CHAPTER 4

Attention, habituation, and antipredator behaviour: implications for urban birds

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4.1 Antipredator behaviour as a key to understanding human impacts

The presence of humans may have a profound effect on the distribution and abundance of animals, including birds (e.g. Marzluff et al., 2001). Why, for instance, when we develop hiking trails does avian biodiversity change (Kangas et al., 2010; Miller et al., 2001)? What explains variation in the tolerance that individuals, populations and species' may have towards humans? And, does habituation play an important role in this? In addition, humans introduce noise to environments and the cities are noisy places (e.g. Kight & Swaddle, 2011). Why do anthropogenic sounds seemingly influence some species more or differently than others and how might this happen (e.g. Francis et al., 2011a)? Given a fundamental understanding of the mechanisms involved in such distraction we may be able to develop novel ways to manage noise and other anthropogenic stimuli so they do not have negative effects on populations of animals.

Predation can have a really bad effect on one's direct fitness! Antipredator behaviour includes those features or phenotypic traits that animals do to reduce the probability of being *detected* by a predator, *attacked* by a predator, or *killed* by a predator (Caro, 2005). It includes adaptations to detect predators (identify them, antipredator vigilance), escape from predators (flee them, use refugia), and communicate about them (Lima & Dill, 1990).

Thus, studying antipredator behaviour is important to understand if we want to manage human impacts because predation is a strong selective force that influences habitat selection and population persistence (Blumstein & Fernández-Juricic, 2010). For instance, marmots (*Marmota* spp.) persist in areas of good visibility and protective rocks (Blumstein et al., 2006). There are also indirect effects of predation risk on populations and communities. Fear—what I will define here as the perceived risk of predation—alone may influence where animals go and what they do and thus fear may structure communities. A recent fascinating paper showed that birds hearing the sounds of predators were less able to feed their young and this decline in feeding was directly responsible for lower reproductive success (Zanette et al., 2011). Thus, simply the presence of predators, or stimuli perceived as predators, may be costly.

A key to understanding how humans impact animals is to view people as predators (Frid & Dill, 2002), as they have been during much of their entire evolutionary history. Predators approach animals, animals flee and hide from them and we can capitalize on these flight responses to gain fundamental insights into how species perceive humans (Møller, 2010; Stankowich & Blumstein, 2005). I will review several studies below.

4.2 Explaining variation in disturbance susceptibility

I want to start by asking a deceptively simple question: why do some species tolerate disturbance

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while others do not? I, and others (e.g. Møller, 2008, 2009a, 2010; 2012; Fernández-Juricic et al., 2009) have used flight initiation distance (FID), the distance at which an individual flees an approaching person, to quantify this. We know that flighty birds suffer from greater risk of raptor predation (Møller et al., 2008), and I assume that it is useful to understand the effects of urbanization because flighty species may be more vulnerable to anthropogenic disturbance (see also Møller, 2008). I will focus here on one key insight that I developed from my studies that created a comparative data set with about 10,000 flushes on >300 species of birds.

Before I do so, however, I would like to acknowledge three key researchers who have adopted similar methods and techniques to study urbanization effects on birds. Joanna Burger conducted a number of pioneering studies using human disturbance on birds, some of which used FID to study avian responses to human disturbance. Among other things, key findings have been to show that the type of approach (direct or tangential) may influence FID (Burger & Gochfeld, 1981, but see Heil et al., 2007), variation in human activity levels are associated with variation in foraging behaviour (Burger & Gochfeld, 1991a), and birds apparently habituate in areas where there are many visitors (Burger & Gochfeld, 1991b). Esteban Fernández-Juricic has also conducted many urbanization studies using FID (and other measures) to draw inferences about human exposure. He too has discovered that birds in urban parks seemingly have habituated (birds tolerate close approaches; a phenomena that could also arise from park populations being comprised of immigrants with little fear of humans) and that visitation in highly visited parks may not actually be disturbing (Fernández-Juricic et al., 2001a), and that alert distance (the distance that birds first detect an approaching threat) may indeed be a superior measure to FID when quantifying disturbance (Fernández-Juricic et al., 2001b). Anders Møller has recently conducted a number of studies that have demonstrated (among other things): that urbanization initially reduces both the mean and variation in FID because intolerant populations decline, before mean and variation increase with increased population size from those animals that tolerated the initial bout of urbanization (Møller, 2010); that urban species (Møller, 2009a) and populations (Møller, 2008) tolerate closer approaches from humans; and that differential FIDs of predators and their prey make urban areas predator-free refugia for some prey (Møller, 2012).

