Journal of Applied Ecology 2005
42, 943–953

Inter-specific variation in avian responses to human disturbance

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Summary

1. Increasing urbanization and recreational activities around and within biodiversity hotspots require an understanding of how to reduce the impacts of human disturbance on more than a single species; however, we lack a general framework to study multiple species. One approach is to expand on knowledge about the theory of anti-predator behaviour to understand and predict how different species might respond to humans.

2. We reviewed the literature and found that only 21% of studies that used a behavioural approach to study human disturbance focused on multiple species. These studies identified a number of potential predictive variables.

3. We developed a simulation model that investigates interspecific variation in different parameters of disturbance with variation in human visitation. We found that fitness-related responses, such as the quantity of food consumed by a species, are relatively sensitive to the distance at which animals detect humans, the frequency of disturbance by humans and the interaction of these factors, but are less sensitive to other characteristics.

4. We examined avian alert distance (the distance animals first orientated to an approaching threat, a proxy for detection distance) across 150 species, controlling for phylogenetic effects. We found that larger species had greater alert distances than smaller species, which could increase local spatial and temporal limitations on suitable habitat with increasing human visitation.

5. *Synthesis and applications*. Our results suggest that body size could be a potential predictor of responses to human disturbance across species, and could be used by managers to make conservation decisions regarding levels of human visitation to a protected site. We suggest that three things are essential to develop predictive models of how different species will respond to human disturbance. First, multiple indicators of disturbance should be studied to select those with lower intraspecific variation for a given study system. Secondly, the species-specific nature of responses should be identified. Thirdly, life history, natural history and other correlates with these species-specific responses must be assessed.

Key-words: alert distance, conservation behaviour, detection distance, ecotourism, flight initiation distance, recreation

Journal of Applied Ecology (2005) **42**, 943–953
doi: 10.1111/j.1365-2664.2005.01071.x

Introduction

Animals are increasingly affected by urbanization processes that modify different aspects of their biology (Wearing & Neil 1999; Marzluff, Bowman & Donnelly 2001). This is likely to worsen because the rate of human visitation to the world's biodiversity hotspots is expected to double by 2020 (Christ *et al*. 2003). However, our ability to predict the effects of humans on wildlife is restricted (Hill *et al*. 1997; Gill, Norris & Sutherland 2001). We need to develop conservation strategies that protect multiple species (Taft *et al*. 2002; Heikkinen *et al*. 2004). Limitations may

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arise when the results of single-species studies are generalized to species with different ecological requirements.

Whilst we acknowledge that behavioural indicators generally used to assess tolerance to disturbance (e.g. flight initiation distance) may not reflect population level responses (Gill, Norris & Sutherland 2001; but see Stillman *et al*. 2000), we believe that a behavioural approach is essential for certain management situations. Visitors to protected areas may reduce the biodiversity they seek via direct or indirect disturbance (Boyle & Samson 1985; Kenchington 1989). Managers who seek to design parks and reserves that maximize the number of species that human visitors can observe should conduct behavioural studies of human disturbance on wildlife to provide information about wildlife uses of particular sites within protected areas under different levels of human visitation. Under this paradigm the question becomes not whether or not a species is negatively affected by human disturbance (Gill, Norris & Sutherland 2001) but what the probabilities are of any given species using a particular site within a protected area under different levels of disturbance.

One useful theoretical framework is the risk–disturbance approach (reviewed in Frid & Dill 2002), which utilizes economic models of anti-predator behaviour to study the responses of single species to human disturbance (Frid & Dill 2002; Beale & Monaghan 2004). Individuals may trade-off the avoidance of disturbance by humans against activities that may increase fitness, such as foraging, mating and parental care (Frid & Dill 2002).

We suggest that the risk–disturbance approach can be incorporated into a multispecies framework to generate predictions about the impact of human disturbance on groups of species. This approach will facilitate the development of strategies for coexistence between humans and wildlife and will lead to a more general understanding of the relationship between the life-history characteristics of species and their response to different aspects of human disturbance.

We developed a multispecies, comparative framework to predict responses of wildlife to recreational activities that could be applied to protected area management. First we reviewed the literature to identify the different approaches used in behaviourally based studies of human disturbance with more than one species. Secondly, we employed a model to examine the sensitivity of fitness correlates of disturbance to quantitative components of the behavioural approach (e.g. flight initiation distance, detection distance and post-disturbance response). We used the model to illustrate how to use correlates of behavioural responses across species to generate testable hypotheses and management recommendations, based on variation in body size in relation to detection distance estimates. Finally, we suggest a three-tiered approach to study multispecies responses' to humans.

Methods

EVIDENCE FOR INTERSPECIFIC VARIATION IN RESPONSE TO HUMAN DISTURBANCE

The Web of Science and Zoological Abstracts were searched from 1980 to 2003 using the key-words 'human disturbance and behaviour or behaviour'. We included some additional reports from federal agencies but not review papers. For each paper reviewed, we classified the number and taxa of the species studied, the location of the study, the type of disturbance, the dependent variables used to assess behavioural responses to humans, and the main conclusions.

