The impact of human disturbance on birds: a selective review

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ABSTRACT

Human disturbance is caused by the mere presence of humans in the environment. As both predation risk and human disturbance redirect time and energy from other fitness-enhancing activities such as reproduction and feeding, perceived predation risk appears to be useful in the understanding of the impact of human disturbance. It is essential to understand how birds react to different levels of human disturbance because riskier human behaviour can have devastating effects on habitat use, community composition, reproduction and fitness. Birds tend to overestimate the risk associated with humans rather than underestimate it and risk injury and therefore are more likely to partially habituate to harmless and repetitive human disturbance rather than lose all 'fear' towards humans. As a bird's response dynamically varies with its current assessment of risk and the response is most likely to be context and species-specific, it is difficult to predict with confidence, how birds will react to increased incidences of human disturbance.

Key words: tolerance, flight initiation distance, habituation, vigilance

Introduction

Human disturbance is caused by the mere presence of people in the environment and is a common, but seldom recognized, form of disturbance. Although it may appear subtle compared to more destructive forms (e.g. deforestation), human presence can have insidious and cumulative effects. The world's population is projected to grow to approximately 9 billion people by 2040 (U.S. Census Bureau 2007) and overpopulation is likely to cause more people to disperse further into remote parts of the world (Gutzwiller and Anderson 1999). With increasingly less habitat for non-human species, remaining wilderness areas will become vital for the conservation of biodiversity. Ecotourism (ecology-based tourism) may potentially provide an avenue to educate the public about sustainable environmental practices and a lucrative economic alternative to more consumptive uses (e.g. logging) for these wilderness areas.

Interestingly, many people believe it is their 'inalienable right' to visit wilderness areas. Although this belief is not wholly unreasonable, many people also consider that their visitation has little or no impact on wildlife or the environment. This is a dangerous assumption and may ultimately counteract the positive conservation benefits of ecotourism. It would be difficult to prevent people from visiting wilderness areas altogether, but we should aim to restrict their potential harm on wild bird species and the environment. Research and careful planning should be conducted prior to the establishment of ecotourism ventures in order to prevent and/or limit the damage on the environment and wildlife (Burger *et al.* 1995). It is essential to have a fundamental understanding of what drives the response of birds to human disturbance to improve future research and management of human disturbance-induced impacts. In this selective review, I consider several aspects of the human disturbance phenomenon from both theoretical and practical perspectives. Important issues addressed include: whether birds respond to humans as though they are predators, how human disturbance affects community composition, whether tolerance of human disturbance is critical to successful urban colonization and the vexed question of researcher impacts on birds' welfare and productivity.

Do birds react to humans as though they are predators?

Many authors argue that birds react to humans approaching on foot as they would to natural predators, by displaying anti-predator responses (see Frid and Dill 2002; Blumstein *et al.* 2003; Beale and Monaghan 2004b). When a bird is confronted by a natural predator, a number of physiological processes and behaviours are activated that prepare the body for combat and/or escape (Sapolsky *et al.* 2000). These processes and behaviours include an increase in HPA (hypothalamic-pituitary-adrenal) axis activity and various defensive tactics, such as immobility, crypsis and distraction. Indeed, the level of HPA activity (also known as the stress response) can be used as an indication of a bird's state of alertness or readiness to either flee or remain and fight. Therefore if birds respond to humans as though they are predators, their reaction should include these elements of typical anti-predator responses.

Holmes *et al.* (2005) found that if Royal Penguins *Eudyptes schlegeli* on Macquarie Island, Antarctica, were approached by a single person to the suggested "safe" distance (5m) recommended for tourists, they showed a 1.23-fold increase in heart rate (from resting rate) and a six-fold increase in vigilance. Interestingly, the authors found that this response was significantly greater than responses to natural aerial predators, Great Skuas *Stercorarius skua*, flying < 15m overhead, suggesting that a person in close proximity was perceived as a greater threat than a known predator flying fairly low overhead (Holmes *et al.* 2005).

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Although a penguin's flight from disturbance is commonly preceded by an increase in heart rate and heightened vigilance, none of the birds fled (Holmes *et al.* 2005), probably because they were nesting at the time. However, the authors did not measure the response of the penguins to an actively hunting skua, which would conceivably be greater than that to one just flying overhead. Royal Penguins thus responded to humans in an apparently similar manner physiologically and behaviourally to that shown to natural predators.

However, some species do not react as dramatically to the presence of humans as they do to natural predators. Eleven species of nesting passerine birds in Europe (Appendix 1) were not negatively affected when their nests were visited by humans every third or fourth day of the breeding season for two years (Mayer-Gross *et al.* 1997). In the presence of an actual predator, these passerines typically exhibit a number of nest defence strategies that deter the predator from attacking their offspring e.g. mobbing, attacking and distraction displays. An increase in the frequency of these defensive behaviours and in the associated physiological regulatory responses could potentially decrease nest attendance levels and result in an increased probability of breeding failure. However, Mayer-Gross *et al.* (1997) found that nesting success was not negatively affected by human visitation. Similarly, the presence of humans in and around a number of penguin breeding colonies in Antarctica has not affected breeding success and population densities (see Carlini *et al.* 2007; Fraser *et al.* 1985; Cobley and Shears 1999).

Frid and Dill (2002) point out that many birds have evolved a generalised anti-predator response to many different, possibly harmful stimuli, such as large and swiftly-moving objects, which could include predators. Members of some bird species exhibit this kind of generalised response towards humans. In this sense, humans and natural predators present some common, threatening, non-specific stimulus properties for birds. When one of these properties (e.g. rapid movement) is exaggerated, the bird's avoidance response correspondingly increases. For example, Piping Plovers *Charadrius melodius* fled more quickly from people running or jogging past them than to those who walked (Burger 1991). Real predation attempts and human disturbance both redirect the target bird's time and energy expenditure away from other important activities, such as reproduction and feeding (Skagen *et al.* 1991; Steidl and Anthony 2000; Frid and Dill 2002), so both are likely to impact negatively on genetic fitness. The difference, however, is that the former are generally more likely to result in mortality, so selection might be predicted to favour more specific, intense and consistent responses to natural predators than to human intruders.

The effect of human presence on avian habitat use and assemblage composition

Resource quality and abundance, and predation risk, should both influence habitat choice by birds, because selection would be expected to favour a choice that optimizes energy and nutrient input and promotes survival (Frid and Dill 2002; Cooper and Frederick 2007). As natural predators and humans appear to share some common 'threatening' properties for many birds, avoidance of human disturbance might also be expected to influence habitat selection, particularly when it is long-lasting and intense. Some raptors have certainly permanently abandoned their territories due to human disturbance, leading eventually to population decline (Verbeek 1982; Grubb and King 1991; Carrete *et al.* 2002). Theoretically, when resource quality is high and the risk of harm from human disturbance is low, birds should be reluctant to leave their foraging or breeding grounds and *vice versa* (Frid and Dill 2002; Cooper and Frederick 2007). A bird might also be expected to flee from localised human disturbance if rich resources are just a short distance away, easy to find or evenly distributed within the bird's home range (Ydenberg and Dill 1986). However, some authors argue that where this alternative does not exist, birds will remain close to the source of human disturbance despite the perceived threat it constitutes (Gill *et al.* 2001; Frid and Dill 2002). These birds will incur increased energetic costs from the inevitable increase in physiological stress (e.g. increased cardiac output) and heightened vigilance. Equally, however, birds that perceive a greater risk in remaining flee to sub-optimal sites and are unable to return soon to their preferred habitat, may also experience short or long-term increases in energetic costs stemming from lost or reduced foraging opportunities. For example, gulls that fled their foraging grounds and retreated to distant, off-shore, inter-tidal flats as people arrived on the beach at Port Liberte (USA) had lower foraging efficiencies than those that remained at the site (Burger 1988). Presumably the perceived risk was high enough for some individuals to retreat far offshore, despite this being a sub-optimal location for foraging, but the gulls that remained on the beach may have also incurred increased costs through heightened vigilance towards the human visitors. In this case the displacement was only temporary, as the birds returned to the beach after the people left each day and the duration of the human disturbance could have been critical in the decision-making process involved in this instance.

Individual variation in evaluation of the threat posed by humans is presumably one of the factors that results in some birds fleeing from a human disturbance, whilst others do not. The 'gaps' in the spatial distribution of species generated by the departure of some individuals in response to human disturbance are not necessarily reflected in significant structural and vegetative modification because the resources are usually left intact (Gutzwiller and Anderson 1999). Thus any effects of human disturbance on bird assemblage composition may be harder to identify than is the case where areas are impacted by more physically destructive types of disturbance (e.g. deforestation) (Burger 1988; Gutzwiller and Anderson 1999). Nevertheless, Fernández-Juricic (2000) found that as pedestrian traffic rate increased in urban parks, bird species richness decreased, evidently as species abandoned the high traffic areas. Using species richness and distribution measures may indicate the effect of human disturbance on bird assemblages, because it takes into account the departing and remaining species.

Although there may be an overall decrease in species richness, some common and non-indigenous species may enter the disturbed areas, altering bird assemblage composition considerably. Some bird species, such as the Australian Noisy Miner *Manorina melanocephala* (Grey *et al.* 1997), may actually thrive in areas with high human disturbance levels and may utilise the 'gaps' left by some departing species.

Using such measures to detect changes in bird assemblage composition, Riffell *et al.* (1996) and Gutzwiller and Anderson (1999) found quite limited, short-term (seasonal) effects of simulated bushwalker traffic on assemblage composition and individual species' abundances of forest birds in Wyoming (USA). The significant effects were restricted to a decline in the abundance of a few of the most common species, but no species entirely disappeared from the area (Riffell *et al.* 1996). Similarly, Price and Lill (in press) found no effect of experimentally simulated bushwalker traffic on bird assemblage composition in mallee woodland in Victoria, Australia. These studies only imposed about 1-3 hours of single-person disturbance per week for 4-10 weeks, but the Wyoming disturbance regime was imposed for several years. The human intruders in these studies did not deliberately try to elicit anti-predator-like responses from the birds, nor did they vocalise in a manner likely to disturb them. In contrast, the densities of 8 of 13 breeding bird species in wooded areas in The Netherlands were negatively affected by increases in 'natural' human recreational activity (totalling 30 pedestrians/dogs/cyclists per day) (van der Zande *et al.* 1984b). It may be difficult to confidently predict the short and long-term effects of pedestrian traffic on avian habitat use and assemblage composition in a particular situation in the absence of targeted field observations. However, the absence of large traffic effects in some of the studies described above does help in determining a traffic level that seems not to be influential in affecting the composition of bird assemblages.

Human disturbance may also influence the abundance of species other than the 'target' (i.e. focus of disturbance) species, that is to say, there may be 'cascading' effects. Any change in the distribution of species among trophic/guild levels is likely to influence the density of their own predators and prey (Frid and Dill 2002; Heil *et al.* 2007). For example, Gutzwiller *et al.* (2002) found that experimental human intrusion on nesting birds in Wyoming (USA) sub-alpine forests increased the number of Gray Jays *Perisoreus canadensis*, a known nest predator. The human intrusion most likely caused other species to temporarily desert their nests, thereby exposing young and increasing the scope for nest predation by the jays. An increase in the number of avian piscivores and frugivores that flee from an area due to an increase in perceived risk of injury would probably modify the proportion of fish and plant biomass being consumed in and near to the disturbed area (Frid and Dill 2002) and may also affect some cohabiting species that benefit from the birds' presence (e.g. symbiosis, commensalism). For example, Bald Eagles *Haliaeetus leucocephalus*, American Crows *Corvus brachyrhynchos* and Glaucous-winged Gulls *Larus glaucescens* exploit the rich concentrations of anadromous salmon *Oncorhynchus* spp. that spawn and then die along North American rivers that flow into the Pacific Ocean (Skagen *et al.* 1991). Only the eagles are powerful enough to open the salmon carcasses; the crows and gulls can only utilise them once the skin has been torn (Skagen *et al.* 1991). Eagles seldom returned to feed on unopened carcasses when disturbed by humans and in their absence the gulls and crows could not utilise these carcasses (Skagen *et al.* 1991). Therefore, frequent disturbance of the eagles would eventually result in less food being available to the gulls and crows and an excess of salmon carcasses along the rivers. Thus, it is highly probable that the effects of human disturbance are often not restricted to one species or trophic guild.

