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REVIEW

What chasing birds can teach us about predation risk effects: past insights and future directions

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Abstract

Birds are the best-studied taxa with respect to our knowledge about predation risk assessment. In the past 4 years, global progress in this field has been made due to a remarkable number of synthetic reviews, meta-analyses, and comparative analyses that are based on databases containing tens of thousands of observations on how birds escape from predators. In addition, novel empirical studies, often on more than one species at a time, have provided new insights into mechanistic diversity. Birds fly, walk, and swim away from approaching threats and the distance at which they do so—quantified as flight initiation distance—reveals much about their perceptions of predation risk. The contexts that influence risk assessment and management in both ecological and evolutionary time have largely been identified by thorough study of the life history, natural history, physiology, environment, and phylogenies of birds. We have also discovered continental and latitudinal differences in risk management. A large set of applied studies now use this knowledge to both increase our understanding of the vulnerability of birds to anthropogenic disturbance, and provide insight into how best to manage it. Future advances require: (1) developing a better understanding of the sensory mechanisms involved in risk assessment, (2) studies of individuals that are sampled repeatedly, and (3) the development of decision-support tools for wildlife managers to help us better coexist with birds in an increasingly urban world.

Keywords Antipredator behavior · Comparative analyses · Conservation · Flight-initiation distance · Management · Meta-analyses

Introduction

When approached by a predator, animals eventually flee (Cooper and Blumstein 2015a, b). Capitalizing on the observation that most species view humans as predators, or at least view humans as providing some predatory threat (Frid and Dill 2002), researchers around the world have conducted many studies quantifying flight initiation distance (FID), i.e., the distance at which animals begin to flee when approached by a human. Most of these studies are on birds (Stankowich and Blumstein 2005; Samia et al. 2015a, b; Møller 2015). Thus, in some respects, we know more about predation risk assessment in birds than any other taxon. In the past 4 years, substantial global progress in this field has been made due to a remarkable number of synthetic reviews, meta-analyses, and comparative analyses that are based on databases containing tens of thousands of observations on how birds escape from predators. The aim of this paper is to summarize some of these insights. By design, this overview is eclectic; not all recent findings will be discussed.

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Methods

On 16 January 2018, I searched all databases on the Clarivate Web of Science platform for papers published in 2014–2018 using the keywords "FID" or "Flight initiation distance" and "birds." Of the 252 initial hits, and after removing duplicates, published abstracts that were later published as papers, papers that were not about FID, papers that were solely about methodology development and did not include any empirical data, and those that were simply reports of data from published papers (the data sets are now published and indexed in Dryad and Figshare), and 132 studies that were not on birds, 72 studies of avian FID remained.

It is important to note that this was not a formal systematic review in that I only searched for these terms in one major database; I did not attempt to see who cited recent papers to find more of them, and because the search was conducted in early 2018, most of the literature published in 2018 is missing. Moreover, relevant chapters from Cooper and Blumstein's (2015a) *Escaping from Predators* did not emerge from this search. Also, while writing the paper, I found several more references that did not result from the formal search. Regardless, this search provides an idea of some of the major topics of FID work in birds conducted since 2014. I summarize the output from the search without the missing references, but do discuss two key book chapters (Møller 2015; Tyrrell and Fernández-Juricic 2015), and a paper by Lomas et al. (2014).

For an index of overall recent work in the field, I also searched using the term "flight initiation distance" between 1986 [the publication date of the foundational Ydenberg and Dill (1986) paper] and 2017.

Results

The field of research on FID, at least as indexed in the Web of Science, has been growing exponentially since 1989 (Fig. 1). Each publication is cited an average of 20.7 times and the h-index for the field is 45, meaning that 45 papers have been cited at least 45 times.

The 72 avian studies on FID published between 2014 and 2017 can be classified in various ways (Supplementary Table 1). Only 38% focused on a single species; most studied more than a single species. The number of species studied per study ranged from one to 650 (average 48 ± 103 SD). Depending upon how viewed, about 6% of the studies were about the development of methodology, 24% asked foundational questions in evolution (including estimating heritability and studying phenotypic correlations), and 44% could be classified as trying to identify or study proximate mechanisms underlying risk perception or the response of birds to human impacts. Indeed, 28% of the studies were directly framed in the context of studying urbanization and another 19% were interested in quantifying human impacts on birds. Many of the studies focused on terrestrial birds (47%), while 24% focused on water birds and shorebirds. Almost a quarter of them (24%) were framed in a way that increased knowledge for conservation or management.