A key assumption of using flight initiation distance to study vulnerability of birds to humans is that we must assume that flight initiation distance is a species-specific trait. A number of years ago, we measured FID of shorebirds at a variety of locations in and around Botany Bay in Sydney, Australia (Blumstein et al., 2003). Botany Bay was a good place to conduct a study of how birds respond to humans because the bay includes areas that are protected and have few visitors, public beaches with many visitors, and private properties with relatively fewer visitors. We asked whether and how species responded to approaching humans at these different sites with different exposures to humans. We expected that species would respond differently as a function of their exposure to humans, but if there were species-specific responses, we expected that flighty species would generally be flighty. We tested this by looking at both the main effects of species and site, and importantly the interaction between species in sight on explaining variation in FID. We found that there was no significant interaction between species and site implying that those species with larger FIDs had larger FIDs at whatever site they were studied. This is illustrated in Figure 4.1 where you can see that few lines cross. From this, we concluded that flighty species are flighty, and this species-specific nature of FID has stimulated a lot of research.

I have focused a number of analyses on the 150 species with >10 independent data points, and therefore a good estimate of FID (Blumstein, 2006). There are other ways to study data sets with variation in sample sizes. For instance Møller (e.g. Møller, 2008, 2009a, 2010) has weighted each species' value by sample size. I shall review a series of phylogenetically based analyses that I conducted that ask what are the natural history and life history correlates of flightiness. In all cases, analyses were conducted using phylogenetically independent contrast values to control for the expected (and documented) similarity among relatives due to common phylogenetic descent.

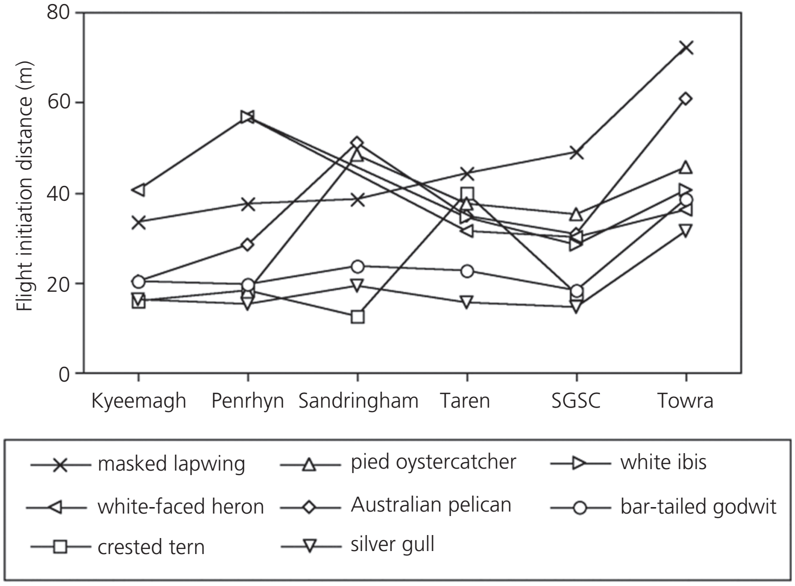

Figure 4.1 The relationship between location and FID for eight species of birds. You can see that few lines cross suggesting that flighty species are typically flighty; indeed, while there were significant effects of site and species, there were no significant interactions between site and species. Modified from Blumstein et al. (2003).

Larger body-sized birds detected approaching humans at greater distances and most of the variation in first response distance is explained by body size (Blumstein et al., 2005; Figure 4.2). Body size explains most of the explained variation in flight initiation distance as well (Blumstein, 2006). Body size is an important life-history trait that has a lot of predictive ability (Bennett & Owens, 2002)—specifically with respect to antipredator behaviour. However, there is some variation that requires further exploration.