The vigilance-foraging time trade-off in responding to human presence

In the presence of humans, birds should dynamically alter their behaviour in an adaptive manner by 'trading off' the costs and benefits of responding to the disturbance in a particular manner (Cooper and Frederick 2007). If individuals perceive the situation to be very risky, they may avoid humans at the expense of a reduction in other fitness-enhancing activities (Frid and Dill 2002; Blumstein *et al.* 2005). Monitoring and constantly evaluating different levels of risk stemming from human disturbance, rather than fleeing immediately, can avoid unnecessary costs of retreating and lost access to foraging and breeding areas (Blumstein *et al.* 2003; Cooper and Frederick 2007). But, equally continuous, intense monitoring of humans can reduce the time and attention that can be allocated to ongoing activities, such as foraging, and may reduce their efficacy (Blumstein 2003). In addition, such a high level of awareness can activate the stress response and prolonged activation of the HPA axis is associated with many acute and chronic diseases (Siegel 1980; Sapolsky *et al.* 2000).

Birds ought to be more vigilant when risk of serious disturbance is perceived as being high. Vigilance reduces the likelihood of the vigilant bird experiencing injury or death, but also reduces the proportion of time the bird can spend foraging or engaged in other essential activities (Frid and Dill 2002). The level of vigilance exhibited varies in response to factors that also affect perceived predation risk, such as predator and prey group size, the amount of time that the predator remains in the area, extent of vegetation cover and distance to that cover (Geist *et al.* 2005). For instance, five species of water birds in the Everglades, Florida (USA) foraged less when people were nearby (Burger and Gochfeld 1998); foraging time decreased as a function of the number of people present and the amount of noise that they created (Burger and Gochfeld 1998). Given that the Everglades is a very popular recreational area, the high level of disturbance by humans would probably result in an increase in the birds' energy expenditure and a reduction in the level of attention paid to real predators (e.g. alligators). A high level of vigilance usually involves a high level of energy expenditure because of the amplification of the stress response (Siegel 1980; Sapolsky *et al.* 2000).

When a large proportion of time and energy are allocated to vigilance and activation of the HPA axis is prolonged, body condition may deteriorate because resource acquisition is necessarily reduced and chronically high levels of glucocorticoids lead to depletion of energy stores (Siegel 1980; Sapolsky *et al.* 2000). Consequently, long-term, intense levels of human disturbance may indirectly cause a population density decline because reduced body condition is likely to negatively impact upon reproductive success and survival (Siegel 1980; Gabrielsen and Smith 1995). Piping Plovers reduce their foraging effort by up to 50% when on beaches with many people and low foraging rates and starvation led to a population crash in Nova Scotia, where numbers almost halved in 4 years (Flemming *et al.* 1988; Burger 1994).

Birds are expected to overestimate a threat rather than underestimating it and risking a number of potentially dramatically fitness-reducing outcomes (Ydenberg and Dill 1986). Although this might be energetically expensive, the costs associated with overestimating a transient threat (e.g. reduced foraging) are much less hazardous than risking injury or death (Frid and Dill 2002). Birds will rarely have perfect information of the threat posed by humans. Therefore, wild birds are much more likely to remain vigilant despite the costs involved and flee when humans approach too closely.

Degree of tolerance of human disturbance

The 'decision' to flee from humans is thought to be based on the relative costs and benefits of escaping or remaining and the probability of being detected and of being captured by humans if detected (Ydenberg and Dill 1986; Cooper and Frederick 2007). The distance at which an individual initiates flight when approached by a human has been known by various names (e.g. instance flush and approach distance), but it is now most commonly referred to as the flight initiation distance (FID; Figure 1) (e.g. Cooke 1980; Burger and Gochfeld 1991; Fernández-Juricic *et al.* 2001; Fernández-Juricic *et al.* 2002; Blumstein 2003; Blumstein *et al.* 2003). Behavioural ecologists have used FID to test assumptions and theories about the tolerance of humans by animals, but also in the practical management of wild bird populations (Blumstein 2003). For example, FID has been used to estimate suitable buffer zones around wild bird populations in order to decrease the degree of exposure to disturbance (Fernández-Juricic *et al.* 2005; Blumstein 2006). Like other responses to human presence, FID will change depending on the bird's current assessment of risk (Ydenberg and Dill 1986; Bonenfant and Kramer 1996; Blumstein 2003; Blumstein *et al.* 2003). For example, a person who suddenly changes direction towards a focal bird may be perceived as a greater threat than one who continues to walk past without changing direction (Burger and Gochfeld 1981). Another measure that has been used in conjunction with FID is the alert distance (AD) (Fernández-Juricic *et al.* 2001). Alert distance is the distance between the bird and the approaching predator or human at which the bird first becomes aware of the approach (Figure 1). Birds monitor predators because this minimizes energy expenditure and time wastage through delaying fleeing until the cost of remaining exceeds the cost of escape (Ydenberg and Dill 1986; Blumstein 2003; Blumstein 2006).

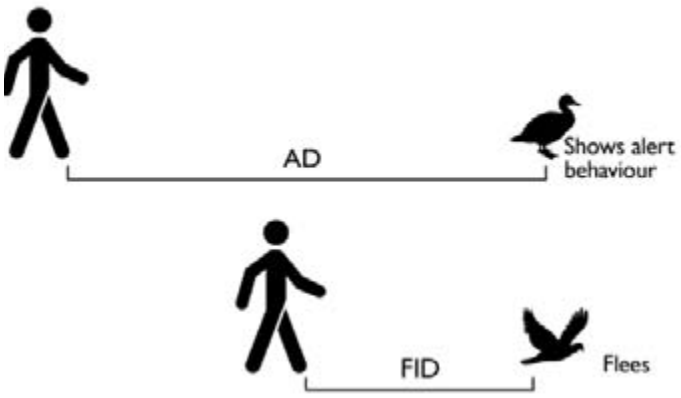

Figure 1. Alert distance (AD) is measured as the distance from the bird exhibiting alert behaviour to the approaching human, and flight initiation distance (FID) is measured as the distance from the approaching person to the fleeing bird.

It appears that FID and AD are highly correlated and can be influenced by many variables (Blumstein *et al.* 2003; Blumstein *et al.* 2005). For example, they can vary with the direction of approach, FIDs being longer when birds were approached directly rather than being passed by at a tangent (Burger and Gochfeld 1981; Burger and Gochfeld 1990b; Burger and Gochfeld 1991; Fernández-Juricic *et al.* 2005). Bird and human group size also influence FID, some birds being more disturbed by larger groups of people and exhibiting larger FIDs as the number of approaching people increased (Burger and Gochfeld 1991; Geist *et al.* 2005). Additionally, a bird's location can influence the magnitude of FID; birds in a location protected by a fence (and possibly other obstacles) had longer FIDs than unprotected individuals (Pfluger and Ingold 1988; Ikuta and Blumstein 2003). Disturbance source (e.g. pedestrian, dog walker, etc.) also appears to affect FID (Burger 1986; Burger and Galli 1987), so that people leading dogs have elicited longer flight distances (Langston *et al.* 2007; Taylor *et al.* 2007).

Life history and morphological traits also affect approach tolerance distances. It has been argued that individuals of longer-lived species are more flighty because they become more wary with time and experience (Blumstein 2006), but equally they may also have more chance to learn that humans pose little threat. Body size affects both FID and AD (Blumstein *et al.* 2005; Adams *et al.* 2006; Blumstein 2006). Testing the FIDs of 150 bird species, Blumstein (2006) found that body size was significantly correlated with approachability by humans, larger species fleeing at greater approach distances than smaller species. Another study demonstrated that AD was also greater for larger birds (Blumstein *et al.* 2005). There are a number of possible reasons why smaller birds are seemingly more tolerant. Flight performance (e.g. speed, duration) decreases as body size increases because smaller birds have a larger power-to-mass ratio that allows them to accelerate rapidly (Adams *et al.* 2006). Better manoeuvrability is also likely to influence a small bird's assessment of risk and should decrease the probability of capture (Adams *et al.* 2006).

Thus less agile, larger-bodied and heavier species should particularly benefit from early predator detection (Lima 1986; Blumstein *et al.* 2005). Furthermore, individuals of smaller species are less likely to be able to store large energy reserves, have a higher mass-specific metabolic rate (Lasiewski and Dawson 1967), usually have a higher cost of flight (Ydenberg and Dill 1986; Blumstein *et al.* 2005) and their shorter flights are relatively energetically expensive (Nudds and Bryant 2000; Nudds and Bryant 2002). Therefore members of smaller species may need to continue foraging and monitoring the predator or human, rather than initiate early escape. It has been suggested that larger species may also be more adept at detecting approaching predators because they have larger eyes and better visual acuity (Blumstein 2006), but prey/predator detection is more likely to vary with type of vision (e.g. violet-sensitive vs. ultra-violet-sensitive) rather than body size. Larger, heavier birds may also flee earlier partly because they are more conspicuous and predators/humans are therefore more likely to detect members of larger species earlier (Blumstein *et al.* 2005; Blumstein 2006). Flight performance in small birds also varies with time-of-day (Metcalfe and Ure 1995). Small birds were found to be over 30% slower at dusk than dawn due to only a slight increase in mass (7%) during the day (Metcalfe and Ure 1995). Differences in tolerance of humans that are related to body size, flight performance and the time of day may have important management implications (Blumstein *et al.* 2005) such as minimising disturbance when birds are foraging at dusk.

As estimated predation risk and available energy vary seasonally, tolerance of humans is also likely to vary (Gill *et al.* 1996; Stillman and Goss-Custard 2002). For example, Australian Magpies *Gymnorhina tibicen* are notorious for attacking passers-by during their breeding season (Warne and Jones 2003), whereas during the non-breeding season they allow close approach (Price 2003). Similarly, Black Grouse *Tetrao tetrix* took flight at greater distances during winter and spring (Baines and Richardson 2007). Eurasian Oystercatchers *Haematopus ostralegus* exhibited shorter FIDs (i.e. greater 'tolerance') to humans when food was scarce in winter and they were thus able to remain near essential resources longer (Stillman and Goss-Custard 2002). Energy availability is also likely to influence flight initiation distances, independently of season. Beale and Monaghan (2004a) also found that Ruddy Turnstone *Arenaria interpres* FIDs were influenced by food availability; birds provisioned with an experimentally supplemented diet were in better condition and took flight at greater approach distances than those present in the same season that were not provisioned. Therefore, when resources are scarce and birds are in poor body condition, it appears that individuals may need to remain at foraging sites longer, even when risk of predation is high, in order to restore lost condition and hence they be more tolerant of people (Beale and Monaghan 2004a). However, this finding is not consistent with Frid and Dill's (2002) argument that FID should increase (i.e. reflect lower tolerance) when prey are at a site that is resource-poor, because the benefits of remaining at a poor resource patch are less likely to outweigh the risk of predation. This argument was formulated from work with Waterstriders *Gerris remigis* by Ydenberg and Dill (1986), who found that individuals in a resource-poor patch were more flighty when approached by a cannibalistic con-specific than when they were located in an abundant resource patch. Birds would rarely have accurate information of the risk posed by a predator (especially the novel presence of humans) and it is possible that the Eurasian Oystercatchers and Ruddy Turnstones did not perceive the risk posed by approaching humans as high. Nevertheless, predictions formulated from observations on how certain species respond to their natural predators should be regarded with caution when applied to human disturbance and further evidence should be sought from field-based experiments.