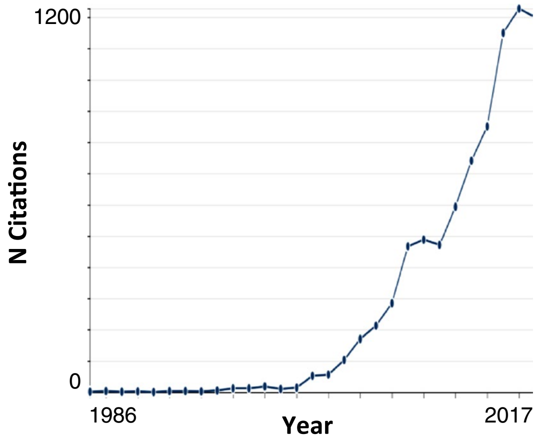

Fig. 1 Number of annual citations referencing 'flight initiation distance' between 1986 and 2017

The data analyzed in these studies came from throughout the world; 14% of the data sets were comparative, global data sets. Most studies (38%) were conducted in Europe. Contributions from North America and Australia/New Zealand/Oceania comprised 18% of the studies. South America, Asia and Africa remain relatively understudied contributing 6, 4 and 4% of the studies, respectively.

What we learned in the past 4 years

Overall, we are now certain that escape decisions are economic decisions, made by individuals that are influenced by both the costs and benefits of remaining and the costs and benefits of flight. Møller (2015) conducted a formal meta-analysis of FID in birds and determined that urbanization is even more important than body mass in explaining avian variation in FID. Møller (2015) also reported that, in birds, FID also varies with predation risk, decreases with increasing latitude, sociality, parasitism, and increases with hunting. There are also effects of habitat openness and life history traits (including coloration).

A few notable trends emerge from recent avian research on FID. Until recently most FID studies were conducted in Europe, North America, and Australia; I am aware of no previously published studies of FID from Africa, and only a few from Asia and South America. Notable among the latter is Carrete et al. (2016), where long-term work on individually marked Burrowing Owls (*Athene cunicularia*) was conducted. It is enlightening to see FID applied to both applied and foundational evolutionary questions throughout the world. There were three African studies, four South American studies, and three studies from China.

Studies undertaken in other continents are important because they both increase the body of literature and provide data on an increasing diversity of species, which can be used in comparative studies. In addition, since some studies suggest different patterns on different continents (e.g., Møller et al. 2014), and since Africa has the longest history of human coexistence with birds, particularly novel insights about human and bird coexistence may shed light on anthropogenic declines of birds on other continents.

The field is unique, in some sense, in that researchers routinely share data sets and combine them for large, comparative, evolutionary studies and formal meta-analyses. I have already discussed Møller's (2015) meta-analysis. Samia et al. (2015b) focused on tolerance, which they defined as the difference in FID in birds between a site with fewer people and one with more people and conducted a phylogenetic meta-analysis to explain variation in tolerance. They found that the type of contrast (e.g., rural–urban) had the largest effect on tolerance, and that the second largest effect was on body size. Unlike the rather universal insight that large birds flush greater distances (e.g., Blumstein 2006; Møller 2015), large birds that can coexist with humans seemingly have the greatest tolerance of humans. The implications of this finding are profound because they suggest that the key remaining question to ask is what explains variation in the probability of coexisting with humans? Large birds, if they can coexist with humans, presumably pay the greatest cost of being disturbed because they flush the greatest distances.