CONSEQUENCES OF INTERSPECIFIC VARIATION IN RESPONSES TO HUMANS

We developed a simulation model to investigate how variation in species-level responses might influence a species' sensitivity to human disturbance, and to explore how potential main effects and their interactions may influence tolerance to disturbance. We chose birds as our model animal to explore the consequences of traits (flight initiation distance, detection distance, landing distance) that are known to vary interspecifically in birds, but the same principles can be applied to other taxa provided information from several species is available. We acknowledge the difference between detection distance (the distance at which approaching humans are detected) and alert distance (the distance at which the animal shows alert behaviours in response to approaching humans). We used detection distance because we were able to specify and manipulate the distance at which birds detected disturbance. Detection distance cannot be measured in the field but can be estimated by quantifying the alert distance (Fernández-Juricic, Jimenez & Lucas 2001a; Blumstein *et al*. 2004). We manipulated the levels of five independent factors: detection distance (25, 55, 85, 115 and 145 m), flight initiation distance (20, 40, 60, 80 and 100 m), landing distance (1, 20, 40, 60 and 80 m), latency period (1, 3, 5, 7 and 9 time intervals spent latent) and pedestrian rate (0, 50 and 100 people crossing the park per day of the simulation). We relied on published and unpublished sources to determine the interspecific variability in these different parameters because of the scarcity of this information in the literature. For detection distances, we used the published estimates of alert distance (Burger & Gochfeld 1983; Fernández-Juricic, Jimenez & Lucas 2001b; Fernández-Juricic & Schroeder 2003; Blumstein *et al*. 2004) and our own data (see below). The variability in flight initiation distance was obtained from published sources (Cooke 1980; Burger & Gochfeld 1981; Burger & Gochfeld 1991; Holmes *et al*. 1993; Rodgers & Smith 1995; Fernández-Juricic, Jimenez & Lucas 2001a; Blumstein 2003; Blumstein *et al*. 2003; Fernández-Juricic, Vaca & Schroeder 2004). The variability in landing distance and latency period was based on published papers (Fernández-Juricic, Jimenez & Lucas 2002; Fernández-Juricic, Vaca & Schroeder 2004) and an unpublished study on the life-history factors affecting interspecific variation in these two parameters conducted in both Europe (15 species) and North America (49 species) (E. Fernández-Juricic & D. T. Blumstein, unpublished data). We examined how certain characteristics of bird responses to humans acted in combination and contributed differently to consumption of a depleting food resource. We simulated comparisons over a wide range of values for a limited number of characteristics.

The model simulated the foraging activities of birds within an insular patch (500 × 500 m) of a protected area (e.g. a park). The park was bisected by a single path running east to west. At the start of each replicate 'season' of 180 days (to simulate the non-breeding season), 10 000 food items were placed randomly throughout the park, where they remained until they were eaten by a bird or that season was completed. The virtual birds were programmed to respond differently to human disturbance. We measured the amount of food left by the virtual birds and its location in the park. Each day of foraging was composed of 144 5-min foraging time steps. At the start of each simulated day, the birds flew into the park, landed at randomly selected points and began foraging. They moved about the park responding to the presence of food by approaching it, and to human pedestrians walking along the path by moving away from them. Importantly, we assumed that the only suitable habitat available to the birds was that within the park.

Each replicate of the simulation tracked 10 birds (the resident population) for a season. Note that these 10 individuals were not unique individuals whose fates were tracked relative to their foraging success. This approach allowed us to address our objective of contrasting the relative impacts of different species-level characteristics of the response to human disturbance upon foraging success without having to parameterize complex details such as species-specific characteristics rates of energy consumption.

During the simulation, pedestrians moved from the western edge of the path to the eastern edge at a randomly selected time step. Once they appeared, pedestrians moved along the path at a rate of 50 m per 5 min time step. If pedestrians passed within a bird's detection distance during a time step, then the bird stopped foraging and moving for that time step (i.e. it froze). If pedestrians passed within a bird's flight initiation distance during a time step, the bird flew for the length of the bird's landing distance directly away from its current position along a line 180° to the approaching pedestrian. If this flight path caused the bird to leave the park, the bird was instead redirected for the appropriate distance along the edge of the park so that it remained within the foraging area but moved the appropriate distance away from the pedestrian. This was realistic behaviour for birds that require specific habitat features found only in a reserve (e.g. wetland birds and those found in remnant forest fragments in urbanized landscapes). Once the bird fled, it did not feed or move for the duration of its latency. After the latency period had elapsed, the bird resumed foraging and moving from its new location.

We set the foraging range (the distance at which birds can effectively capture food items during a time step) constant at 1 m, and the probability that birds could capture a food item within their foraging range constant at 0·5 during each time step when the birds were not latent or alert. The simulation recorded the number of food items consumed by birds during the season, distance from the pedestrian path to food items consumed by birds, number of times pedestrians passed within detection distance of birds, and the number of time periods birds spent latent after fleeing pedestrians. The distance from the path spatially described the loss of previously suitable habitat as a result of human disturbance.

Movements by foraging birds were simulated using a biased random walk model (equation 1) that was modified by rules described below (equation 2 and equation 3). Note that while the model tracked the movements and activities of 10 individual birds during each day they should not be considered the same birds on successive days. All movements were simulated without respect to other birds, although simulated birds did change their movements based upon the spatial pattern of food and encounters with pedestrians. Furthermore, if a bird's foraging movements caused it to cross the edge of the park it was reflected back into the park because we assumed that there was no food outside the park. The number of food items a bird encountered within its foraging range during each time step altered both the degree of correlation between successive steps (equation 2) and the length of steps taken by the bird (equation 3). These changes were made to cause birds to move straighter and further when not finding food and to mimic area-restricted searching (moving slower and turning more) when encountering lots of food. Foraging movements by the bird were simulated as vectors of varying lengths and directions between successive steps. Movement patterns were simulated using a correlated ra ndom walk:

$$\beta = 2\arctan[((1-\rho)/(1+\rho))\tan(\Psi)] \qquad \text{eqn 1}$$

where β is the random angle at which birds move between successive steps, ρ the degree of correlation between successive moves taken by the bird, and Ψ the uniform distribution of angles between –90° and 90° from which β was randomly drawn. After each step there was a change in direction by a random angle β. The default value of ρ for each time step was set equal to 0·95 unless foraging success or failure changed the bird's behaviour. Changes in the degree of correlation between successive steps taken by the bird were defined by:

$$\rho = 0{\cdot}95 - (\mathrm{NF} \times 0{\cdot}05) \qquad \text{eqn 2}$$

where NF is the number food items encountered in the last time step. Whenever foraging success reduced ρ so that it was lower than 0·5, ρ was automatically set to a value of 0·5. We defined the length of steps taken by the bird for each time step as:

$$DM = (1 - (NF \times 0{\cdot}1)) \times (SD) \qquad \text{eqn 3}$$

where DM is the distance moved in a time step, NF is the number food items encountered in a time step and SD is the standard distance moved when searching for food and always set equal to 1 m for this application of the simulation. Whenever foraging success reduced DM so that it was less than 0·005 × SD, DM was set equal to 0·005 × DM.

We analysed our simulation results in SAS 6·0 (SAS 1989) by fitting a general linear model to quantify the variation explained by the main effects and their interactions. All possible combinations of all levels of all five variables produced 1875 unique sets of parameter space, replicated (with unique random number seeds) 50 times. We acknowledge that our design resulted in some parameter combinations that are not likely to be seen in nature. Specifically, virtual birds whose flight initiation distance exceeded their detection distance might be considered unrealistic. We therefore excluded those combinations of flight initiation distance and detection distance from analyses, resulting in 1275 sets of possible parameter space.

A COMPARATIVE APPROACH TO PREDICT INTERSPECIFIC RESPONSES

Our model suggests that the distance animals become aware of approaching threats (i.e. detection distance) is a key biological factor explaining variation in the responses to human disturbance. Comparative approaches can help us understand the vulnerability of species to disturbance. For instance, many different ecological, behavioural and life-history traits are associated with body size (Gaston & Blackburn 2000; Bennett & Owens 2002). We used body size to illustrate the predictive power of certain traits to explain variation in species' tolerance to disturbance and make specific management predictions based on disturbance tolerance.

Our methods followed those reported in Blumstein (2003) and Blumstein *et al*. (2004). We focused on birds in Australia, Europe, North America and South America that were foraging or engaged in 'relaxed behaviours' such as preening and roosting. Highly vigilant and obviously alarmed birds were not approached, nor were nesting birds or endangered species. To estimate alert distance, we identified individual birds and then walked at a steady pace of *c*. 0·5 m s^{-1} towards them. We noted the distance that we started walking towards birds (starting distance) and the distance at which the focal bird looked up in response to our approach. This was usually obvious, with the exception of some species that actively move their heads while foraging (e.g. shorebirds). We ensured that all observers collected data consistently. New observers were trained until their observations were very similar to an experienced observer. Additionally, all observers were instructed to discard data if there were any doubts about any of the variables collected.

Subjects were not marked; however, we avoided resampling individuals by focusing on birds in different geographical locations and not resampling the same location. Birds were studied in both 'pristine' environments, with few if any visitors, and in areas with human activity. Analyses excluded observations on individuals in highly visited city parks and individuals that approached humans (for handouts) rather than fleeing. To our knowledge, none of the species included in our analyses was actively hunted at the locations where we studied them.

From a database of more than 350 species, we selected 150 species (representing 107 genera and 40 families) for which we had at least 10 observations and calculated a species' mean alert distance. Maximum body mass was tabulated from Dunning (1993) or values were obtained from species' accounts published in the multi-authored series *The Birds of North America* (www.aou.org/birdsofna.php3) and the *Handbook of Australian*, *New Zealand*, and *Antarctic Birds* (www.birdsaustralia.com.au) with supplementary data from Geffen & Yom-Tov (2000) and Clement (2000).

All variables were $\log_{10}$-transformed for analysis. The distance a human begins walking towards a bird explains significant variation in an animal's response to approaching threats and must be incorporated into subsequent analyses (Blumstein 2003). Importantly, this relationship logically should be forced through the origin. This is because a person beginning to approach a bird at 0 m could only elicit a 0-m detection distance. We regressed the $\log_{10}$ of body size and the $\log_{10}$ of starting distance against the $\log_{10}$ of alert distance. We included both main effects and the interaction of starting distance and body size as independent variables. Our data included species with a range of mean alert distances (mean ± SD, 24·5 ± 18·5 m, range 4·5–86·2 m), masses (30 ± 1053 g, range 5–8700 g) and starting distances (33·0 ± 22·4 m, range 8·0–103·8 m). Because values of related species are not phylogenetically independent (i.e. species may resemble each other because of shared ancestry) but differences between them are, we then calculated phylogenetically independent contrasts (Felsenstein 2004) and fitted the same models to contrast data. We used the Sibley & Ahlquist (1990) phylogeny and the Sibley & Monroe (1990) taxonomy. Unresolved congeners not specifically included in the Sibley & Ahlquist (1990) phylogeny were left as polytomies that were later resolved randomly using MacClade 4·03 (Maddison & Maddison 2001). We assumed a punctuational model of evolution, calculated contrasts using COMPARE 4·5 (Martins 2003), and, as required by the method, forced the regression through the origin (Felsenstein 2004). Once we $\log_{10}$-transformed values, we met key statistical assumptions of the regression analyses. Specifically, there were no outliers with substantial leverage and there was no relationship between the absolute value of the contrasts when plotted against the standard deviation of the raw contrasts (suggesting that residual variation is constant across the relationships).