A basic assumption made when managing wild bird populations is that direct approaches are more disturbing than tangential ones (Fernández-Juricic *et al.* 2005). Theoretically, direct approaches should be more disturbing because they will usually indicate that the prey has been detected and hence there is greater likelihood of attack. In addition, substantial exposure to a human face can increase flightiness. For example, Black Iguanas *Ctenosaura similis* ran earlier and further when approached by an experimenter with an exposed, as opposed to a covered face (Burger and Gochfeld 1993). Fernández-Juricic *et al.* (2005) believe that the rate of approach is slower when approaching tangentially and hence birds may need more time (leading to a shorter FID) to detect a threat that is moving slowly. In addition it may be more difficult to detect predators in the periphery of the visual field, which would vary according to a species' visual acuity (Fernández-Juricic *et al.* 2005). Some studies have provided evidence supporting the direct approach hypothesis (Burger and Gochfeld 1981; Burger and Gochfeld 1990b; Cooper 1997), but Fernández-Juricic *et al.* (2005) found that four of the five bird species that they studied increased their FIDs when approached tangentially (Appendix 1). Many terrestrial predators stalk their prey by approaching slowly and, if necessary, change direction to avoid being detected before making the final attack. Thus indirect approaches may elicit the most severe response because they mimic the behaviour of a natural stalking predator. It is possible that the hunting techniques of a species' natural predator (e.g. aerial pursuit vs. terrestrial stalking) will influence how birds respond to direct or tangential approaches by humans. Alternatively, some species may have learnt that humans approaching directly pose a greater threat than those who appear to be walking by because directly approaching humans have, in the past, been more disruptive (Burger and Gochfeld 1981). The finding that some species are less tolerant of tangential approaches may require a review of this assumption.

Documenting flight initiation and alert distances may prove to be essential in gauging the birds' tolerance of humans, but many of the above factors must be considered when using such methods. Blumstein (2003) argues that the interpretation of FID is confounded by the distance at which the investigator commences walking toward the focal subject. He found that there was a significant, positive, linear relationship between investigator starting distance and FID in 64 of 68 bird species studied.

Gutzwiller and Marcum (1997) also suggest that approach distance measures may be influenced by the colour of the investigator's clothing and/or the bird's plumage colour, because birds lacking orange or red in their plumage were less tolerant when people wore orange vests. It is evident that approach tolerance indicators can be influenced by a number of factors and managing bird populations based on these measurements without factoring in their variability may reduce or eliminate their effectiveness. Many studies have indicated that FID and other spatial tolerance indicators vary inter-specifically and most likely intra-specifically (Blumstein 2003; Blumstein *et al.* 2003; Fernández-Juricic *et al.* 2005; Blumstein 2006; Tarlow and Blumstein 2007). Therefore it is difficult to predict with confidence how tolerant a certain species is of human disturbance without field observations.

Is tolerance of humans a major contributing factor to the success of urban invaders?

Urbanisation can directly influence bird populations and communities by affecting habitat, food supply and the number of predators, competitors, parasites and pathogens (Marzluff 1997). Urbanisation favours some species more than others, so that urban bird assemblage composition can be very different from assemblages in the original pre-urban environment. One of the most striking differences between urban and ex-urban areas is the population density of people. This raises the question: Is tolerance of humans a major factor contributing to the success of some urban species? If it is, urban birds should either perceive little risk from human proximity or tolerate that risk to a greater extent than their ex-urban counterparts and only flee when humans actually breach their threshold distance (i.e. where a human is so close that it poses risk of actual physical threat/capture).

Birds that inhabit urban areas are likely to encounter relatively harmless people more often than rural con-specifics. It would therefore be highly advantageous for urban birds to react less intensely to human presence, because repeatedly fleeing needlessly from distant humans would reduce the time and energy commitment to vital activities. The urban/ex-urban comparison is hard to test rigorously because the species' tolerance indicators (e.g. FID) need to be scaled for numerous possibly confounding variables, such as body size/mass. However, it has been found that some British and Australian urban passerine species were significantly more tolerant of human approach than rural con-specifics (Cooke 1980; Price 2003) and many urban birds do allow humans to approach within 1m, provided that certain behavioural constraints apply (e.g. slow, cautious movement) (Price 2003). The extent to which such greater tolerance is a pre-adaptation or learned is unclear. This issue could be explored by studying recent re/invaders of the urban environment, such as the newly-arrived parrot species in many of Australia's capital cities (e.g. corellas, lorikeets). Systematically monitoring the tolerance of humans of these new arrivals over time could help to determine the extent to which it is genetically based or learned through direct experience or by observation. Experimental transfers of birds between urban and ex-urban environments (with appropriate ethical safeguards) could also be illuminating.

Although some urban birds appear behaviourally to be very tolerant of humans (i.e. shorter FIDs), a reduction in the typical physiological stress response elicited by human presence may not have occurred. Urban Rufous-collared Sparrows *Zonotrichia capensis* exhibited a Heterophil/Lymphocyte (H/L) ratio (an accepted indicator of chronic stress) ten times greater than that of rural con-specifics (Ruiz *et al.* 2002), suggesting that living in urban areas was much more stressful. Furthermore, rural sparrows that were placed in captivity to simulate urban conditions became chronically stressed after only two weeks, exhibiting similar H/L ratios to urban sparrows (Ruiz *et al.* 2002).

The ability of a minority of bird species to successfully live commensally with humans has led to the dominance of cities by a few particularly tolerant species, many of them exotics, which is of concern with respect to the conservation of urban biodiversity. In eastern Australia these species include the introduced Common Myna *Acridotheres tristis* and the native Noisy Miner. Noisy Miners and Common Mynas can be particularly aggressive towards other bird species and it has been suggested that they compete with other native birds for resources (Grey *et al.* 1997; Jones and Wieneke 2000). However, recent evidence suggests that Common Mynas do not negatively influence cohabiting bird species, at least with respect to competition for food (Crisp and Lill 2006; Parsons *et al.* 2006). However, ten bird species were less likely to be present when Noisy Miners were in the vicinity in urban Sydney, including Willie Wagtails *Rhipidura leucophrys*, Superb Fairy-wrens *Malurus cyaneus* and New Holland Honeyeaters *Phylidonyris novaehollandiae* (Parsons *et al.* 2006).

There is a real need for further research in this area, because if intolerance of humans is one of the factors causing many native species to abandon or avoid urban areas, biodiversity is likely to decrease further as human urban populations increase and spread. Additionally, species that thrive in human-disturbed areas may limit the amount of resources available to other tolerant natives, thereby decreasing species richness even further.

Habituation to anthropogenic disturbance

The assessment of predation risk allows prey to dynamically alter their response to predators, depending on prior experience of a particular predator (Stankowich and Blumstein 2005). If the risk has been low for a substantial period, it is beneficial for the prey to reduce anti-predator behaviour. Similarly, prey should be able to recognize humans who pose no real threat and, with repeated exposure, be able to down-regulate their response accordingly.

Habituation is the progressive waning of a response to a repeated and/or constant stimulus (Thorpe 1963; Burger and Gochfeld 1983; Walker *et al.* 2006). Given the recent dramatic growth in the human population, some wildlife will certainly encounter humans more frequently. The response of wildlife to humans does appear to be strongly influenced by the degree to which they have previously been exposed to them (Knight and Cole 1995; Holmes *et al.* 2005). It has been suggested that wild vertebrates are more likely to partially habituate than to lose all 'fear' of a potential threat (see Steidl and Anthony 2000; Frid

and Dill 2002; Walker *et al.* 2006). Recent studies have indicated that repetitive and predictable visitation by people can facilitate such partial habituation (Walker *et al.* 2005; Walker *et al.* 2006). For example, tourist-visited Magellanic Penguins *Spheniscus magellanicus* at Punta Tombo, Argentina, were significantly less 'fearful' of people than penguins not exposed to human disturbance (Walker *et al.* 2006). Tourists have been visiting the Punto Tombo colony for 30-40 years, with more than 70,000 people visiting the site annually. However, visitors are restricted to paths within a small section of the colony and this appears to have facilitated partial habituation to people who abide by guidelines set by the management agency (Walker *et al.* 2006). During a 15 min visit by researchers, tourist-exposed penguins displayed fewer defensive head-turns and had lower circulating blood corticosterone concentrations than undisturbed penguins (Walker *et al.* 2006). However, when researchers captured and restrained penguins of both groups, baseline corticosterone concentrations did not differ between the two groups of penguins (Walker *et al.* 2006) showing that tourist-exposed penguins did not lose all 'fear' of people. Partial habituation should not be considered as inevitable in wildlife that are regularly exposed to human disturbance (Holmes *et al.* 2005); for example, a number of gull species *Larus* have not habituated despite relatively harmless human visitation (see Anderson and Keith 1980; Burger 1981).

There are varying types of habituation, such as habituating to a generalised stimulus. For example, a bird may habituate to the presence of cows, but also generalize this response to other similar animals, which are of a broadly similar size and shape (e.g. horse) (McLean *et al.* 1999; McLean *et al.* 2000). On the other hand, wild vertebrates may habituate to a specific stimulus, such as the presence of a particular person. Moreover, the nature of the encounter with people may habituate wildlife to so specific a stimulus (i.e. people with food) that without it the situation can become dangerous for both parties. For example, Brown Bears *Ursus arctos* in North America that were habituated to human presence later became food-conditioned and were more likely to look for food from people, damage or destroy property or be killed (non-sporting kills) than non-habituated bears (Herrero 1985; Olson *et al.* 1997).

Physiological habituation can occur concurrently with behavioural habituation, because decreasing unnecessary activation of the stress response reduces energy wastage and unwanted side-effects. Members of species may react initially to human presence much as they might react to a natural predator, but rapidly habituate to it in a way that is unlikely to occur with real predators. This habituation is not necessarily a lengthy process when birds are repeatedly exposed to people who constitute no threat. Physiological and behavioural habituation occurred after as little as 5 days of continuous exposure to people in adult Magellanic Penguins (Walker *et al.* 2005). However, the duration or frequency of disturbance to achieve partial habituation to people varies widely among species; Herring Gull *Larus argentatus* chicks that were handled by researchers more often (daily for 35 days) actually moved farther away from the nest when disturbed (i.e. responded more strongly) than did weekly disturbed and undisturbed chicks (Burger 1981).

Nevertheless, experimentally habituating animals to human disturbance as the above studies did might be a very effective management technique to accustom naïve wildlife to the presence of humans. Several authors have successfully taught naïve birds and mammals to 'fear' predators and to exhibit evasive or alarm behaviours in response to either specific or generalised threatening stimulus (Maloney and McLean 1995; McLean *et al.* 1999; McLean *et al.* 2000; Griffin *et al.* 2001; Griffin and Evans 2003; Shier and Owings 2006). Therefore, similar techniques could potentially be used to teach birds to either respond to the high level of risk involved with potentially threatening humans or to habituate to and disregard harmless people. However, would such techniques be practical and economical? Each generation of animals would probably have to be taught to recognise and 'fear' predators. Many captive carnivore reintroductions have had little success in reducing excessive confidence towards humans (Rodriguez *et al.* 1995). For example, captive-raised Pumas *Puma concolor* in Florida were less fearful of people than wild individuals, and were consequently more likely to engage in dangerous and harmful interactions with humans and livestock than wild individuals (Beldon and McCown 1996). Similarly, Sea Otter *Enhydra lutris* pups raised in captivity and released into the wild frequently interacted with, and attacked people (Miller *et al.* 1999).