Comparative analyses have also generated some key findings. For instance, brain size seems to be a major driver of avian escape strategies. Samia et al. (2015a, b) applied the Samia and Blumstein (2014) phi-index, which is a metric that quantifies the degree to which animals escape immediately upon detection or whether they delay escape after detecting an approaching threat, and found that birds with larger brains delay escape longer than birds with smaller brains. Symonds et al. (2014), using a relatively smaller data set that contained parameters related to brain size, noted that most of the variation in FID explained by brain size is a function of cerebellum size, although they also noted that the results depended to some extent on the specific phylogeny used. Møller and Erritzøe (2016) noted that brain size has consequences in that smaller brained individuals are more likely to be shot!

In a comparative study Garamszegi and Møller (2017) found that both between-population and within-population variation in FID, not simply average FID, has consequences. Importantly, when between-population variation in FID increases, birds live shorter lives. In addition, the probability of natal dispersal and the type of habitats used are also associated with variation in FID.

Jiang and Møller (2017) compared close relatives where one was relatively more threatened than the other, and found that the threatened species typically had larger FIDs than their non-threatened close relatives. However, continental patterns of expanding and declining populations are not consistently associated with FID (Møller et al. 2014). In both Europe and Australia, birds with longer FIDs are declining in number, but North American birds show the opposite relationship: birds there with longer FIDs are increasing in number. Additional work is warranted to understand how variation in FID is associated with population trends in birds at the continental scale.

Over the past few years there have been a number of exciting empirical findings. Amongst them are those about the genetic basis of FID variation. In animals, at least two genes, the dopamine D4 receptor gene (*DRD4*) and the serpentine receptor, class T gene (*SRT*) are associated with fear. Three avian studies on individually marked birds (Garamszegi et al. 2014; van Dongen et al. 2015; Holtmann et al. 2016) studied the underlying genetic correlates with FID. Two genes, *DRD4* and *SERT*, have been identified as being associated with fear in animals. van Dongen et al. (2015) found that in Black Swans (*Cygnus atratus*), there was no inter-individual variation in *SERT* but that there was a significant association between *DRD4* and FID. More importantly, they found that *DRD4* varied as a function of urbanization. In more rural populations of swans around Melbourne, Australia, the birds were more wary, whereas in more urban populations they were less wary. These differences were associated with specific *DRD4* genotypes, which suggests that swans might be classified according to the degree of disturbance they can tolerate. Garamszegi et al. (2014) found specific single nucleotide polymorphisms of *DRD4* associated with variation in FID in Collared Flycatchers (*Ficedula albicollis*), while Holtmann et al. (2016) found that both *DRD4* and *SERT* were associated with Dunnock (*Prunella modularis*) FID. Because Dunnocks were studied in their native UK population as well as in an introduced New Zealand population, Holtmann et al. (2016) asked whether there were population differences in genes associated with this successful introduction. Indeed, the New Zealand population of Dunnocks had more bold-related *SERT* individuals, which either reflected the fact that bolder animals were caught and transported or that there has been selection against shy individuals associated with their translocation to New Zealand.

Both Møller (2014) and Carrete et al. (2016) found significant heritability in FID in Barn Swallows and Burrowing Owls, respectively. These were the first two studies that quantified heritability, a discovery only made possible because individually marked animals were studied. This is notable because the vast majority of FID studies are conducted on unmarked animals. Heritability is reasonably high, suggesting that there is sufficient opportunity for selection in FID.

However, not all plasticity need be associated with evolutionary changes, e.g., phenotypic plasticity is another way that animals may respond to changing conditions. Another notable study that capitalized on individually marked birds focused on quantifying the process of habituation in urban and rural House Sparrows (Vincze et al. 2016). After demonstrating that urban sparrows tolerated closer approaches than rural populations, the authors brought animals into captivity and began to approach them repeatedly, measuring FID with each approach. Urban populations were not plastic—there was no evidence of habituation. By contrast, the rural population was shown to become habituated to repeated approach when FID was measured in several ways. More work quantifying phenotypic reaction norms in urban and rural populations of birds should help us better understand some of the mechanisms underlying their tolerance to humans.

Rebolo-Ifran et al. (2015) found that Burrowing Owls appear to be distributed across urban and rural habitats based on their tolerance to human disturbance. What was particularly notable about this study was that corticosterone measured in owl feathers did not differ across the environments where the owls were found, which suggests that their distribution was determined by their degree of tolerance to human disturbance.