One might expect that relative eye size influences the ability of birds to respond to threats. This ultimately is because eye size is associated with higher visual acuity (Kiltie, 2000), and higher visual acuity is associated with a greater ability to resolve objects from farther away (Land & Nilsson, 2002). One analysis suggests that after controlling for body size, eye size does not explain variation in FID (Blumstein et al., 2004), while another analysis suggests that it does (Møller & Erritzøe, 2010). Another couple of studies measured visual acuity of passerines (considering both eye size and the density of retinal ganglion cells) and found that species with higher visual acuity were able to detect a predator model from farther away (Dolan & Fernández-Juricic, 2010; Fernández-Juricic & Kowalski, 2011). My suspicion is that birds have large eyes for several reasons, and there may be a relatively small effect of eye size on vulnerability to humans. Note, however, the effect reported by Møller and Erritzøe (2010) accounted for 11% of the variance, which is not an insignificant amount. However, in other analyses (Blumstein, 2006) I found that flightiness coevolved with capturing live prey (as did Møller & Erritzøe, 2010), and being a cooperative breeder. Thus, perhaps having eyes that detect movement (which ultimately is about how the retina functions), not eye size, per se, is associated with flightiness.

And, after controlling for body mass and starting distance (the distance that the observer started an experimental approach to a bird), statistically, birds that reproduce at an older age are more flighty (also see Møller & Garamszegi, 2012). I examined a variety of other life history traits but found that most did not have a large effect. For instance, there was no effect of clutch size, no effect of the number of days young were fed, no effect of longevity (although

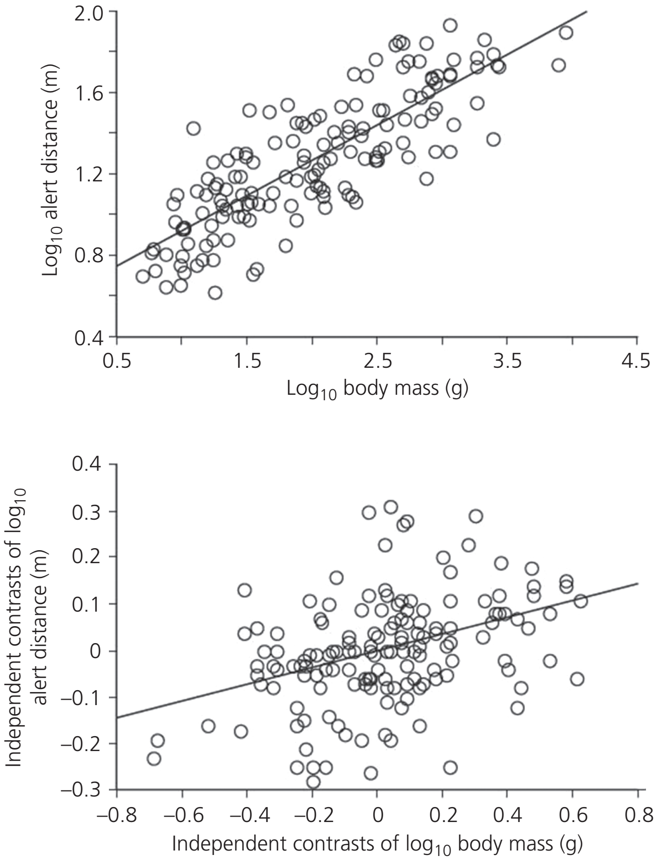

Figure 4.2 Larger body-sized birds first detect approaching humans at a greater distance whether quantified with species values or by calculating phylogenetically independent contrast values. Modified from Blumstein et al. (2005).

these are notoriously difficult to estimate), and no effect of habitat openness (Blumstein, 2006; but see Møller & Erritzøe, 2010 who report an effect of habitat openness). These results were somewhat surprising. However, being social, which I quantified by noting whether a species was a cooperative breeder or not, was associated with enhanced flightiness.

In a recent analysis, with different data, Møller (2009b) found that after controlling for body size, birds with greater basal metabolic rates have greater FID estimates. This is an important finding because it suggests that risk taking is part of a life-history syndrome of traits. And this life-history variation has important implications for how species respond to humans.

Thus, while life history variation is an important factor in explaining the evolution of species-specific differences in flight initiation distance, body size is the single biggest predictor yet identified. And, recent work by Møller (2012) suggests that this has important consequences for coexistence of smaller prey and larger predators in urban areas. I conclude from these analyses that body size has a profound effect on species vulnerability, and suggest that, without any other knowledge, body size alone may be a useful surrogate for vulnerability; large species are more vulnerable to human disturbance than smaller species (Bennett & Owens, 2002).