Although habituation may have serious consequences for interactions between humans and captive-raised carnivores, it might reduce the incidence of unnecessary, energetically-expensive behaviour in wild birds where people pose little threat. Without experimental habituation, Black-crowned Night Heron *Nycticorax nycticorax* nestlings moved, on average, 1 m from the nest when disturbed by people, whereas habituated young would remain near or on nests (Parsons and Burger 1982). Non-habituated young would also defecate or regurgitate eaten food, possibly providing an additional cue for potential predators and certainly increasing energy and nutrient loss (Kury and Gochfeld 1975; Parsons and Burger 1982). This was not an isolated case; Farallon Western Gull *Larus occidentalis* chicks that were more frequently disturbed by humans were less likely to be attacked and killed by con-specific adults, as the they did not run as far into other territories as less frequently disturbed chicks (Robert and Ralph 1975).

Reproductive success of wild birds subject to human disturbance

To maximise fitness, birds should balance the costs and benefits of alternative reproductive strategies and/or behaviours (Cooper and Frederick 2007). Human disturbance can influence reproductive success because most adult birds must make 'decisions' about the optimal level of parental investment (Frid and Dill 2002). Theoretically, parents must balance the costs and benefits of certain reproductive strategies, given that there will be a trade-off between current reproductive success and the probability of the parent's survival and therefore future reproductive output (Montgomerie and Weatherhead 1988; Blumstein 2006). Breeding adults employ various tactics that deter predators and protect young, such as

performing distraction displays, alarm calling and making direct attacks, which inevitably involve an additional energy expenditure and sometimes increased risk of injury (Montgomerie and Weatherhead 1988).

Life history traits may influence the trade-off between parental investment and survivorship when the bird is subject to the threat of predation or human disturbance (Blumstein 2006). Iteroparous species are more likely to abandon current offspring, whereas semelparous species and those that invest heavily in a few offspring may be less likely to desert their young and should defend their nests vigorously (Frid and Dill 2002). In addition, the number of parents or helpers that raise the brood may influence the degree to which an individual defends the nest, because in some species as the parental group size increases, the cost of nest defence per individual should decrease. Thus mobbing intruders should be an effective defence strategy in these species.

Intensity of nest defence is also thought to vary with stage of the breeding cycle. Therefore the presence of humans is likely to impact on reproductive success differently depending on the breeding stage (Knight and Temple 1986; Montgomerie and Weatherhead 1988; Tarlow and Blumstein 2007). Defence of offspring should increase as the investment in young increases, so parents should avoid risky behaviours early in incubation, but defend more intensely at hatching and during chick rearing (Montgomerie and Weatherhead 1988). Vos *et al.* (1985) found that Great Blue Herons *Ardea herodias* were much more approachable by people late in the breeding season when cumulative investment in the offspring was high, young were more likely to survive and it was too late in the season to re-lay.

Nest defence is most likely to peak at hatching in precocial species, as young are at their most vulnerable because chicks are mobile and leave the nest soon after hatching. Theoretically, altricial offspring will be defended until fledging because the probability that the young can survive on their own increases after fledging (Montgomerie and Weatherhead 1988). In addition, parents should be reluctant to flee when their young are most vulnerable and cannot be relocated to hide in cover. For example, ground-nesting Golden Plovers *Pluvialis apricarius* tolerated closer human approach when incubating eggs than when rearing chicks (Yalden and Yalden 1990), suggesting that the investment in their young was high and they could not risk leaving the eggs exposed to the approaching human. Although the cost of guarding chicks was high (15% higher when disturbed by humans) (Yalden and Yalden 1990), adults were probably reluctant to leave eggs because they could not be relocated and were therefore considerably more vulnerable than highly mobile young that could flee from humans. Likewise, if adults are unable to avoid disturbances when nesting, they should relocate when their chicks are more mobile. Burger and Gochfeld (1990a) found that Least Tern *Sternula antillarum* parents led chicks away from the nesting area when subjected to human disturbance and to the protection of the dunes upon hatching. However, if the perceived predation risk is too high, precocial and altricial species may nevertheless abandon their eggs, despite the actual threat being minimal (e.g. regulated tourism). When approached by people, nesting Herring Gulls left eggs unprotected and they were then exposed to either predation (by other gulls) or hyper/hypothermia (Hunt 1972; Burger 1981).

Parents should also nest in areas that will increase their current reproductive success, reduce the chance of predation and/or decrease the number of encounters with people (Frid and Dill 2002). Safina and Burger (1983) found that many adult Black Skimmers *Rychops niger* that had yet to lay avoided colonies disturbed by people and eventually nested in undisturbed areas. In addition, some adults were observed to abandon nests in disturbed colonies during early incubation (Safina and Burger 1983). Adélie Penguins *Pygoscelis adeliae* also shifted their colony away from areas of high human visitation (Woehler *et al.* 1994).

In addition to stimulating increased nest defence and altering nest site choice, the presence of humans can increase egg and chick mortality, nest desertion, premature fledging and acute and chronic stress and decrease parental care, singing frequency and nestling mass gain rate (Verbeek 1982; Boellstorff *et al.* 1988; Keller 1990; Gutzwiller *et al.* 1997; Perry and Gilmour 1999; Sapolsky *et al.* 2000). Stress may not only affect breeding adults, it can also be stimulated in offspring by transference of stress hormones deposited in the yolk and through higher embryonic heart rates during incubation (Gillet *et al.* 1975; Siegel 1980). Young birds are particularly vulnerable to the effects of high concentrations of stress hormones in the body because hormones play a pivotal role in the development of behaviour, neurology and growth. Testosterone has been found to pass from mother to egg; although increased concentrations of testosterone in young may increase subsequent competitive ability in adulthood through effects on aggression, male-male competition and growth rates, persistently elevated concentrations of testosterone have been associated with reduced parental care, reduced survivorship and perioxidative tissue damage from free radicals (Ros *et al.* 1997; Royle *et al.* 2001). Increased stress in young birds can also increase sensitivity to stress in their adulthood, inhibit skeletal calcification and induce osteoporosis later in life (Urist and Deutsch 1960; Liu *et al.* 2000). Even moderate levels of stress can have detrimental effects on cognition, behavioural development and learning ability that can continue into adulthood (Kitaysky *et al.* 2003).

The impact of human disturbance on reproduction is influenced by several factors, including life history events, and will most likely be the result of longer-term cumulative effects on hatching and fledging success, and nest site choice (Lafferty 2001; Tarlow and Blumstein 2007). Although some short-term studies have found that human disturbance can limit reproductive success, it is more likely that fitness is subtly being eroded over time. Therefore an important research focus should be on longer-term studies and/or those that re-visit colonies/birds previously impacted by human disturbance to determine population level effects.

The (often forgotten) effects of researcher disturbance

Wildlife research is critical to the conservation of biodiversity. Some researchers may consider that their investigative techniques have little or no impact on the wildlife they are studying, particularly when their focus is not on the effects of humans. Thus in a review of the effects of investigators on nesting success, Götmark (1992) found that less than one per cent of 17,353 papers examining breeding biology examined the possible effects of researchers on reproductive success.

The impacts of scientific investigators may be even more severe than those of tourists, because the methods used to study birds are often very invasive. Theoretically, a bird should assess the current level of risk to itself and its young posed by the investigator disturbance and respond in a way that will reduce the impact on its current reproductive success or its survival. For example, reproductive productivity was severely reduced when researchers entered an American White Pelican *Pelecanus erythrorhynchos* colony to collect eggs for chemical analysis (Boellstorff *et al.* 1988). Breeding success almost halved (0.5 young per nest attempt) in investigator-disturbed areas compared to that in undisturbed colonies (1.2 and 1.1 y/nest), and this decline was not only as a result of egg removal (Boellstorff *et al.* 1988). Researchers have also caused declines in nesting Brown Pelican *P. occidentalis* productivity (young fledged per nest) of 67 to 100% (Anderson and Keith 1980). After the pelicans had fled from researchers and abandoned their nests, eggs and young were lost to predators and nestlings often died from hypo/hyperthermia (Anderson and Keith 1980). The increased calling of gulls around investigators also attracted other predators, which panicked the pelicans further and exacerbated the situation (Anderson and Keith 1980).

Research does not necessarily have to be as invasive as egg collecting, blood sampling or banding to impact on breeding. Robert and Ralph (1975) found that hatching success in a Farallon Western Gull colony (San Francisco, USA) was negatively affected by the disturbance created by their research activities of simply recording nest location/contents and number of chicks in the colony. Therefore the costs and benefits of such research should be considered carefully before investigations are initiated, including the fact that any data collected may be biased or skewed by the disturbance created. Thus if a researcher was collecting eggs to determine the corticosterone concentration of eggs laid at different times or by mothers under different environmental stressor regimes, frequently entering the colony during egg-laying would probably increase the amount of corticosterone transferred to the yolk and hence results would be skewed towards higher concentrations.

It has been suggested that techniques to monitor nesting birds may alter the natural clutch predation rate and therefore conclusions about nesting success drawn from the data may be misleading (Schaub *et al.* 1992; Hannon *et al.* 1993; O'Grady *et al.* 1996; Mayer-Gross *et al.* 1997). For example, Major (1990) used artificially-positioned, abandoned nests of the White-fronted Chat *Epthianura albifrons* to determine whether researcher visits impacted on predation rates and found that visiting nests daily for 14 days resulted in significantly higher losses (9 of 20 nests) from predation than nests visited only once (2 of 20 nests). Götmark (1992) found that experimental nests in studies that demonstrated an effect of investigator disturbance on nesting birds had higher visitation rates than experimental nests in studies that demonstrated no effect. This result may be expected because nest defence is most likely positively correlated with the intensity of disturbance.

Including controls in the experimental design could allow the measurement error associated with investigator disturbance to be defined. However, when Götmark (1992) reviewed literature examining various methods of determining the effect of investigator disturbance on nesting birds, he found that only 27 of 100 studies included undisturbed control nests (e.g. observed from afar or using a mirror on a pole). Although 33 studies compared two levels of nest disturbance (but without controls) and 12 compared three or more levels, the others used less rigorous methods, such as comparing current success with previous studies/years. However, it is admittedly difficult to include control nests in such investigations, as nests often need to be visited to establish parameters that cannot be observed from a distance. Nonetheless, these failings should be acknowledged, especially if the ultimate aim of research is to determine the natural nesting success of a species.

It has been calculated that ignoring investigator disturbance effects underestimates nesting success, whereas if observer effects are included in the analysis, bias is substantially reduced (Rotella *et al.* 2000). Obviously, any negative impact on fledging success may not only bias the data, but may indicate that the methods used are ethically inappropriate for monitoring the focal species and should be revised, especially if one is working with rare or endangered birds (Hannon *et al.* 1993). One way to reduce investigator disturbance effects may be to use remote monitoring equipment. The use of radio-tags to monitor the nests of Ring-necked Pheasants *Phasianus colchicus* and Grey Partridges *Perdix perdix* significantly reduced nest abandonment compared with invasive nest examinations (Carroll 1990). Global positioning satellite (GPS) units, data loggers, video and audio equipment are becoming smaller, more reliable and cheaper, and providing some alternatives to previously invasive investigation techniques.

The interaction between predation and human disturbance

Breeding individuals of many species will flee from approaching humans, leaving eggs or young unprotected and vulnerable to predators. For example, North-western Crows *Corvus caurinus* prey upon the eggs and young of species disturbed by humans, including Double-crested Cormorants *Phalacrocorax auritus*, Pelagic Cormorants *P. pelagicus*, Glaucous-winged Gulls and Pigeon Guillemots *Cepphus columba* (Verbeek 1982). This increased predation often occurs in mixed-species colonies, where not only hetero-specific, non-breeding visitors take advantage of the lapse in parental care, but other breeding con- and hetero-specific individuals prey on abandoned eggs and young. In fact, Heermann Gulls *Larus heermanni* are so intensely territorial that when human intruders entered a colony, gulls attacked and killed con-specific young that

wandered out of their natal territory and trampled eggs and young in neighbouring nests when fleeing from the intruders (Anderson and Keith 1980). Human intruders also walked through the gull colonies to obtain access to Elegant *Thalasseus elegans* and Royal *T. maximus* terneries, and in the ensuing chaos the gulls attacked and killed terns (Anderson and Keith 1980). Both Heermann Gulls and Elegant Terns are restricted to breeding on just a few islands and apparently experienced population declines as a result of such human disturbance (Anderson *et al.* 1976; Villa-Ramirez 1976; Anderson and Keith 1980).