Urbanization is a focus of much work and we know that risk assessment may be modified in urban environments. For instance, urban birds flush at similar, closer distances in response to either direct or tangential approaches (Møller and Tryianowski 2014). Ducatez et al. (2017) discovered that more innovative species (they studied nine species of Barbados birds for which they had previously, and for different subjects, developed foraging innovation scores) tolerated closer approach in rural areas but behaved more similarly in urban areas. The relationship between cognitive ability and urban tolerance is an area ripe for more study.

Simply because species have lived with humans in cities for a long time does not mean that the duration of coexistence explains patterns of tolerance to humans. In Melbourne, Gendall et al. (2015) found that the bird species with the longest relationship with humans, the Rock Dove (*Columba livia*), had the shortest FID and showed the least alarm when escaping from humans (they walked away from approaching humans). By contrast, Spotted Doves (*Spilopelia chinensis*) and Crested Pigeons (*Ocyphaps lophotes*) have more recently colonized Melbourne with the latter being the most recent colonist. Lengths of residency of these two species were not associated with escape responses; both species were more wary of humans than Rock Doves but did not differ from each other in their escape responses.

Humans disturb birds in a variety of ways. Glover et al. (2015) found that people in canoes are less threatening to water birds than people approaching on foot. Such insights permit us to better develop management strategies to reduce human impacts associated with tourism and recreation.

FID has been used to shed light on nest predation in Red-capped Plovers (*Charadrius ruficapillus*) (Lomas et al. 2014). Plovers have either covered or uncovered nests and nest cover has important thermal consequences. Covered nests are cooler, but are more detectable at a distance. Birds on covered nests permit humans (and presumably natural predators) to approach closer. Thus, thermal risks are traded-off against predation risks.

A particularly fascinating line of applied work has sought to identify the mechanisms by which birds estimate time to impact with a vehicle, and use these to understand and potentially reduce vehicular collisions with birds. Bird strikes are a multi-million dollar cost to the aviation industry alone (Dolbeer 2018). If birds have not evolved mechanisms that permit them to detect speeding vehicles at a distance, then they will be particularly vulnerable to collision. This is also an emerging theme in work by DeVault et al. (2015). For instance, at higher speeds, cowbirds cannot quickly flee over a distance of 3 m to avoid a rapidly approaching truck (DeVault et al. 2015).

The field of FID is also notable because data are frequently shared to create management tools. For instance, Livezey et al. (2016) developed a database of North American FID data to help managers calculate buffer areas to reduce or manage human disturbance to birds. Guay et al. (2016) developed an online management tool, AvianBuffer, which uses all available FID data in Australia to suggest buffer zones for birds based on FID. Such management tools are highly promising but do require proper evaluation.

The future

I believe a greater mechanistic understanding of the sensory mechanisms involved in risk assessment will help us to both develop predictive models of bird escape behavior and improve our ability to use escape behavior to conserve and manage avian populations. Tyrrell and Fernández-Juricic (2015) built the case for why visual sensory mechanisms matter. We know that birds vary in their probability of escape at a given distance, but why? Tyrrell and Fernández-Juricic (2015) make a convincing case that variation in sensory systems can explain variation in escape. Indeed, the assumptions made about equal visual abilities of birds in all directions is certainly incorrect. Also, a better understanding of avian visual perception will enhance our understanding of escape in birds and enhance our ability to manage it by designing specific stimuli that best capture birds' attention.

I think much can be gained, as illustrated by both heritability and phenotypic reaction norm studies, by studying escape in individually marked birds. With individually marked birds, and multiple generations of data, proper variance decomposition methods (e.g., Wilson et al. 2010) can be applied, and we will be able to expand our understanding of factors affecting variation in avian FID. Importantly, such studies will permit us to better study the limits of plasticity. Many bird species are the subject of long-term studies where the fate of marked individuals is followed throughout their life. Adding an FID component to these long-term studies could be an excellent first step towards expanding our knowledge of plasticity.