4.3 The natural history of habituation

4.3.1 Habituation and the geography of fear

Psychologists have formally studied habituation and its doppelganger, sensitization, for over 100 years. Yet even the ancients knew that animals may habituate to repeated exposure. Thompson

(2009) quoted an Aesop's Fable about the fox and the lion:

> A fox who had never yet seen a lion, when he fell in with him for the first time in the forest was so frightened that he was near dying with fear. On his meeting with him for the second time, he was still much alarmed, but not to the same extent as at first. On seeing him the third time, he so increased in boldness that he went up to him and commenced a familiar conversation with him.

Habituation is seen when a response declines over repeated exposures to a particular stimulus. By contrast, sensitization is seen when the response is enhanced with repeated exposure to stimuli. While this is well known, what is not really well understood is what I will refer to as 'the natural history' of these phenomena. For instance, under what conditions do animals habituate, and under what conditions do animals sensitize? What are the life history and natural history correlates or predictors of habituation or sensitization in different individuals, populations and species? I will first discuss some insights from studying ungulates, and then about several studies of birds, including one that I have not previously reported.

Günther's dik-diks (*Madoqua guentheri*) are small, monogamous, African ungulates that are eaten by about 36 species of mammals and birds—assessing risk to them is *essential*. Many species respond to the sounds of their predators and take evasive action. We (Coleman et al., 2008) capitalized on this expected response to predator sounds and broadcast jackal calls (a potential predator) and non-alarming bird song (a benign sound) within 0.5 km of human habitation, and >0.5 km of human habitation. We found that unhabituated dik-diks were unable to discriminate between the sounds of predators and benign sounds. This is important because ecotourists at more pristine places are likely to disturb animals and interfere with their risk assessment. What was interesting was the observation of this 0.5 km discrimination ability threshold.

To follow up on this, and in a study of how mule deer (*Odocoileus hemionus*, a North American ungulate) respond to marmot alarm calls (a form of interspecific communication) we (Carasco & Blumstein, 2012) found that deer discriminated marmots and white-crowned sparrow (*Zonotrichia leucophrys)* song when they were relatively close to people, *again within 0.5 km of houses*, while they failed to discriminate farther away, suggesting that there was some sort of a ceiling effect.

These two studies raise an interesting question that is ripe for study: is 0.5 km a 'magic number' for ungulates? What about other taxa?

Working along the beaches of Santa Monica, California, we (Webb & Blumstein, 2005) found that there were quantitatively different patterns of human visitation on either side of a very popular pier. Interestingly, FID to humans varied on either side of the pier (Figure 4.3). On the side with reasonably constant visitation, FID was reasonably constant. On the side with decreasing visitation, gulls were more flighty when there were fewer people. This pattern is evident over several kilometres and it illustrates the scale and pattern of human impacts on wildlife.

However, the scale of human disturbance can be much shorter. Working in two southern California wetlands, we (Ikuta & Blumstein, 2003) found that the presence of a fence that separated an area where ecotourists were common from an area where there were few visitors was sufficient to explain variation in avian FID. Indeed, species responded in a similar way to their responses in a nearby, protected wetland with very few human visitors. And, Fernández-Juricic et al. (2009) found that other wetland birds had shorter FID in areas with greater visitation.

I think that these studies suggest that we need to know much more about the spatial ecology of fear. How generalizable is the 0.5 km threshold for making biologically important discriminations? Are there different thresholds in highly urbanized areas? Over what distances do humans influence FID—a biologically important antipredator behaviour? And, what factors explain variation in the scale of interference.