Analyses were conducted using SPSS 10 and linear models were fitted using the GLM univariate method (SPSS Inc. 2000). We interpreted all two tailed *P*-values < 0·05 as significant. Residuals from general linear models were scrutinized visually and did not deviate substantially from normal.

Results

EVIDENCE FOR INTERSPECIFIC VARIATION IN RESPONSE TO HUMAN DISTURBANCE

We found 147 studies that used a behavioural approach to investigate the effects of human disturbance, of which 31 (21·1%) involved more than one species (mean 11·25 species, range 2–68; see the Appendix). Of the interspecific studies, 28 studies used birds as model species, two used mammals and one study used a combination of mammals and birds. Interestingly, we found no studies that focused on fish. Of the bird studies, 17 (58·6%) were exclusively devoted to birds that spent part of their life cycle in association with water (waterfowl, shorebirds, etc.).

The majority of studies were conducted in North America (16, 51·6%) and Europe (seven, 22·6%), while Asia (seven, 22·6%) and South America (one, 3·2%) were not well represented given their relative sizes. Most of the studies evaluated the effects of pedestrians on wildlife (28, 90·3%). As for the variables that assessed responses to humans, flight initiation distance, the distance at which animals flee an approaching threat, was by far the most frequently used variable (22 studies, 71%). Other variables employed less frequently included alert distance (three studies), distance moved during flight (two studies), patterns of vigilance or foraging (two studies), variation in activity period (two studies), the time required to resume initial activity (two studies) and various behavioural responses (such as nesting behaviour, vocalizations, escape tactics, etc.; four studies).

Most of the studies found interspecific variation in the behavioural responses to human disturbance (29, 93·5%). Body size was the most often cited factor accounting for these interspecific patterns (10 studies). Six studies showed that larger species had greater flight initiation distances than smaller species, and only one found the opposite pattern. Body size was also involved in other behavioural responses. Larger species were reported to have greater alert distances (two studies), they moved farther away after being disturbed (one study), and they also moved to less-disturbed areas (one study). Larger bird species used higher landing substrates (one study) and flew higher after fleeing (one study). Other biological factors explaining the interspecific variation in the responses to disturbance included crypsis (two studies), habituation (two studies) and patterns of habitat use (two studies). Results from these studies suggested that conspicuous species tended to move away immediately after disturbance, and had greater flight initiation distances, than cryptic species, which usually stopped feeding and remained still for longer periods of time. Habituation effects were related to the frequency with which different species interacted with humans: migratory species tended to have greater flight initiation distances than resident species. Finally, habitat selection patterns also affected some responses. Species that foraged in the water had greater flight initiation distances than those that used water solely for resting. Forest species that were active relatively close to the ground had greater flight initiation distances than those that used the upper canopy. None of these studies controlled for potential phylogenetic biases.

CONSEQUENCES OF INTERSPECIFIC VARIATION IN RESPONSES TO HUMANS

All factors (and their interactions) were significant, which was not surprising given the large sample size (n = 63 750) of simulated runs. Thus, we focused specifically on interpreting the main effects and interactions that explained greater than 5% of the total variation in our dependent variables.

The combination of pedestrian rate (number of people crossing the park in a given time period) and detection distance (Table 1) explained more than 84% of the variability in the number of food items consumed during the season. These two factors also interacted significantly (Table 1 and Fig. 1) to explain an additional 14% of the variation in the number of food items eaten: when no pedestrians were present, the number of food items consumed did not vary with detection distances. However, at higher pedestrian rates (50–100) there was a decrease in the number of food items consumed with increasing detection distances (Fig. 1).

Variation in the distance from the path to food consumed was mainly explained by pedestrian rate,

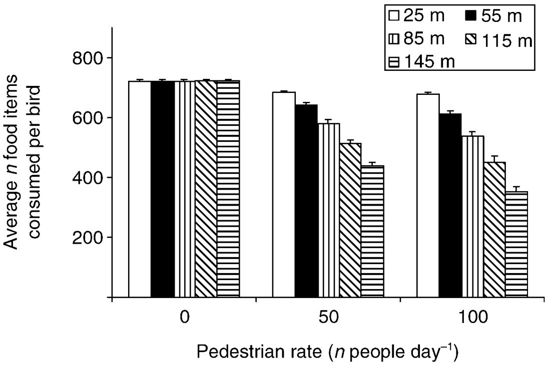

Fig. 1. Effects of number of pedestrians per day and detection distance (different bar shadings indicate detection distances investigated in metres) upon the average number of food items consumed by 10 virtual birds feeding in a 25-ha virtual park during a simulated 180-day non-breeding season. Shown are means ± SD.

Table 1. Results of a fully factorial ANOVA testing for parameters influencing the response of 10 virtual birds feeding in a 25-ha virtual park during a simulated 180-day non-breeding season to patterns of human disturbance. Values are shown for all main parameters and interactions where partial $R^2 > 0·05$