What attracts predators to a colony disturbed by humans if they are not nearby at the time? Are they directly attracted by the noise, confusion and chaos or have they learned to associate human presence with access to deserted nests? Anecdotal reports suggest that many gull species associate the approach of humans with access to abandoned eggs and young in seabird colonies. Kury and Gochfeld (1975) argued that Dolphin Gulls *Leucophaeus scoresbii* were conditioned to follow humans entering colonies by previous human disturbance events. The authors reached this conclusion after observing the gulls patrolling the perimeter of King (Imperial) Shag *Phalacrocorax atriceps* colonies shortly after the arrival of humans. This is not uncommon; researchers report having to be vigilant to ensure that Crested Terns *Sterna bergii* returned to their nests after being disturbed by the scientists because Silver Gulls Larus novaehollandiae were very capable of pilfering nest contents within a few seconds (A. Lill, pers. comm.). Visitors and investigators should be particularly careful when entering and leaving colonies that may be subject to monitoring by such predators and also should be alert to any particular human behaviour that may elicit this focus.

A number of factors affect the risk of predation and so it is likely that they will also affect the vulnerability of birds to predation when subject to human disturbance. For instance, King Shags were less likely to abandon eggs and young in response to human disturbance when most of the colony was brooding young (Kury and Gochfeld 1975; Ellison and Cleary 1978; DesGranges and Reed 1981). Investment in young was high at this time, which made shags more likely to remain when approached by people. Therefore, Kury and Gochfeld (1975) and Ellison and Cleary (1978) argue that tourist visits to birds' nesting colonies should be restricted to late in the reproductive cycle, when the young are partially grown, to reduce human impact and predation. This may reduce nest abandonment and consequently predation, but on the other hand the nesting adults are more likely to risk injury to themselves (remain to protect offspring) at this time because cumulative investment in the young is high and breeding attempts are more likely to succeed. Therefore, adults may jeopardise future reproductive effort to protect current offspring when disturbed by humans. Achieving the optimal timing of human visits to a breeding colony is not likely to result just from restricting visitors to late or early in the season.

Another factor that may influence the likelihood of human-induced predation is prey group size. Other than dilution of risk (Ydenberg and Dill 1986), an increase in the number of adults defending young may decrease the cost per individual and probably make the attack more effective as a deterrent to predation. Hence human disturbance should be reduced or prevented when (a) the young are most vulnerable, (b) human behaviour is likely to attract predators (c) colony/family numbers are lower than normal and (d) parents show less inclination to flee from people.

So far we have seen that predators are attracted by the presence of humans, but is it also possible that predators sometimes perceive too much risk in associating with humans? Black-legged Kittiwakes *Rissa tridactyla* have recently been the subject of several studies investigating chick growth and adult mass loss (Sandvik and Barrett 2001). However, a natural predator of kittiwake eggs and young, the Herring Gull, appeared to be intolerant of the increased investigator presence (Sandvik and Barrett 2001). Consequently, the normal level of gull predation in the kittiwake colony may have inadvertently been reduced by human disturbance, not increased (Sandvik and Barrett 2001).

Nevertheless, people should be careful to avoid altering the natural level of predation around human-disturbed nests. A number of techniques that may help to reduce disturbance or avoid attracting predators include constructing or laying down a tunnel/piping (e.g. collapsible dog agility tunnels) to reach nests, so that the researchers/visitors are not observed entering or exiting. However, this may also scare the birds and preliminary observations should be conducted before considering such tactics. In addition, researchers should ensure that the parents have returned to the nest after the disturbance so that predators do not have access to any offspring and, if necessary, should withdraw slowly, avoiding any jerky, sudden movements that would flush parents from their nests and possibly attract predators. Åhlund and Götmark (1989) suggest that covering nests exposed to human disturbance may reduce predation. The authors found that covering Common Eider *Somateria mollissima* nests with down reduced predation of exposed nests (Åhlund and Götmark 1989). A final point to consider is that it is still unclear which species will be affected by human disturbance-induced predation and what human behaviour/activity actually attracts the predators. Although human disturbance may not always increase predation (see Verboven *et al.* 2001), people should recognise the possibility that their presence may have this effect.

The future focus and objectives of human disturbance research and management

The response of birds to human disturbance appears to be highly variable and may depend on many factors (Appendix 1). Much of this variation may be explained by life history events and morphological traits (e.g. body size) and identifying these factors may help to develop models to predict how species will react to human disturbance events (Blumstein 2006). There are many parameters that researchers could use to gauge different aspects of the response to human disturbance. For example, physiological parameters (e.g. peripheral blood leukocytes) could be used to detect changes in the stress response, distance measures (e.g. FID) may indicate the degree of tolerance or habituation, and vigilance can indicate the amount of time devoted to essential activities (e.g. foraging). However, care should be taken when applying the results of one study or species to another, especially if

natural history characteristics are different (Blumstein *et al.* 2005). In addition, management of wild birds should be conservative, because there may be significant inter- and intra-specific variation and birds are likely to alter their responses to humans with changes in season, energy availability and risk assessment.

Although a number of studies have looked at different types of human disturbance (e.g. joggers, walkers or dog walkers), knowledge is still limited in certain areas of human disturbance research (Blumstein *et al.* 2005). There are various examples of the effect of people on sea and water bird species, but it is reasonable to assume that species less popular with tourists are also disturbed by humans, and research should be directed to investigate a wider range of species and population level effects. There is a large volume of literature on various aspects of the effect of human disturbance on Northern Hemisphere species (see Appendix 1), but there is little information on Australasian species. Götmark (1992) found that of 225 studies, 71% were conducted within North America, 22% in Europe and 6% in other regions. Although Australasian species probably respond to human disturbance similarly to other species in their respective families, there is too much variability in the response of birds to humans to be confident about using knowledge derived from other species to manage Australasian species without some field observation. In addition, Australia is home to many endemic families of birds.

Approximately 40% of published studies (Appendix 1) have found either no effects or even positive effects of human disturbance on birds. Since science puts a great emphasis on the reporting of so-called significant results, non-significant results are often disregarded as 'unimportant'. It is difficult to publish 'non-significant' results on the effect of human disturbance, despite their obvious importance to the conservation of birds exposed to human activities. It is important to understand what levels of human disturbance do and do not affect birds to provide management agencies with the tools and information to manage populations. Presumably it would be better to at least identify a level of human disturbance that is not detrimental, rather than leave management to guess at such values. How many studies yielding no significant effects of human disturbance on birds have gone unreported and what is a more realistic estimate of the proportion of species affected by human disturbance?

In 2005, United Kingdom policy-makers identified 100 ecological questions that were considered significant (Sutherland *et al.* 2006). One question was of particular relevance to human disturbance research: 'What are the impacts of recreational activities upon biodiversity?' (Sutherland *et al.* 2006). Policy-makers may be becoming more open to advice regarding the impact of human disturbance on biodiversity and may be more willing to fund high quality research of global relevance.

Conclusion

It is essential to understand how birds react to humans because wild birds are more likely to encounter people more frequently as the human population grows. Humans and natural predators present some common, threatening, non-specific stimulus properties for birds and thus birds should respond to humans in a way that resembles anti-predator behaviour. Exploration of these common stimulus properties should enable better management and conservation of wild bird populations exposed to human disturbance.

Nisbet (2000) argues that published papers and reviews overstate the adverse effects of human disturbance and that habituation should be promoted as a way of minimising disturbance effects. However, it should be remembered that humans will still hunt and kill wild birds, regardless of local laws. Therefore, wild birds should only be habituated if human behaviour can be tightly regulated or if it is highly unlikely that the birds will encounter predatory humans.

Although visits to nature-based tourism destinations are no longer 'truly' exploitative and consumptive, an increased environmental consciousness has increased the public's desire to see animals in their natural habitats, and many believe it is their 'right' to visit wilderness areas. This has been considered by some as 'conservation backfire'. While people may be genuinely interested in wildlife, many still retain the belief that non-consumptive wildlife recreation has insignificant effects on animals (Anderson and Keith 1980). As we have seen, the mere presence of humans can have significant impacts on the behaviour, physiology and demography of wild birds. Nevertheless, current and future research is, and should be, facilitating discussion and developing strategies for the coexistence of humans and wild birds.

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APPENDIX 1

Appendix 1. A summary of studies (1975-2007) investigating the effect of human disturbance on the physiology, behaviour and demography of bird species worldwide. Considering the spread of literature in many journals/books some studies have inevitably, but not intentionally, been excluded. Common and scientific names were sourced from del Hoyo *et al.* (1992), Christidis and Boles (1994), AOU (1998), Banks *et al.* (2006), Remsen *et al.* (2007) and Dudley *et al.* (2006). Any common names in parentheses indicate the name preferred by the author/s.

Common and scientific name	(Sub)family	Effect of human disturbance	Reference
Emperor Penguin *Aptenodytes forsteri*	Spheniscidae	Human disturbance increased body temperature, stress and metabolic rate (3x that of basal metabolic rate)	(Regel and Pütz 1997)
		Chicks became more vigilant and fled from helicopters and aeroplanes, but would remain as a group	(Giese and Riddle 1999)
King Penguin *A. patagonicus* Adélie Penguin *Pygoscelis adeliae*	Spheniscidae	Human activities, including construction of new buildings, have regionally decreased their populations, but they are stable elsewhere	(Micol and Jouventin 2001)
Adélie Penguin	Spheniscidae	Breeding success (chicks fledged per marked nest) at Esperanza Bay, Antarctica was not significantly affected by high levels of human disturbance.	(Carlini *et al.* 2007)
		Penguin heart rates increased when approached and captured by humans	(Culik *et al.* 1990)
		Localised long-term decreases in populations were most likely due to environmental fluctuations not human disturbance	(Fraser *et al.* 1985)
		Heart rates increased when people approached (76 to 135 bpm), but doubled again when captured (287 bpm). A single observer invoked an extra 70m travel for birds returning from foraging	(Wilson *et al.* 1991)
		Penguins are susceptible to researcher disturbances, particularly any devices fitted to the birds	(Wilson *et al.* 1989)
		Penguins rarely re-colonised areas that were disturbed by humans	(Wilson *et al.* 1990)
		Human visitors reduced overall breeding success at Shirley Island and Casey station, Antarctica	(Woehler *et al.* 1994)
		Hatching and chick survival were lowest at colonies with human activity (also nest checking)	(Giese 1996)
Chinstrap Penguin *P. antarctica*	Spheniscidae	Juveniles fled a researcher sooner when far from the sub colony	(Martín *et al.* 2004)
Gentoo Penguin *P. papua*	Spheniscidae	Human disturbance did not influence populations at Port Lockroy, Antarctica	(Cobley and Shears 1999)
		Well-behaved visitors temporarily altered heart rates of birds with no prior adverse experience of humans	(Nimon *et al.* 1995)
		Penguins increased vigilance and displays when approached by humans, but returned to pre-disturbance levels after 5mins. Breeding was not affected by pedestrians	(Holmes *et al.* 2006)
Royal Penguin *Eudyptes schlegeli*	Spheniscidae	Heart rate (23%) and vigilance (600%) increased at 5m (recommended tourist viewing distance)	(Holmes *et al.* 2005)

