodia</i>	Song sparrow	12.9±5.5	8.2±3.9	17
Emberizidae	<i>Zonotrichia leucophrys</i>	White-crowned sparrow	16.1±8.2	8.6±5.3	43
Emberizidae	<i>Junco hyemalis</i>	Dark-eyed junco	15.1±6.6	8.9±3.8	17
Emberizidae	<i>Pipilo crissalis</i>	California towhee	19.8±10.9	11.9±7.9	46
Emberizidae	<i>Pipilo maculatus</i>	Spotted towhee	15.8±10.5	9.8±6.4	32
Parulidae	<i>Dendroica coronata</i>	Yellow-rumped warbler	14.8±5.7	9.4±4.1	28