An important caveat, and opportunity for future research, is that to really understand whether habituation, differential recruitment, or local adaptation to human disturbance is occurring, one must study marked individuals; something that is rarely done with studies of avian FID. My group has shown that marmot FID is repeatable, and that some individuals may habituate (Runyan & Blumstein, 2004; M. Petelle et al., in review). Recent work with birds

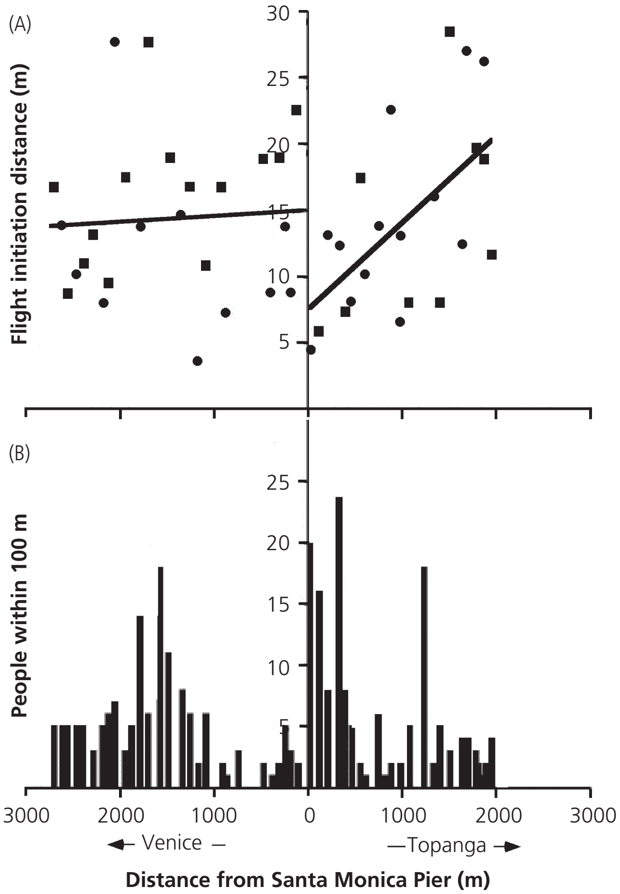

Figure 4.3 Flight initiation distance of Western gulls varies rapidly with distance on a side of a popular pier where visitation drops off compared to the side where visitation is more constant. Modified from Webb and Blumstein (2005).

has shown that FID may be significantly repeatable (Carrete & Tella, 2010), and other work (e.g. Møller 2008) suggests that local adaption to human disturbance is possible in the long run.

4.3.2 Sensitization and the contiguous habitat hypothesis

But not all species habituate. My work at both very patchy wetlands and very contiguous chaparral habitat in California led me to develop a novel hypothesis. While I suspected that increasing human visitation would typically habituate birds, this is not what I found.

Rina Fernandez, an undergraduate student working in my lab, visited six different sites weekly over 10 weeks. Sites were trails and fire roads in the Santa Monica Mountains (outside Los Angeles, California) that had different degrees of human visitation that she quantified by counting the number of pedestrians she encountered. Two sites, Albertson Motorway and Zuma Canyon, were classified as high impact based on the number of pedestrians encountered during censuses while Lower Chesboro, Palo Comodo Social Trail, Sage Hill, Morrison Ranch Road, and the Zuma Loop trail were considered lower impact areas. Thus, we had some replication for our two levels of impact.

While at the sites, birds were experimentally approached and FID was estimated. Of 49 species studied, we focused on 14 species with ≥4 observations per impact level (the majority of species had many more observations and California towees (*Melozone crissalis*) had a total of 208). We expected to see that there would be significant differences whereby increased human disturbance would be