Yellow-eyed Penguin *Megadyptes antipodes*	Spheniscidae	Regulated tourism did not negatively impact breeding, fledging success and feeding of the chicks. Adults and chicks habituated to tourists in trenches and hides, but would flee if approached	(Ratz and Thompson 1999)
		Chicks in tourist-visited areas had lower fledging weights than chicks in undisturbed areas	(McClung *et al.* 2004)
		Penguins exposed to unregulated tourism showed significantly lower breeding success, fledging weights and increased stress-induced corticosterone concentrations	(Ellenberg *et al.* 2007)
Magellanic Penguin *Spheniscus magellanicus*	Spheniscidae	Birds readily habituated, showed fewer defensive behaviours and had lower stress in tourist areas	(Walker *et al.* 2006)
		High tourist disturbance levels over a long period may lead to some tolerance by penguins	(Fowler 1999)
		Breeding penguins in tourist areas allowed closer approach than those in undisturbed areas, but fled if approached with jerky/quick movements. Fledging weights were similar in and out of tourist area	(Yorio and Boersma 1992)
		Chicks in tourist areas exhibited stress responses in people's presence, undisturbed chicks did not	(Walker *et al.* 2005)
Jackass (African) Penguin *S. demersus*	Spheniscidae	Frequently approached penguins reacted less severely to humans than partially disturbed or undisturbed groups. Minimum approach distance was 30m	(van Heezik and Seddon 1990)
		Human visitation of colonies caused egg predation by Kelp Gulls (*Larus dominicanus*). Minimum approach distance was 30m. Adults reacted most to a slow but direct approach	(Hockey and Hallinan 1981)
Humboldt Penguin Spheniscus humboldti	Spheniscidae	Penguin breeding success was significantly reduced at frequently visited sites. Increased heart rates during and after human presence indicated birds more disturbed than other penguin species studied	(Ellenberg *et al.* 2006)
Black Grouse *Tetrao tetrix*	Phasianidae	Radio-tagged grouse assigned to experimental disturbance flushed at greater distances from people, especially in spring and winter	(Baines and Richardson 2007)
Common Loon *Gavia immer*	Gaviidae	Loons that were subject to human disturbance exhibited decreased hatching success	(Heimberger *et al.* 1983)
Great Crested Grebe *Podiceps cristatus*	Podicipedidae	Nesting success lower on lakes with recreation, adults took flight later and covered nests less frequently than those on undisturbed lakes. Pairs with shorter FIDs were more successful breeders	(Keller 1990)
New Zealand Dabchick *Poliocephalus rufopectus*	Podicipedidae	Number of human-made structures positively correlated with number of chicks, human structures may provide protected nesting areas	(Bright *et al.* 2004)
Wandering Albatross *Diomedea exulans*	Diomedeidae	Research focal birds and those closest to the research station at Marion Island, Antarctica, responded most intensely to approach by humans	(de Villers *et al.* 2005)
Northern Giant Petrel *Macronectes halli*	Procellariidae	Petrels experienced increased heart rates in response to human approach (204%), much higher than natural disturbance (97%) at Marion Island	(de Villers *et al.* 2006)
Short-tailed Shearwater *Puffinus tenuirostris*	Procellariidae	Human disturbance did not affect chick growth	(Saffer *et al.* 2000)
American White Pelican *Pelecanus erythrorhynchos*	Pelecanidae	Breeding success was halved when researchers entered colonies	(Boellstorff *et al.* 1988)
		Especially disturbed in early incubation by low flying aircraft	(Bunnell *et al.* 1981)
California Brown Pelican *P. occidentalis californicus*	Pelecanidae	Pelican nests abandoned were abandoned in response to humans	(Anderson 1988)

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Double-crested Cormorant *Phalacrocorax auritus*	Phalacrocoracidae	Abandoned nests when disturbed by people and underwent greater predation	(Ellison and Cleary 1978)
		Increased loss of eggs due to predation by gulls when disturbed by investigators. Cormorants on the periphery of colony lost most eggs to predation	(DesGranges and Reed 1981)
Great Blue Heron *Ardea herodias*	Ardeidae	Herons had greater FID early in the breeding season, while at the end of they rarely left their nests	(Vos *et al.* 1985)
Black-crowned Night-heron *Nycticorax nycticorax*	Ardeidae	Nestlings and chicks responded intensely to human disturbance, but experimentally habituated young remained on the nest	(Parsons and Burger 1982)
Common Eider Duck *Somateria mollissima*	Anatidae	Gull egg and nestling predation and encounter rate increased when boats disturbed crèches	(Åhlund and Götmark 1989)
		Experimental human disturbance and gull (predator) nest density impacted on nesting success. Timing of visits also impacted on nesting success, most nest failures occurred after first visit	(Bolduc and Guillemette 2003)
		Found no significant attraction of predators as a result of investigator-induced flushing of incubating birds. Nests experimentally covered with down were preyed upon less	(Åhlund and Götmark 1989)
Greater Snow Goose *Chen caerulescens atlanticus*	Anatidae	Disturbed by low flying aircraft	(Belanger and Bedard 1989)
Dark-bellied Brent Goose *Branta bernicla bernicla*	Anatidae	Anthropogenic equipment/vehicles induced the greatest energy expenditure. Geese were more vigilant and foraged less when disturbance was high	(Riddington *et al.* 1996)
Common (Green-winged) Teal *Anas crecca* Wigeon *A. penelope* Mallard *A. platyrhyncha* Spot-billed Duck *A. poecilorhynchoa* Gadwell *A. strepera* Northern Shoveller *A. clypeata* Falcated Duck *A. falcata* Mandarin Duck *Aix galericulata* Common Pochard *Aythya ferina* Tufted Duck *Ay. fuligula* Bewick's Swan *Cygnus columbianus bewickii*	Anatidae	Green-winged Teals, Wigeons, Mallards, Spot-billed Ducks, Gadwalls and Pochards had short FIDs in response to an approaching human compared to the other species, suggesting that they were more tolerant than the other members of the same family	(Mori *et al.* 2001)
Osprey *Pandion haliaetus*	Accipitridae	Reproductive success increased further away from humans and by the establishment of a reservoir	(van Daele and van Daele 1982)

Bald Eagle *Haliaeetus leucocephalus*	Accipitridae	Eagles most disturbed by pedestrians and least by aircraft	(Grubb and King 1991)
		No evidence human activities have impacted on reproductive success at Chippewa National Forest	(Fraser *et al.* 1985)
		Eagles decreased preening, sleeping, nest maintenance, time devoted to feeding themselves and their young and increased brooding time when humans present	(Steidl and Anthony 2000)
Sharp-shinned Hawk *Accipiter striatus*	Accipitridae	Sharp-shinned Hawks, Cooper's Hawk, Merlin, Northern Harrier and Osprey prefered to inhabit areas that are off-limits to large numbers of people, whereas American Kestrels, Red-tailed Hawks and Broad-winged Hawks did not show this preference	(Niles and Clark 1989) cited in (Burger *et al.* 1995)
Cooper's Hawk *A. cooperi*	Accipitridae		
Merlin *Falco columbarius*	Falconidae		
Northern Harrier *Circus cyaneus*	Accipitridae		
Osprey	Pandionidae		
American Kestrel *Falco sparverius*	Falconidae		
Red-tailed Hawk *Buteo jamaicensis*	Accipitridae		
Broad-winged Hawk *B. platypterus*	Accipitridae		
Osprey	Pandionidae	Nesting success was not negatively affected by researchers visiting the nests of each of the raptor species	(Steenhof and Kochert 1982; Grier and Fyfe 1987; Poole 1989)
Bald Eagle	Accipitridae		
Ferruginous Hawk *Buteo regalis*	Accipitridae		
Prairie Falcon *Falco mexicanus*	Falconidae		
Golden Eagle Aquila chrysaetos	Accipitridae	Nests of Golden Eagles and Red-tailed Hawks were more likely to fail if visited by researchers early in the breeding season	(Steenhof and Kochert 1982)
Red-tailed Hawk			
Willow Ptarmigan *Lagopus lagopus*	Tetraonidae	Did not find a significant effect of visiting nests on predation rate	(Hannon *et al.* 1993)
Ring-necked Pheasants *Phasianus colchicus*	Phasianidae	Nest abandonment was significantly reduced by using radio-tags to monitor nests rather than invasive nest examinations by researchers	(Carroll 1990)
Grey Partridge *Perdix perdix*			
Hoatzin chicks *Opisthocomus hoazin*	Opisthocomidae	Chick survival much lower in tourist areas compared to undisturbed. Young hatchlings seemed to be unaffected by disturbance, but juveniles had lower body masses and were highly stressed	(Müllner *et al.* 2004)
Eurasian Coot *Fulica atra*	Rallidae	Daily nest visitation by investigators increased Coot egg predation by crows	(Salathé 1987)
Sandhill Crane *Grus canadensis*	Gruidae	Cranes closer than 70m to the road and vehicles, interrupted feeding, became alert and walked or flew away, whereas birds more than 300m showed no response	(Burger and Gochfeld 2001)

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Eurasian Thick-knee (Stone-curlew) *Burhinus oedicnemus*	Burhinidae	Probability of flushing a bird increased exponentially as the disturbing agent moved from 500 to 50m, where a walker with a dog elicited the greatest reaction	(Taylor *et al.* 2007)
New Zealand dotterel *Charadrius obscurus aquilonius*	Charadriidae	Although birds were somewhat habituated on human-frequented beaches, the approach of people leading a dog was particularly threatening	(Lord *et al.* 2001)
Golden Plover *Pluvialis apricarius*	Charadriidae	Plovers tolerated closer human approach when incubating eggs than at other times. Chick-guarding 15% more expensive for adults when disturbed by humans	(Yalden and Yalden 1990)
Ringed Plovers *Charadrius hiaticula*	Charadriidae	Birds avoided disturbance areas. From population models, fencing nests would increase population by 8%, completely excluding people, 85% and doubling number of people, a decrease of 23%.	(Liley and Sutherland 2007)
Piping Plover *Charadrius melodus*	Charadriidae	Adults increased vigilance, and young decreased foraging, increased vigilance and running	(Burger 1991)
		Plovers decreased feeding, foraging rate of chicks and brooding, and increased vigilance. Population almost halved in 4 years	(Flemming *et al.* 1988)
		Plovers selected sites with fewer people and vigilance was related to the number of people nearby	(Burger 1994)
Hooded Plover *Thinornis rubricollis*	Charadriidae	Chick foraging was reduced in the presence of humans	(Weston and Elgar 2005)
		Human disturbance more frequent than natural disturbances, and humans decreased nest attendance	(Weston and Elgar 2007)
Golden Plover Dunlin *Calidris alpine*	Charadriidae Scolopacidae	No evidence that nest location, clutch survival or chick growth reduced near footpaths, or that plovers avoided human-disturbed areas. Dunlins used disturbed habitats after footpaths had been resurfaced	(Pearce-Higgins *et al.* 2007)
Northern Lapwing *Vanellus vanellus*	Charadriidae	Experimenter nest visits every 4 days during incubation did not reduce Lapwing clutch survival	(Fletcher *et al.* 2005)
Eurasian Oystercatcher *Haematopus ostralegus*	Haematopodidae	Birds spent more time at greater distances from nests when people present, but no increased egg loss	(Verboven *et al.* 2001)
		Adults compensated for lost feeding time by remaining at the foraging site longer	(Urfi *et al.* 1996)
		FIDs shorter when food was scarce, suggested food availability related to flight distance	(Stillman and Goss-Custard 2002)
Short-billed Dowitcher *Limnodromus griseus*	Scolopacidae	Species that preferred the heavily used front beach (Dowitcher, Sanderling, Sandpiper and Knot) showed displacement of resting area and/or abandonment of the migratory staging area in response to human disturbance. There were also greater declines in abundance of front beach species	(Pfister *et al.* 1992)
Sanderling *Calidris alba*	Scolopacidae		
Semipalmated Sandpiper *C. pusilla*	Scolopacidae		
Red Knot *C. canutus*	Scolopacidae		
Ruddy Turnstone *Arenaria interpres*	Scolopacidae		
Black-billed Plover *Pluvialis squatarola*	Charadriidae		
Semipalmated Plover *Charadrius semipalmatus*	Charadriidae		