Response variable	Contributing effects	Statistics
Number of food items consumed		
	Pedestrian rate	$F_{2,256} = 7\ 639\ 328$, $P < 0·0001$, $R^2 = 0·58$
	Detection distance	$F_{4,256} = 1\ 678\ 750$, $P < 0·0001$, $R^2 = 0·26$
	Pedestrian rate × detection distance	$F_{8,256} = 455\ 409$, $P < 0·0001$, $R^2 = 0·14$
Distance from path to food consumed (m)		
	Pedestrian rate	$F_{2,256} = 5\ 170\ 603$, $P < 0·0001$, $R^2 = 0·70$
	Detection distance	$F_{4,256} = 605\ 310$, $P < 0·0001$, $R^2 = 0·16$
	Pedestrian rate × detection distance	$F_{8,256} = 185\ 416$, $P < 0·0001$, $R^2 = 0·10$
Number of times pedestrians passed within the detection distance		
	Detection distance	$F_{4,256} = 5\ 208\ 100$, $P < 0·0001$, $R^2 = 0·38$
	Pedestrian rate	$F_{2,256} = 7\ 938\ 948$, $P < 0·0001$, $R^2 = 0·27$
	Pedestrian rate × detection distance	$F_{8,256} = 1\ 724\ 356$, $P < 0·0001$, $R^2 = 0·24$
	Flight initiation distance	$F_{4,256} = 945\ 269$, $P < 0·0001$, $R^2 = 0·07$
Time spent latent		
	Landing distance	$F_{4,256} = 1\ 285\ 807$, $P < 0·0001$, $R^2 = 0·28$
	Pedestrian rate	$F_{2,256} = 1\ 702\ 641$, $P < 0·0001$, $R^2 = 0·19$
	Landing distance × pedestrian rate	$F_{8,256} = 343\ 565$, $P < 0·0001$, $R^2 = 0·15$
	Flight initiation distance	$F_{4,256} = 451\ 463$, $P < 0·0001$, $R^2 = 0·10$
	Landing distance × flight initiation distance	$F_{16,256} = 103\ 593$, $P < 0·0001$, $R^2 = 0·09$
	Flight initiation distance × pedestrian rate	$F_{8,256} = 116\ 539$, $P < 0·0001$, $R^2 = 0·05$

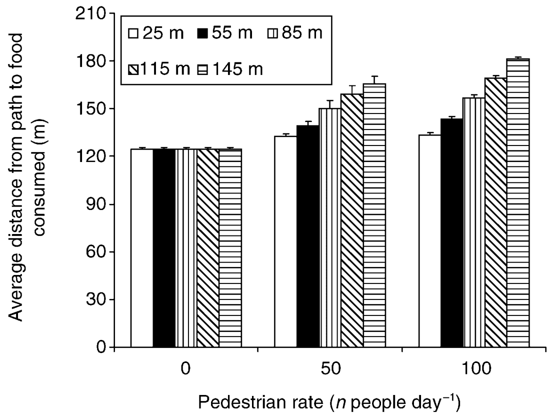

Fig. 2. Effects of number of pedestrians per day and detection distance (different bar shadings indicate detection distances investigated in metres) upon the distance from the pedestrian path to the food items that were consumed by 10 virtual birds feeding in a 25-ha virtual park during a simulated 180-day non-breeding season. Shown are means ± SD.

detection distance and the interaction between them (Table 1). When no pedestrians were present, the virtual birds did not vary the distance from the path to food consumed across the range of simulated detection distances; however, average distance from the path to consumed food increased significantly with higher pedestrian rates and increasing detection distances (Fig. 2).

Variation in the number of times pedestrians passed within the birds' detection distance was mainly accounted for by detection distance and pedestrian rate and their interaction (Table 1). When no pedestrian was present, obviously animals did not become alert (Fig. 3a). An increase in the number of human visits increased the

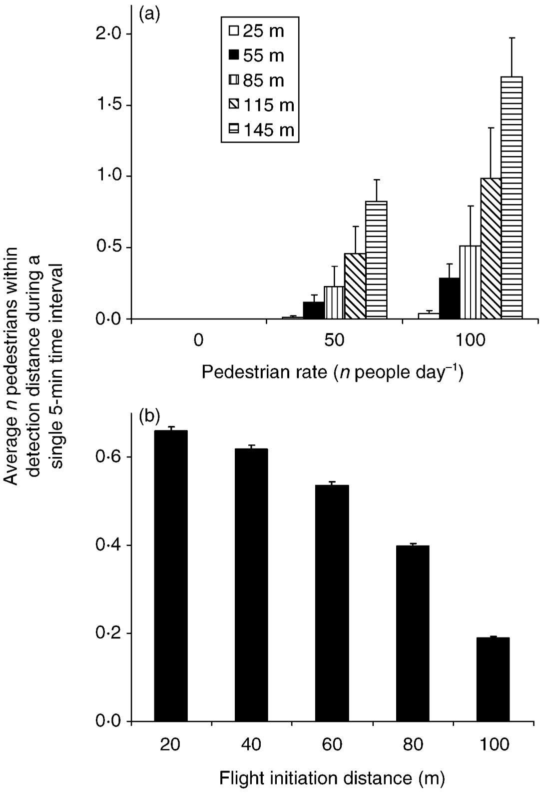

Fig. 3. Effects upon the number of pedestrian encounters per day causing birds to enter alert status for a 5-min time period (during which time they do not forage) by 10 virtual birds feeding in a 25-ha virtual park during a simulated 180-day non-breeding season of (a) number of pedestrians per day and detection distance (different bar shadings indicate detection distances investigated in metres) and (b) flight initiation distance for birds simulated with a detection distance of 115 m as an example. Shown are means ± SD.

frequency of encounters by 46% and this effect was more pronounced in virtual birds with larger detection distances (Fig. 3a). Flight initiation distance also had a minor effect on frequency of encounters (Table 1), with fewer pedestrians passing within the birds' detection distance as flight initiation distance increased (Fig. 3b).