Finally, we need to develop decision-support tools for wildlife managers. Such tools, like AvianBuffer (Guay et al. 2016), should help us better coexist with birds in an increasingly urban world in which annual visits to protected terrestrial areas exceed the number of humans on Earth (Balmford et al. 2015). All such applied studies, however, must be conducted in an explicitly adaptive management framework (Holling 1978), where experiments inform management and management actions are set up as testable hypotheses.

The study of FID in birds is a success story that combines foundational insights into the drivers of antipredator behavior with applied management. This field of research wonderfully illustrates the productive interplay between mathematical modeling, empirical tests of models, comparative studies and meta-analyses. It also illustrates how collaborations can lead to much larger insights than single-species, single-investigator studies. It also details, in many ways, highly successful avian behavioral ecology.

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References

Balmford A, Green JM, Anderson M, Beresford J, Huang C, Naidoo R, Walpole M, Manica A (2015) Walk on the wild side: estimating the global magnitude of visits to protected areas. PLoS Biol 13:1002074

Blumstein DT (2006) Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. Anim Behav 71:389–399. https://doi.org/10.1016/j.anbehav.2005.05.010

Carrete M, Martinez-Padilla J, Rodriguez-Martinez S, Rebolo-Ifran N, Palma A, Tella JL (2016) Heritability of fear of humans in urban and rural populations of a bird species. Sci Rep 6:31060. https://doi.org/10.1038/srep31060

Cooper WE, Blumstein DT (eds) (2015a) Escaping from predators: an integrative view of escape decisions. Cambridge University Press, Cambridge

Cooper WE Jr, Blumstein DT (2015b) Escape behavior: importance, scope, and variables. In: Cooper WE, Blumstein DT (eds) Escaping from predators: an integrative view of escape decisions. Cambridge University Press, Cambridge, pp 3–14

DeVault TL, Blackwell BF, Seamans TW, Lima SL, Fernandez-Juricic E (2015) Speed kills: ineffective avian escape responses to oncoming vehicles. Proc R Soc B 282:2188. https://doi.org/10.1098/rspb.2014.2188

Dolbeer R (2018) Wildlife strikes to civil aircraft in the United States 1990–2016. Serial report 23. Federal Aviation Administration National Wildlife Strike Database, Federal Aviation Administration

van Dongen WFD, Robinson RW, Weston MA, Mulder RA, Guay P-J (2015) Variation at the *DRD4* locus is associated with wariness and local site selection in urban black swans. BMC Evol Biol 15:253. https://doi.org/10.1186/s12862-015-0533-8

Ducatez S, Audet J-N, Rodriguez JR, Kayello L, Lefebvre L (2017) Innovativeness and the effects of urbanization on risk-taking behaviors in wild Barbados birds. Anim Cognit 20:33–42. https://doi.org/10.1007/s10071-016-1007-0

Frid A, Dill LM (2002) Human-caused disturbance stimuli as a form of predation risk. Cons Ecol 6:11. [online] https://www.consecol.org/vol16/iss11/art11.

Garamszegi LZ, Møller AP (2017) Partitioning within-species variance in behaviour to within- and between-population components for understanding evolution. Ecol Lett 20:599–608

Garamszegi LZ, Mueller JC, Markó G, Szász E, Zsebők S, Herczeg G, Eens M, Török J (2014) The relationship between *DRD4* polymorphisms and phenotypic correlations of behaviors in the Collared Flycatcher. Ecol Evol 4:1466–1479

Gendall J, Lill A, Beckman J (2015) Tolerance of disturbance by humans in long-time resident and recent colonist urban doves. Avian Res 6:7. https://doi.org/10.1186/s40657-015-0018-x

Glover HK, Guay P-J, Weston MA (2015) Up the creek with a paddle; avian flight distances from canoes versus walkers. Wetl Ecol Manage 23:775–778

Guay P-J, van Dongen WFD, Robinson RW, Blumstein DT, Weston MA (2016) AvianBuffer: an interactive tool for characterising and managing wildlife fear responses. Ambio 45:841–851. https://doi.org/10.1007/s13280-016-0779-4

Holling CS (1978) Adaptive environmental assessment and management. Wiley, Berlin