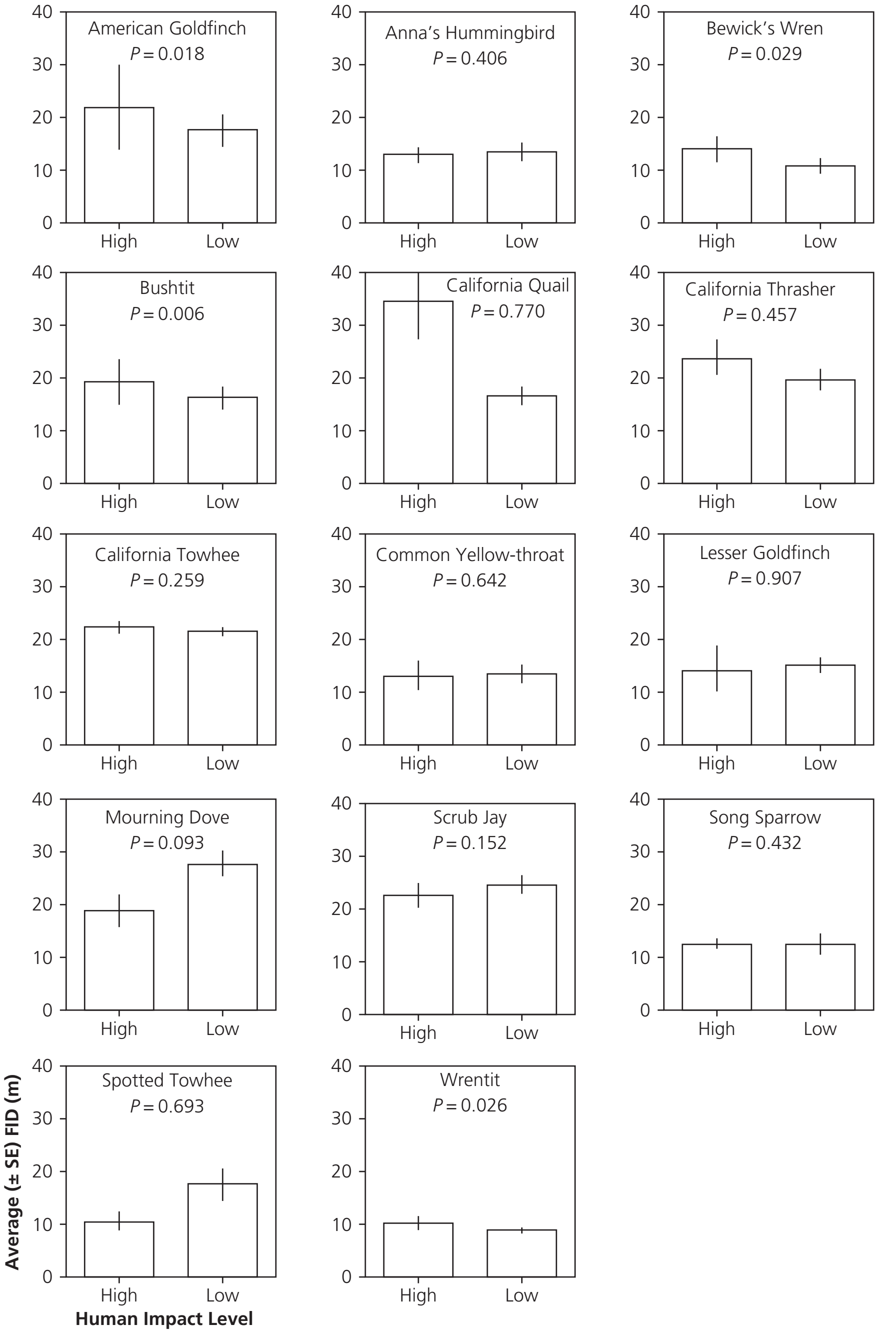

Figure 4.4 The effect of human visitation on avian flight initiation distance (± SE) (m) for 14 species of chaparral birds. In only four species, American goldfinch, Bewick's wrens, bushtits, and wrentits did human visitation have any impact on FID. Results suggest that these three species were sensitized to human visitation in that their FID was greater with increased human visitation. *P*-values are from a general linear model after explaining significant variation accounted for by the distance the observer began walking towards the focal bird.

associated with decreased FID. *We found the opposite*. Indeed only 4 of these 14 species of chaparral birds had significantly different FID estimates as a function of high or low human disturbance levels. And, for the four species that varied, they sensitized, rather than habituated (Figure 4.4).

By contrast, all of the species of shorebirds habituated to increased visitation in the Ikuta and Blumstein (2003) study. A number of factors might influence this difference including (but not limited to) the degree to which species are territorial, group living, etc. However, perhaps there is something about the options that individuals have that explains this difference.

I would like to suggest a novel hypothesis to explain these patterns: 'the contiguous habitat hypothesis'. The contiguous habitat hypothesis states that 'species living in limited habitats (e.g. wetland fragments), may be more likely to habituate than those living in more contiguous habitats (e.g. chaparral)'. If this is generally true, it seems to provide a mechanistic model that may explain species vulnerability to urbanization.