Finally, variation in the time spent latent was mostly explained by (in order of importance): landing distance, the number of pedestrians in a given time period, flight initiation distance and their interactions (Table 1). Virtual birds only spent time latent when pedestrians were present. However, the time spent latent decreased substantially as pedestrians increased from 50 to 100 day^{-1} (Fig. 4a–b). One interpretation of this result is that, as the number of pedestrians increased, virtual birds moved away from the path, thus spending less time in its proximity, and consequently reduced the amount of time spent latent. Greater landing distances reduced the time spent latent because animals moved away from the path more quickly (Fig. 4). There was also an interaction between landing distance and pedestrian rate (Table 1): virtual birds with large flight initiation distances and very small landing distances were scared many times in succession by the same pedestrians, and thus spent a considerable amount of time latent, while virtual birds with very small flight initiation distances and large landing distances fled the path once and were not influenced again by pedestrians.

A COMPARATIVE APPROACH TO PREDICT INTERSPECIFIC RESPONSES

In general, larger bird species responded to approaching humans by showing alert behaviours at significantly greater distances than smaller species (Fig. 5). After explaining variation in alert distance accounted for by starting distance ($P_{\text{raw data}} < 0{\cdot}001$, $P_{\text{contrasts}} < 0{\cdot}001$), body mass did not explain significant variation in alert distance in the analysis of log-transformed species values ($P_{\text{raw data}} = 0{\cdot}061$) according to statistical convention, but did for the analysis of phylogenetically independent contrasts ($P_{\text{contrasts}} = 0{\cdot}006$). Interestingly, there was a significant interaction between body mass and starting distance in the analysis of species values ($P < 0{\cdot}001$) but not in the analysis of independent contrasts ($P = 0{\cdot}734$). Thus, in both analyses, body mass had some effect on alert distance: for a given starting distance, larger birds responded to approaching threats by showing alert behaviours at greater distances than smaller birds. We also noted that alert distance and

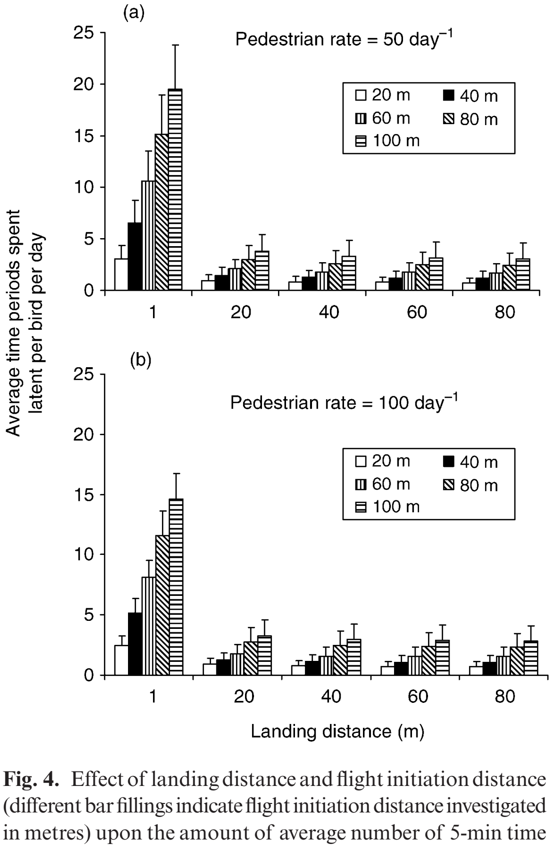

Fig. 4. Effect of landing distance and flight initiation distance (different bar fillings indicate flight initiation distance investigated in metres) upon the amount of average number of 5-min time periods spent latent (i.e. not foraging following flight response) per bird per day by 10 virtual birds feeding in a 25-ha virtual park during a simulated 180-day non-breeding season under two levels of human visitation: (a) 50 pedestrians day^{-1} and (b) 100 pedestrians day^{-1}. Shown are means ± SD.

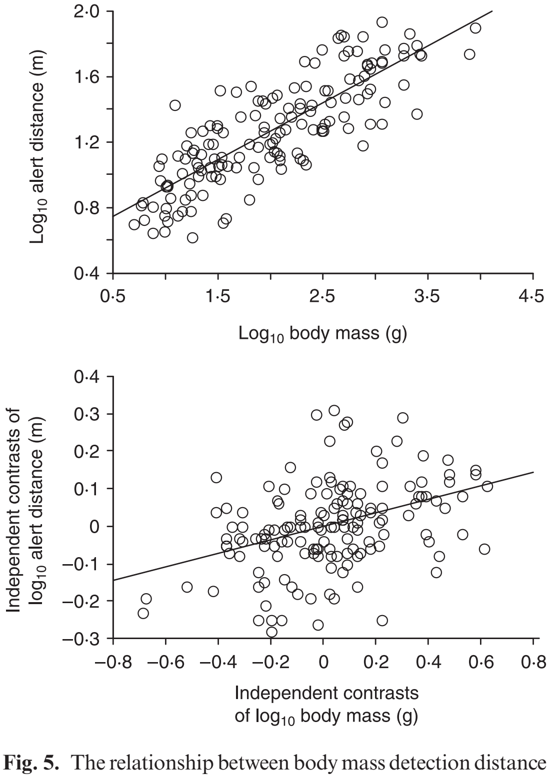

Fig. 5. The relationship between body mass detection distance in (a) log$_{10}$-transformed raw data ($R^2 = 0{\cdot}672$; log$_{10}$ alert distance $= 0{\cdot}574 + 0{\cdot}347 \times$ log$_{10}$ body mass) and (b) phylogenetically independent contrasts ($R^2 = 0{\cdot}156$; contrast of log$_{10}$ alert distance $= 0{\cdot}180 \times$ contrast of log$_{10}$ body mass). After accounting for significant variation explained by starting distance (see text), prediction equations are: log$_{10}$ alert distance = 0·802(log$_{10}$ starting distance) – 0·0435(log$_{10}$ mass) + 0·0714(log$_{10}$ starting distance × log$_{10}$ mass); contrast of log$_{10}$ alert distance = 0·970 (contrast of log$_{10}$ starting distance) + 0·047(contrast of log$_{10}$ mass) + 0·046(contrast of log$_{10}$ starting distance × contrast of log$_{10}$ mass).

flight initiation distance were correlated ($r = 0{\cdot}957$, $n = 150$ species, $P < 0{\cdot}001$).