Ruddy Turnstone	Scolopacidae	Higher body condition from supplementing diet increased FID suggested FID influenced by food availability	(Beale and Monaghan 2004a)
Brown (Subantarctic) Skua *Stercorarius antarcticus lonnbergi*[1] South Polar (Antarctic) Skua *S. maccormicki*	Stercorariidae	Humans indirectly and directly killed and maimed skuas and deliberately removed eggs from colonies. Construction of airfields and stations resulted in the disturbance of breeding skuas, leading to population declines	(Hemmings 1990)
Glaucous-winged Gulls *Larus glaucescens*	Larinae	Experimenter presence increased chick mortality, but had no effect on egg mortality	(Gillet *et al.* 1975)
		Egging highest cause of mortality and caused total reproductive failure in 1 of 18 colonies studied	(Vermeer *et al.* 1991)
Laughing Gull *L. atricilla* Herring Gull *L. argentatus*	Larinae	Avian distribution affected by demolition workers; gull foraging efficiency decreased when workers appeared	(Burger 1988)
Herring Gull	Larinae	Hatching success negatively affected by disturbance, eggs exposed to sufficient solar radiation	(Hunt 1972)
Western Gull *L. occidentalis*	Larinae	Investigator disturbance caused greater egg losses, often from intra-specific predation, but chicks were more likely to survive, presumably through habituation	(Robert and Ralph 1975)
		Gulls had shorter FIDs when in heavily visited tourist areas	(Sutherland *et al.* 2006)
Yellow-footed Western Gull *L. o. livens*	Larinae	Adults that lost their eggs or chicks to human disturbance would later take eggs and chicks of other nests	(Hand 1980)
Ring-billed Gull *L. delawarensis*	Larinae	Aggression increased due to investigator activity. No chicks fatally attacked during disturbances, but often fled investigators. Fledging success in disturbed and undisturbed areas did not differ	(Brown and Morris 1995)
Black-legged Kittiwake *Rissa tridactyla*	Larinae	Investigator disturbance decreased adult nest attendance and increased daily chick loss rates	(Sandvik and Barrett 2001)
Heermann Gull *Larus heermanni* Elegant Tern *Thalasseus elegans* Royal Tern *T. maximus*	Laridae Sterninae Sterninae	Tourists that walked through gull colonies into the terneries caused confusion, where gulls killed terns. Gulls also trampled eggs and young of neighbouring nests, and attacked and killed young gulls that wandered into their territory	(Anderson and Keith 1980)
Common Tern Sterna hirundo Little (Least) Tern *Sternula albifrons* Black Skimmer *Rychops niger* Herring Gull	Sterninae Sterninae Rynchopinae Laridae	Human disturbance influenced nest site choice due to habitat reduction. Herring Gulls feed on human rubbish and therefore future population increases may have negative impacts on smaller nesting gull species and other nesting seabirds in the area	(Erwin 1980)
Little Tern	Sterninae	Nesting was up to 34x more likely to succeed with disturbance-reducing protective measures	(Medeiros *et al.* 2007)
Least Tern *Sternula antillarum*	Sterninae	Off-road vehicles ran over nests and consequently vehicles affected hatching success	(Burger and Gochfeld 1990a)
Bridled Tern *Sterna anaethetus*	Sterninae	Experimental human intrusion did not negatively affect breeding success, terns may have habituated	(Gyuris 2004)
		Terns allowed closer human approach when breeding on people-frequented islands	(Dunlop 1996)

Herring Gull	Larinae	Nesting Herring Gulls in disturbed areas responded more quickly to an approaching human. When disturbed male Herring Gulls and Skimmers resumed nesting some time after the disturbance, but females were replaced by their mate. Human presence increased intra-specific aggression in Great Black-backed and Herring Gull colonies. Franklin's and Brown-hooded Gull chicks left the nest and swam when disturbed, often becoming lost in the vegetation. Herring Gull chicks that were handled more often moved farther away from the nest when disturbed, rather than habituating	(Burger 1981)
Great Black-backed Gull *Larus marinus*	Larinae		
Brown-hooded Gull *L. maculipennis*	Larinae		
Franklin's Gull *L. pipixcan*	Larinae		
Black Skimmer	Rynchopinae		
Black-legged Kittiwake	Larinae	Nesting success was substantially affected by human disturbance but Kittiwakes were more sensitive than Guillemots, both the number and distance of people negatively effected these species	(Beale and Monaghan 2004b)
Common Guillemot *Uria aalge*	Alcidae		
Common Tern	Sterninae	Skimmer chicks ran away more often and further than tern chicks. Skimmer chicks seldom returned to nests once they had run far. Handling increased the likelihood that chicks would run from the nest	(Gochfeld 1981)
Black Skimmer	Rynchopinae		
Black Skimmer	Rynchopinae	Nest density, late incubation, hatching and fledging success was negatively affected	(Safina and Burger 1983)
Silver gull *Larus novaehollandiae*	Larinae	FID was found to vary between species and the authors suggest that FID can be viewed as a species-specific trait. Species, such as the Silver gull, were less flighty than others and may be able to habituate to human habitation than other more sensitive species	(Blumstein *et al.* 2003)
Bar-tailed Godwit *Limosa lapponica*	Scolopacidae		
Crested Tern *Sterna bergii*	Sterninae		
White Ibis *Threskiornis molucca*	Threskiornithidae		
Australian Pelican *Pelecanus conspicllantus*	Pelecanidae		
White-faced Heron *Egretta novaehollandiae*	Ardeidae		
Masked Lapwing *Vanellus miles*	Charadriidae		
Pied Oystercatcher *Haemtopus longirostris*	Haematopodidae		
Tufted Puffin *Fratercula cirrhata*	Alcidae	Breeding success was lower and chick growth was retarded in the heavily disturbed area	(Pierce and Simons 1986)
Mourning Dove *Zenaida macroura*	Columbidae	Nesting success was significantly reduced after investigator disturbance	(Westmoreland and Best 1985)
		Researchers did not negatively affect nesting success	(Nichols *et al.* 1984)
European Nightjar *Caprimulgus europaeus*	Caprimulgidae	Nests failed close to paths, main access points and in more sparsely vegetated areas. Predation main cause of nest failure. Flushing was associated with height of vegetation and nest cover	(Langston *et al.* 2007)

Woodlark *Lullula arborea*	Alaudidae	Woodlark density (per ha) lower on sites with high disturbance. Density-dependent breeding success partially balanced negative effects of disturbance	(Mallord *et al.* 2007)
Dartford Warbler *Sylvia undata*	Sylviidae	Disturbance only impacted on the productivity of birds in heather territories. An average of 13-16 people passing/hour would delay breeding pairs, making multiple brooding less likely	(Murison *et al.* 2007)
White-fronted Chat *Epthianura albifrons*	Meliphagidae	Daily visits over 14 days resulted in significantly higher losses to predators (9 of 20 nests) than nests visited only on the 14th day (2 of 20 nests). Predators probably corvids	(Major 1990)
Song Thrush *Turdus philomelos*	Turdidae	Researcher nest visiting had no overall effect on nest success of these open-nesting passerines	(Mayer-Gross *et al.* 1997)
Eurasian Blackbird *T. merula*	Turdidae		
Blackcap *Sylvia atricapilla*	Sylviidae		
Garden Warbler *S. borin*	Sylviidae		
Common Whitethroat *S. communis*	Sylviidae		
Hedge Accentor (Dunnock) *Prunella modularis*	runellidae		
Winter Wren *Troglodytes troglodytes*	Troglodytidae		
European Greenfinch *Carduelis chloris*	Fringillidae		
Eurasian Linnet *C. cannabina*	Fringillidae		
Eurasian Bullfinch *Pyrrhula pyrrhula*	Fringillidae		
Eurasian Chaffinch *Fringilla coelebs*	Fringillidae		
Chestnut-collared Longspur *Calcarius ornatus*	Emberizidae	Researcher visitation did not significantly increase predation of eggs and young	(O'Grady *et al.* 1996)
Pied Currawong *Strepera graculina*	Artamidae	Currawong FID variability not influenced by starting distance or intruder number. Rosella FIDs were significantly greater when approached by two intruders, than by one	(Geist *et al.* 2005)
Crimson Rosella *Platycerus elegans*	Psittacidae		
Gray Jay *Perisoreus canadensis*	Corvidae	Experimental human intrusion increased the number of Jays, thereby increasing potential nest predation by the Jays	(Gutzwiller *et al.* 2002)
Florida Scrub Jay *Aphelocoma* coerulescens	Corvidae	Frequency of researcher visits to nests did not increase predation rates	(Schaub *et al.* 1992)

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Grey-backed Sparrow (Finch)-lark *Eremopterix verticalis*	Alaudidae	Researcher visits did not increase mammalian predation on these ground nesting bird species	(Lloyd *et al.* 2000)
Black-eared Sparrow (Finch)-lark *E. australis*	Alaudidae		
Namaqua Sandgrouse *Pterocles namaqua*	Pteroclididae		
Ruby-crowned Kinglet *Regulus calendula*	Regulidae	Human intrusion had limited effects on the seasonal timing of songs during breeding periods. Kinglets sang earlier on intruded sites, but authors admit that results were conservative	(Gutzwiller *et al.* 1997)
Yellow-rumped Warbler *Dendroica coronata*	Parulidae		
Dark-eyed Junco *Junco hyemalis*	Emberizidae		
Gray Jay	Corvidae	Detectability period was positively associated with the number of con-specifics nearby and approach distance was greater for more conspicuous species	(Gutzwiller *et al.* 1998b)
Mountain Chickadee *Poecile gambeli*	Paridae		
American Robin *Turdus migratorius*	Turdidae		
Yellow-rumped Warbler	Parulidae		
Dark-eyed Junco	Emberizidae		
Mountain Chickadee	Paridae	Human intrusion did not significantly affect the vertical distribution of these species and appeared to tolerate low levels of disturbance	(Gutzwiller *et al.* 1998a)
Ruby-crowned Kinglet	Regulidae		
Yellow-rumped Warbler	Parulidae		
Dark-eyed Junco	Emberizidae		
Magpie-lark *Grallina cyanoleuca*	Dicruridae	Rural birds were significantly less tolerant (greater FID) than urban birds	(Price 2003)
Willie Wagtail *Rhipidura leucophrys*	Dicruridae		
Australian Magpie *Gymnorhina tibicen*	Artamidae		
Eurasian Blackbird	Turdidae		
Adélie Penguin	Spheniscidae	Breeding skuas were unaffected by station construction, and were tolerant of people. The number of breeding penguins nearest to the station declined, but the overall population was relatively stable	(Young 1990)
South Polar (Antarctic) Skua	Stercorariidae		

Adélie Penguin	Spheniscidae	Breeding populations of Adélie Penguins increased despite nesting near engines and helicopters. Regional populations of Emperor Penguins decreased due to human activities. Cape and Snow Petrel breeding sites were destroyed by the building of an airstrip, but overall population increased. South Polar Skua population increases closely related to Adélie increases, as Skuas prey on penguin eggs and chicks. Human activities near Southern Giant Petrels limited establishment of breeding sites, 87% decrease in population at Point Géologie.	(Micol and Jouventin 2001)
Emperor Penguin	Spheniscidae		
Cape Petrel *Daption capense*	Procellariidae		
Snow Petrel *Pagodroma nivea*	Procellariidae		
South Polar Skua	Stercorariidae		
Southern Giant Petrel *Macronectes giganteus*	Procellariidae		
Common Loon	Gaviidae	Human disturbance and lake characteristics influenced piscivorous bird species richness and species presence of 98 lakes in Wisconsin and Michigan, USA. Three species, Osprey, Common Merganser and Common Loon were not found on lakes with high levels of human disturbance.	(Newbrey *et al.* 2005)
Great Blue Heron *Ardea herodias*	Ardeidae		
Common Merganser *Mergus merganser*	Anatidae		
Hooded Merganser *Lophodytes cucullatus*	Anatidae		
Osprey	Pandionidae		
Bald Eagle	Accipitridae		
Ring-billed Gull	Laridae		
Great Crested Grebe	Podicipedidae	Grebes were more sensitive to landside intrusions; Coots were more sensitive to disturbances originating from the waterside	(Pfluger and Ingold 1988)
Eurasian Coot	Rallidae		
Magnificent Frigatebird *Fregata magnificens*	Fregatidae	Heartbeat rates doubled or increased four-fold above the normal rate when visitors approached within 18m	(Jungius and Hirsch 1979)
Great Frigatebird *F. minor*	Fregatidae		
Blue-footed Booby *Sula nebouxii*	Sulidae		
Masked Booby *S. dactylatra*	Sulidae		
Waved (Galapagos) Albatross *Phoebastria irrorata*	Diomedeidae		
Swallow-tailed Gull *Creagrus furcatus*	Larinae		
Lava Gull *Larus fuliginosus*	Larinae		