Holtmann B, Grosser S, Lagisz M, Johnson SL, Santos ESA, Lara CE, Robertson BC, Nakagawa S (2016) Population differentiation and behavioural association of the two "personality" genes *DRD4* and *SERT* in Dunnocks (*Prunella modularis*). Mol Ecol 25:706–722. https://doi.org/10.1111/mec.13514

Jiang Y, Moller AP (2017) Antipredator escape distances of common and threatened birds. Behav Ecol 28:1498–1503. https://doi.org/10.1093/beheco/arx114

Livezey KB, Fernandez-Juricic E, Blumstein DT (2016) Database of bird flight initiation distances to assist in estimating effects from human disturbance and delineating buffer areas. J Fish

Fish Wildl Manage 7:181–191. https://doi.org/10.3996/082015-jfwm-078

Lomas SC, Whisson DA, Maguire GS, Tan LX, Guay P-J, Weston MA (2014) The influence of cover on nesting Red-capped Plovers: a trade-off between thermoregulation and predation risk? Vic Nat 131:115–127

Møller AP (2014) Life history, predation and flight initiation distance in a migratory bird. J Evol Biol 27:1105–1113. https://doi.org/10.1111/jeb.12399

Møller AP (2015) Birds. In: Cooper WE, Blumstein DT (eds) Escaping from predators: an integrative view of escape decisions. Cambridge University Press, Cambridge, pp 88–112

Møller AP, Erritzøe J (2016) Brain size and the risk of getting shot. Biol Lett 12:20160647

Møller AP, Tryjanowski P (2014) Direction of approach by predators and flight initiation distance of urban and rural populations of birds. Behav Ecol 25:960–966. https://doi.org/10.1093/beheco/aru073

Møller AP, Samia DSM, Weston MA, Guay P-J, Blumstein DT (2014) American exceptionalism: population trends and flight initiation distances in birds from three continents. PLoS One 9:e107883. https://doi.org/10.1371/journal.pone.0107883

Rebolo-Ifran N, Carrete M, Sanz-Aguilar A, Rodriguez-Martinez S, Cabezas S, Marchant TA, Bortolotti GR, Tella JL (2015) Links between fear of humans, stress and survival support a non-random distribution of birds among urban and rural habitats. Sci Rep 5:13723. https://doi.org/10.1038/srep13723

Samia DSM, Blumstein DT (2014) Phi index: a new metric to test the flush early and avoid the rush hypothesis. PLoS One 9:e113134. https://doi.org/10.1371/journal.pone.0113134

Samia DSM, Moller AP, Blumstein DT (2015a) Brain size as a driver of avian escape strategy. Sci Rep 5:11913. https://doi.org/10.1038/srep11913

Samia DSM, Nakagawa S, Nomura F, Rangel TF, Blumstein DT (2015b) Increased tolerance to humans among disturbed wildlife. Nat Commun 6:8877. https://doi.org/10.1038/ncomms9877

Stankowich T, Blumstein DT (2005) Fear in animals: a meta-analysis and review of risk assessment. Proc R Soc Lond B 272:2627–2634. https://doi.org/10.1098/rspb.2005.3251

Symonds MRE, Weston MA, Robinson RW, Guay P-J (2014) Comparative analysis of classic brain component sizes in relation to flightiness in birds. PLoS One 9:e91960. https://doi.org/10.1371/journal.pone.0091960

Tyrrell LP, Fernández-Juricic E (2015) Sensory systems and escape behavior. In: Cooper WE, Blumstein DT (eds) Escaping from predators: an integrative view of escape decisions. Cambridge University Press, Cambridge, pp 322–342

Vincze E, Papp S, Preiszner B, Seress G, Bokony V, Liker A (2016) Habituation to human disturbance is faster in urban than rural House Sparrows. Behav Ecol 27:1304–1313. https://doi.org/10.1093/beheco/arw047

Wilson AJ, Réale D, Clements MN, Morrissey MM, Postma E, Walling CA, Kruuk LEB, Nussey DH (2010) An ecologist's guide to the animal model. J Anim Ecol 79:13–26

Ydenberg RC, Dill LM (1986) The economics of fleeing from predators. Adv Study Behav 16:229–249