We know from many studies that the spatial scale of habituation can be stark (e.g. with a fence), or gradual and occur over several kilometres. Animals that have no options other than to remain in a small, constrained habitat type (as exemplified by wetland birds in Southern California) should be more likely to habituate. Alternatively, there has already been some species-sorting on these wetlands that has led to the loss of species that are unable to habituate. By contrast, species that have more contiguous habitat may actually be more vulnerable to human disturbance because it is likely that the first response for many species is to sensitize to increased human disturbance.

Gill et al. (2001) noted that we must be careful when assume that a behavioural response indicates that there has been a population consequence, and, importantly, the lack of response indicates no population consequence. They also emphasized that the availability of alternative habitat was likely a key feature in determining how human disturbance was reflected in observed differences. The contiguous habitat hypothesis differs in emphasis: I assume that habituating to humans allows coexistence of those populations and species that are able to habituate. Thus, the contiguous habitat hypothesis may help explain an equilibrium condition. We need to know more about how individuals and individual species respond across a range of human disturbances and those researchers who adopt a reaction norm approach will likely make fundamental discoveries.

The contiguous habitat hypothesis requires proper testing and I hope that by articulating it here, other data sets will be examined to see if and how it explains variation in habituation/sensitization with increased human disturbance and if, ultimately, populations and species that tolerate disturbance because of limited options, are more likely to persist in areas with humans.

4.4 Noise and its varied effects

Let us change topics a bit and think about the effects of anthropogenic noise, which is present in the seas and on land. Noise may mask biologically important signals and is associated with changes in signal structure (reviewed in Chapter 6). Noise is associated with physiological stress (Campo et al., 2005). Noise is associated with a decline in avian reproductive success (reviewed in Chapter 7), with changes in population distributions (Bayne et al., 2008; Bejder et al., 2006; Reijen et al., 1998), and noise may directly harm animals (Popper & Hastings, 2009). Avian community structure (Francis et al., 2009, 2011b; Slabbekoorn & Halfwerk, 2009), and important species interactions—like pollination and seed dispersal (Francis et al., 2012), can be influenced by anthropogenic noise. Noise may also provide distracting stimuli that interfere with biologically important assessments. I will focus first on masking and then discuss how noise may be distracting.

4.4.1 Noise masks important signals

While the importance of the acoustic environment on signal structure has long been recognized, it has only been since Slabbekoorn and Peet (2003) that conservation and behavioural biologists have been particularly sensitive to the idea that urban noise can influence the structure of bird song. Birds sing at higher frequencies (Parris & Schneider, 2009) and at greater amplitudes (Brumm, 2004) to sing over background noise. Those that naturally sing above the lower-frequency noise may be less likely to be impacted less by urban noise than those that sing at higher frequencies. However, other than Francis et al. (2011a) who focused on well compressor noise, I am not aware of a systematic test of this hypothesis in urban ecosystems. Indeed, if we look at how species avoid biological noise in their environment, we see a number of potential adaptations to avoid noise (Kirschel et al., 2009) that may be used by birds encountering anthropogenic noise.

The initial Slabbekoorn and Peet result has created a cottage industry in studying birds' responses to urban noise (as of March 2012, the article has been cited 290 times). But, I believe, that this cottage industry has largely emphasized bottom-up perceptual processes (Miller & Bee, 2012), in that researchers have gone out and focused on quantifying the noise spectra and the frequencies produced in noisy areas and more rural and presumably more quiet areas. This is fine, but there are a variety of top-down cognitive processes (Miller & Bee, 2012) that have been neglected. Below I will discuss attentional processes.

4.4.2 Noise competes for limited attention

Stimuli, in any modality, that do not provide information about biologically important features of the environment, may distract individuals from making biologically important assessments (Chan & Blumstein, 2011). I shall first explain this in the context of signal detection theory (Green & Swets, 1966) and then discuss how attention may also be modified.

Animals must discriminate useful and informative stimuli from those that are not useful or informative. To make such discrimination, individuals must set a decision threshold which will, inevitably have two types of error: false positives mean that individuals respond to non-informative stimuli and false negatives means that individuals miss responding to informative stimuli. Signal detection theory is a statistical framework to understand and quantify this tradeoff (Wiley, 2006).