Brown Pelican *Pelecanus occidentalis*	Pelecanidae	15 species nesting at 17 colonies of mixed species nesting assemblages, exhibited greater flight distances when approached on foot compared to motor boats. Wood Storks exhibited the smallest flight distances, whereas Great Blue Herons had the greatest. The authors concluded that set back distances should be 100m for wading bird colonies and 180m for tern/skimmer colonies	(Rodgers and Smith 1995)
Double-crested Cormorant	Phalacrocoracidae		
Anhinga *Anhinga anhinga*	Anhingidae		
Great Blue Heron	Ardeidae		
Great Egret *Casmerodius albus*	Ardeidae		
Snowy Egret *Egretta thula*	Ardeidae		
Tricolored Heron *E. tricolor*	Ardeidae		
Little Blue Heron *E. caerulea*	Ardeidae		
Cattle Egret *Bubulcus ibis*	Ardeidae		
Black-crowned Night-heron	Ardeidae		
American White Ibis *Eudocimus albus*	Threskiornithidae		
Wood Stork *Mycteria americana*	Ciconiidae		
Least Tern *Sternula antillarium*	Sterninae		
Black Skimmer	Rynchopinae		
Laughing Gull	Larinae		
Northwestern Crow *Corvus caurinus*	Corvidae	Eagles were easily disturbed by humans and consequently flew over neighbouring colonies, scaring cormorants, gulls and guillemots off their nests, where crows took advantage of their absences and raided nests	(Verbeek 1982)
Double-crested Cormorant	Phalacrocoracidae		
Pelagic Cormorant *P. pelagicus*	Phalacrocoracidae		
Glaucous-winged Gull	Larinae		
Pigeon Guillemot *Cepphus columba*	Alcidae		
Bald Eagle	Accipitridae		

Blue-footed Booby	Sulidae	Seven factors were identified to contribute to partial or total breeding failure including predation by mammals, flooding, intra-specific predation by Laughing Gulls, movement of livestock, human visitation on foot or in vehicles, harvesting of eggs for human consumption and killing of fledglings by fishermen (to provide bait for crabbing)	(Muñoz Del Viejo *et al.* 2004)
Laughing Gull	Larinae		
Least Tern	Sterninae		
Royal Tern	Sterninae		
Gull-billed Tern *Gelochelidon nilotica*	Sterninae		
Black Skimmer	Rynchopinae		
American Oystercatcher *Haematopus palliatus*	Haematopodidae		
Kentish (Snowy) Plover *Charadrius alexandrinus*	Charadriidae		
Wilson's Plover *C. wilsonia*	Charadriidae		
Double-crested Cormorant	Phalacrocoracidae	When humans entered the Cormorant, Great Black-backed and Herring Gull colonies birds regurgitated fish and crushed eggs while fleeing. While the intruder remained cormorants would not return but gulls would eat the regurgitated fish, and eggs and young. When Shags were disturbed, Dolphin Gulls waited at the periphery for the adult Shags to flee, once they had fled, the gulls took unguarded eggs. However, when brooding nestlings, Shags were more reluctant to leave, but when threatened with human touch they fled. Dolphin Gulls only took eggs, not young	(Kury and Gochfeld 1975)
Imperial (King) Shag *Phalacrocorax atriceps*[2]	Phalacrocoracidae		
Great Black-backed Gull	Larinae		
Herring Gull	Larinae		
Dolphin Gull *Leucophaeus scoresbii*	Larinae		
Indian Pond-heron (Pied) Heron *Ardeola grayii*	Ardeidae	Flight distance was related to migratory status and there was a negative correlation between flight distance and number of people nearby	(Burger and Gochfeld 1991)
Eurasian Collared-dove *Streptopelia decaocto*	Columbidae		
Red-vented Bulbul *Pycnonotus cafer*	Pycnonotidae		
House Crow *Corvus splendens*	Corvidae		
Carrion Crow *C. corone*	Corvidae		
Jungle Babbler *Turdoides striata*	Timaliidae		
Common Myna *Acridotheres tristis*	Sturnidae		
Bank Myna *A. ginginianus*	Sturnidae		
House Sparrow *Passer domesticus*	Passeridae		

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Common Gallinule (Moorhen) *Gallinula chloropus*	Rallidae	Time devoted to foraging decreased while people were present and further decreases observed when the noise made by people increased	(Burger and Gochfeld 1998)
Sora Rail *Porzana carolina*	Rallidae		
Glossy Ibis *Plegadis falcinellus*	Threskiornithidae		
Little Blue Heron	Ardeidae		
Louisiana Heron	Ardeidae		
Bald Eagle	Accipitridae	Eagles were most disturbed by humans and reduced their foraging; gulls and crows rely on eagles to open salmon carcasses for them, so would eventually be adversely affected by the eagles absence	(Skagen *et al.* 1991)
American Crow *Corvus brachyrhynchos*	Corvidae		
Glaucous-winged Gull	Laridae		
Black-bellied Plover *Pluvialis squatarola*	Charadriinae	Birds that were protected and separated from humans by a fence had similar FIDs to birds at a site with low levels of human intrusion and significantly different FIDs from birds at a high human intruded site	(Ikuta and Blumstein 2003)
Black-necked Stilt *Himantopus mexicanus*	Recurvirostridae		
Great Blue Heron	Ardeidae		
Great Egret *Ardea alba*	Ardeidae		
Greater Yellowlegs *Tringa melanoleuca*	Scolopacinae		
Least Sandpiper *Calidris minutilla*	Scolopacinae		
Ring-billed Gull	Larinae		
Snowy egret *Egretta thula*	Ardeidae		
Western Sandpiper *Calidris mauri*	Scolopacinae		
Willet *Catoptrophorus semipalmatus*	Scolopacinae		
Plumbeous Sierra-Finch *Phrygilus unicolor cyaneus*	Emberizidae	Four of the five species showed greater FIDs to tangential rather than direct approaches. Southern Lapwings was more sensitive to direct approach. Sensitivity to direction approach appeared to be species-specific	(Fernández-Juricic *et al.* 2005)
Cordoba (Chestnut-winged) Cinclodes *Cinclodes comechingonus*	Furnariinae		
Rufous-banded Miner *Geosita rufipennis ottowi*	Sclerurinae		
Longtailed Meadowlark *Sturnella loyca obscura*	Icteridae		
Southern Lapwing *Vanellus chilensis*	Charadriidae		

Black-billed Magpie *Pica pica*	Corvidae	Pedestrian rate negatively related to species richness, foraging was reduced in presence of people	(Fernández-Juricic 2000)
Blackbird	Turdidae		
Spotless Starling *Sturnus unicolour*	Sturnidae		
Common Woodpigeon *Columba palumbus*	Coumbidae		
Common Woodpigeon	Columbidae	All but the abundances of *Phylloscopus trochilis* showed a negative difference between control and experimental sites	(van der Zande and Vos 1984)
Winter Wren	Troglodytidae		
Hedge Accentor	Prunellidae		
Song Thrush	Turdidae		
Eurasian Blackbird	Turdidae		
Icterine Warbler *Hippolais icterina*	Sylviidae		
Blackcap	Sylviidae		
Garden Warbler	Sylviidae		
Common Whitethroat	Sylviidae		
Lesser Whitethroat *Sylvia curruca*	Sylviidae		
Willow Warbler *Phylloscopus trochilis*	Sylviidae		
Common Chiffchaff *P. collybita*	Sylviidae		
Common Woodpigeon	Columbidae	The densities of the Common Woodpigeon, European Turtle-dove, Song Thrush, Blackcap, Garden Warbler, Willow Warbler, Common Chiffchaff and Eurasian Chaffinch were negatively correlated with increased human recreation intensity	(van der Zande *et al.* 1984a)
European Turtle-dove *Streptopelia tutur*	Columbidae		
Song Thrush	Turdidae		
Blackcap	Sylviidae		
Garden Warbler	Sylviidae		
Willow Warbler	Sylviidae		
Common Chiffchaff	Sylviidae		
Eurasian Chaffinch	Fringillidae		
Eurasian Collared-dove	Columbidae		
Winter Wren	Troglodytidae		
Eurasian Blackbird	Turdidae		
European Robin *Erithacus rubecula*	Muscicapidae		
Great Tit *Parus major*	Paridae		

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17 Species	11 Families	Mean FIDs were significantly lower (more tolerant) in urban than in rural areas for 7 species (there was insufficient data for the other 10)	(Cooke 1980)
45 Species	19 Families	Species richness was lower in areas of high human disturbance. The abundances of 6 species were negatively affected by human intrusion	(Heil *et al.* 2007)
50 Species	22 Families	Australian mallee species richness and abundance was unaffected by low levels of experimental human intrusion	(Price and Lill in press)
57 Species	-	People did not alter the distribution of Southern Californian shorebird species	(Lafferty 2001)
59 Species	-	Experimental human intrusion had limited effects on Wyoming bird species richness and abundance, only the most common species showed significant declines in abundance	(Riffell *et al.* 1996)
68 Species	35 Families	There was a significant positive linear relationship between FID and approaching starting distance in 64 of the 68 Australian species. But there was inter-specific variation in FID	(Blumstein 2003)
83 Species	29 Families	FID and post-escape behaviour were positively associated with body mass and wing morphology	(Fernández-Juricic *et al.* 2006)
150 Species	55 Families	Body size was related to flight distance, larger species took flight at greater distances than smaller birds	(Blumstein 2006)

[1.] Sub-antarctic *Skua S. lonnbergi* was once considered a separate species but is now included as a sub-species of the Brown Skua

[2.] The King Shag *P. albiventer* is now considered to be a colour morph of the Imperial Shag *P. atriceps*.

APPENDIX 2

Australian Pelicans on Mud Islands, Port Phillip Bay. Pelicans become very vigilant as people pass by their rookeries and will take flight to the safety of off-shore sand banks, leaving young exposed. Often older chicks will accompany their parents and carers. Although great care is taken to avoid this by walking far from the edge of the rookery, some pelicans will flee at the first sight of humans.

Photo: M. Price

Silver Gulls wait on the periphery of Caspian and Crested Tern colonies for an opportunity to raid nests on Mud Islands, Port Phillip Bay. It is possible to wade off-shore to prevent flushing the terns, thereby avoiding increased human-induced predation. Silver Gulls are probably less likely to raid Caspian Tern nests but the gulls are often observed mobbing pelicans, so it is best not to give them the opportunity.

Photo: M. Price

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Caspian Tern in flight above the sand banks of Mud Islands, Port Phillip Bay. Although it is possible to wade offshore to avoid flushing the terns from their nests, the Caspian Terns are quite protective of their young and will bombard anyone in the vicinity. This tern is coming around for another pass.

Photo: M. Price

Megan Price holding a Scarlet Robin in Kooyoora State Park.

Photo: N. Takeuchi