Discussion

Our literature review detected relatively few studies on human disturbance effects where more than one species was studied simultaneously. The number of model species was relatively small, and most of the studies focused on only one potential indicator of tolerance (flight initiation distance). There is a need for studies that consider the response of many species to human disturbance events. Future comparative studies should use phylogenetically rigorous methods (Blumstein *et al.* 2004), such as independent contrasts, that 'control' for expected similarity between related species (Felsenstein 2004). None the less, because there is variation among species in behavioural responses to human disturbance, we believe that this species-level variation must be considered in management decisions. Our simulation model demonstrated how resource use might be affected by interspecific variation in responses to human disturbance.

Our model showed that detection distance, the frequency of disturbance by humans and the interaction between these two factors are likely to drive most of the variation in important fitness-related response variables such as the number of food items eaten. Such effects would probably be exaggerated if our model also accounted for the fact that disturbance restricts the space available for foraging, thereby increasing interference competition for limited depleting food resources (Stillman *et al.* 2001). Other complexities, such as allowing food reserves to replenish or redistribute themselves in space during the simulation, could have been included but they would not have altered the relative nature of these relationships. The point of this modelling exercise was to define, within the subset of scenarios where patterns of human disturbance do alter foraging success, the relative impacts of the different characteristics of the response of wildlife to human disturbance. Refinements of this simulation into more of a truly individual-based modelling approach represent a potentially fruitful future direction for this research.

Time spent latent was the only response variable that was not primarily driven by detection distance and the number of pedestrians, but was influenced by interactions between landing distance, flight initiation distance and pedestrian rate. Thus time spent latent is likely to be a complex response requiring further study.

It is noteworthy that more complex interaction terms between these predictor variables explained very little (< 5%) of the variation in the response variables apart from time spent latent. This implies that empirical studies focused on complex interactions will be less valuable than studies aimed at understanding how detection distance (or any other relevant biological factor that could be used as a proxy) interacts with the frequency of human disturbance for a variety of species in a variety of settings. Furthermore, conservation managers interested in the interactions between wildlife and human disturbance in specific locations should focus their efforts on these two crucial factors and their interactions. The emphasis on these variables is supported by anecdotal observations, for example red deer *Cervus elaphus* Linnaeus, 1758 are known to use areas of parks that are farther away from paths on days when pedestrian traffic is greater and to forage closer to paths on days when pedestrian traffic is light (Sibbald *et al.* 2001; Gill, Sutherland & Watkinson 1996). Finally, our simulation model demonstrates that human disturbance can dramatically reduce food consumption by wildlife foraging within a park setting, and thus disturbance might reduce fitness.

Our comparative study demonstrated that alert distance (a proxy for detection distance) is influenced by body size: larger birds have greater alert distances than smaller birds. Furthermore, alert distance and flight initiation distance are highly correlated. This may be because larger birds are more conspicuous than smaller birds and therefore less likely to depend on crypsis. If large-bodied species are less agile than smaller-bodied species (Marden 1987; Witter, Cuthill & Bonser 1994) they would benefit from early response and flight to escape predators. Thus, for any given risk, large-bodied species may be more wary (Fig. 5; Fernández-Juricic & Schroeder 2003). If large-bodied species have a lower cost of flight than small-bodied species, then we might expect them to fly away at greater distances (Ydenberg & Dill 1986). It is conceivable that small-bodied species must allocate proportionally more time to foraging than larger-bodied species because of their relatively greater energy requirements (Bennett & Harvey 1987). If so, then small species that are disturbed would tolerate a greater risk before flight. If available energy varies seasonally, the cost of responding to disturbance may also vary seasonally (Stillman & Goss-Custard 2002). Thus, birds of a given body size might seem more tolerant of humans during the winter when the cost of flight is higher. Therefore, in multispecies management scenarios, it is important to consider not only interspecific differences in responses to disturbance but also seasonal differences.

Body size may also be related to detection distance because the ability to detect a given disturbance visually is likely to covary with known interspecific variations in visual systems. One recent study reported that alert distance was affected by body size (Fernández-Juricic, Jimenez & Lucas 2001a) but a more comprehensive phylogenetic analysis of a larger data set found no such relationship (Blumstein *et al.* 2004). None the less, the amount of interspecific variation requires explanation and our simulation results suggest that detection distance should have a large effect on tolerance and habitat use.

Body size could also explain interspecific variation in post-disturbance responses (Lima 1993). First, small-bodied species with high metabolic rates may be unable to tolerate long periods of time spent without foraging (Suarez & Gass 2002) and thus will resume foraging relatively quickly following disturbance. Secondly, larger species may move further following disturbance. A study of ground-foraging birds found that larger species tended to land further away and in higher ground vegetation than smaller species after being disturbed by humans (Fernández-Juricic, Jimenez & Lucas 2002). Another study, examining post-disturbance responses of species perching in trees, found that large species landed further away than small species (Fernández-Juricic *et al*. 2003). Although these studies are not conclusive, they underscore the role of body size as a potential predictor of specific responses to human disturbance.