Using signal detection theory we can view stimuli as having certain potentially overlapping characteristics. For instance, both predators and non-predators move through the air, and to discriminate a predator from a non-predator some threshold about how to respond to these stimuli must be set (Figure 4.5).

The more perceivable stimuli in the environment are, the greater the risk of an error. And, the relative cost of the two sorts of errors might cause several things to happen. First, a predetermined threshold might be unchanged. This will cause individuals to have more false positive responses and if these responses are costly, it will cause a waste of both time and energy. Of course, in response to these costly responses, thresholds may change which would reduce the false positive responses but at the cost of more false negative responses! Thus, animals may simply not respond to the presence of real predators and this too may have a fitness cost.

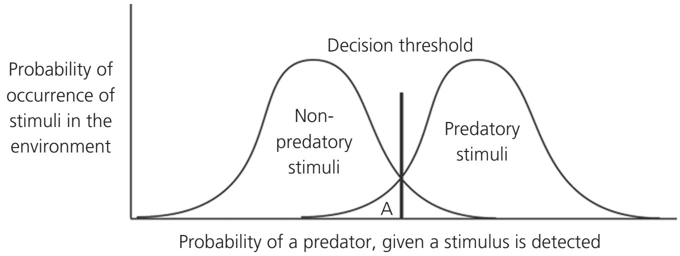

Figure 4.5 Fundamental signal detection problem that all species face when trying to detect predators. Predatory and non-predator stimuli overlap in characteristics (e.g. raptors and leaves both move through the air but only raptors are dangerous). To differentiate between them, animals must set a response threshold which inevitably trades-off certainty with error. Area A, to the left of the decision threshold, illustrates missed detections because predatory stimulus characteristics fully overlap non-predator stimulus characteristics. If these errors are costly, then we expect natural selection will shift the decision threshold further to the left.

Another view of competing stimuli is how they may act on attention. Attention is viewed as a limiting resource: individuals must allocate it among biologically important tasks such as looking for suitable habitat, food, mates, and detecting predators. Given these competing demands, extraneous stimuli can capture valuable attention and distract it from tasks at hand. I think that to understand how humans impact wildlife and to manage these impacts we must develop mechanistic hypotheses (Blumstein & Fernández-Juricic, 2010).

Chan et al. (2010) developed the 'distracted prey hypothesis' that states that: 'Any stimulus an animal can perceive is capable of distracting it by reallocating part of its finite attention and thus preventing it from responding to an approaching threat'.

The main idea of the distracted prey hypothesis is that attention is finite (e.g. Dukas, 2004), and that attention can be compromised by stimuli in multiple modalities. We know that birds, mammals, reptiles, and invertebrates all use attention to focus on relevant stimuli. Thus, and as discussed above, cities create many extraneous stimuli that may distract animals.

While studies of hermit crabs (Chan et al., 2010) and lizards (Huang et al., 2011) found that boat motor noise and camera sounds (respectively) distracted these species, we need studies focusing directly on birds to better understand how anthropogenic stimuli can distract birds. Thus, there are many research opportunities that may generate novel insights that will better allow us to manage urbanization and its deleterious consequences on birds. And, it is essential to try to properly quantify fitness consequences of limited attention, a potential challenge to much urbanization work.

4.5 Conclusions

Ultimately, human coexistence with wildlife in urban settings will require active management. I have focused largely on my own studies to suggest that by focusing on antipredator behaviour, we can gain valuable mechanistic insights into how birds are likely to respond to urbanization. Mechanistic studies are particularly important because if we know the mechanism, we should be able to manipulate the impacts (Blumstein & Fernández-Juricic, 2010). For instance, if we know that prey are distracted, and that this distraction increases predation risk, then we can better understand and manage causes of decline for threatened or endangered species. If we know that species on contiguous habitat are more sensitive to increased human visitation, vulnerable species will be managed by reducing visitation. And, if we know that large body-sized birds are generally going to be more vulnerable to disturbance, we know that larger patches are required to contain them.

The future will determine whether such management interventions work and I (Blumstein, 2007, 2013) strongly advocate the use of evidence-based evaluation (Sutherland et al., 2004) because this will be the most efficient way to test these management recommendations. Finally, I believe these studies suggest that there is a very fruitful collaboration between behavioral biologists and wildlife managers and I hope that this review helps stimulate these collaborations.

Acknowledgements

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