The interspecific variation in tolerance to human disturbance based upon body size could have important management implications. The same amount of human disturbance may affect species of different body sizes in different ways by differentially influencing detection abilities, flight initiation distance and post-disturbance behaviour. Large species are predicted to have greater detection distances, greater flight initiation distances and to move further following disturbance. Note that the simulation results demonstrated that wildlife species with these characteristics may obtain less food than smaller species during the course of a non-breeding season as a direct result of human disturbance.

We also expect larger species to have more spatial and temporal limitations on suitable habitat if tourists visit most of the suitable area available for wildlife in a protected area. For instance, if the management targets include the protection of relatively large species it would be advisable to reduce the frequency of human–wildlife interactions by reducing the percentage of the habitat open to visitors. If relatively small species are more important, the frequency of human–wildlife interactions may be reduced by advising tourists to walk in larger groups but without necessarily restricting the spatial extent of the visit, because smaller species might in general be less disturbed by human presence. Buffer areas may be a useful management tool for large species, whereas small species are likely to be more resilient to human disturbance.

SYNTHESIS AND APPLICATIONS

We suggest that three things are essential to develop predictive models of how different species will respond to human disturbance. First, multiple indicators of disturbance should be studied to select those with lower intraspecific variation for a given study system. Secondly, the species-specific nature of responses should be identified. Thirdly, life history, natural history and other correlates with these species-specific responses must be assessed.

In any disturbance study, it is important to include several variables that reflect different stages involved in the disturbance process: (i) detection of disturbance (e.g. alert or detection distance); (ii) tolerance to the disturbance before vacating the patch (e.g. flight initiation distance); (iii) spatial displacement (e.g. landing distance); and (iv) temporal displacement (e.g. time to resume pre-disturbance activities). These measures may be highly correlated (e.g. as alert distance is with flight initiation distance) and in some cases variables can serve as surrogates for each other.

It is also important to study behavioural responses under different disturbance conditions. For example, humans should approach directly and tangentially, alone and in groups, and there should be different intervals between disturbances. Different types of human disturbance (e.g. people alone or with dogs, bikers vs. pedestrians) should also be included. Such a comprehensive approach is necessary to predict how different species will respond to different human visitation levels (Fernández-Juricic 2002).

It is essential to understand how these response traits vary among species. Some measures have higher degrees of intraspecific variation than others (e.g. flight initiation distance in relation to alert distance, Fernández-Juricic, Jimenez & Lucas 2001b), which could affect comparative analyses. Thus it is important to select response traits that enhance our ability to estimate species-specific traits. For instance, we found evidence for interspecific variation in alert distances and reviewed studies on interspecific variation in flight initiation distance and landing distance. Identifying variation associated with these species-specific traits will improve our ability to predict species' responses to human disturbance.

It is also essential to identify life history, natural history and other correlates of measures of disturbance that may allow us to predict species' vulnerability. One example is the relationship between body size and a species' response to human disturbance. Other traits (e.g. diet, developmental mode, migration, parental care, brain size) might also influence predation hazard assessment (Lima & Dill 1990) and should be considered in the context of human disturbance (D. T. Blumstein, in press).

In summary, by incorporating this comparative approach into the intraspecific framework presented by Frid & Dill (2002), we generated testable management predictions about body size that can help managers understand and regulate human visitation in ways that can promote coexistence.

Acknowledgements

We thank L. Anthony, L. Antolin, Y. Attia, Y. Cárdenas, J. Craanen, J. Daniel, M. Edgerton, R. Fernandez, C. Geist, K. Gilmour, L. Ikuta, C. Konig, E. Larsen, O. LeDee, J. Liao, S. Libby, C. Madrileo, T. Morgan, N. Murillo, B. Shen, S. Robertson, I. Rodriguez-Prieto, C. Zugmeyer, L. Zung, T. Morgan and Y. Attia for help collecting and processing data. Research protocols were approved by the Macquarie University Animal Research Committee (99021), the Rocky Mountain Biological

Laboratory AND the UCLA Animal Research Committee (2000-147-01). Field research permits were issued by Booderee National Park (BDR03/00012), the California Department of Fish and Game, the New South Wales National Parks and Wildlife Service (A2712), Orange County Harbor Beaches and Parks, the US Fish and Wildlife Service (32154), the Parks and Wildlife Service of Tasmania (FA 00060), Seal Beach National Wildlife Refuge, the US National Parks Service (SAMO-2001-SCI-0004), the University of California Natural Reserve System and the Queensland Parks and Wildlife Service (FA/000379/00/SA). Support for this project to D. T. Blumstein came from Macquarie University (2001 Research Discovery Scheme grant with R. Harcourt), the University of California Los Angeles Division of Life Sciences, The Lida Scott Brown Ornithology Trust, the University of California Los Angeles Office of Instructional Development and The University of California Los Angeles Council on Research. E. Fernández-Juricic acknowledges the support of the College of Natural Sciences and the Department of Biological Sciences at California State University Long Beach. P. A. Zollner thanks the landscape ecology project (4153) of the North Central Research Station for support. We thank E. J. Gustafson, L. Dill, two very constructive referees and a remarkably helpful editorial team for comments on previous versions of this manuscript.

Supplementary material

The following supplementary material is available online:

Appendix. Summary of studies that simultaneously studied human disturbance in more than a single species.

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Received 7 October 2004; final copy received 12 May 2005
Editor: Steve Rushton