Alert distance as an alternative measure of bird tolerance to human disturbance: implications for park design

ESTEBAN FERNÁNDEZ-JURICIC¹*, MARÍA DOLORES JIMENEZ² AND ELENA LUCAS¹

¹ Depto de Biología Animal I, Facultad de Biología, Universidad Complutense de Madrid, Madrid, E-28040, Spain, and ² Centro de Investigaciones Ambientales de la Comunidad de Madrid 'Fernando Gonzalez Bernaldez', C/ San Sebastián, 17, 28791 Soto del Real, Madrid, Spain Date submitted: 17 November 2000 Date accepted 3 May 2001

Summary

Animal tolerance to human approaches may be used to establish buffers for wildlife that can minimize the probability that animals will be disturbed by human activity. Alert distance (the distance between an animal and an approaching human at which point the animal begins to exhibit alert behaviours to the human) has been proposed as an indicator of tolerance mainly for waterbirds; however, little is known about its utility for other bird species. The factors that influenced alert distances of four bird species to pedestrian approaches in five large wooded fragments in the city of Madrid (Spain) were analysed. Location of human activity affected only Passer domesticus alert distances, which increased in the proximity of pathways. Habitat structure modified alert distances of all the species (Passer domesticus, Turdus merula, Columba palumbus, and *Pica pica*), increasing bird tolerance with greater availability of escape cover (shrub and coniferous cover, and shrub height). Alert distances varied among species, with large species being less tolerant of human disturbance than small ones. Alert distance appears to be a more conservative indicator of tolerance than flight distances, because it includes a buffer zone (the difference between alert and flight distance) in which birds may adapt their reaction to the behaviour of visitors. Alert distance may be used in the determination of minimum approaching areas, allowing people to enjoy their visit to parks, and birds to use patches for foraging and breeding without being displaced.

Keymords: alert distance, bird tolerance, flight distance, human disturbance, park design

Introduction

Nowadays, many natural areas surrounded by human-modified landscapes serve not only as refuges for wildlife, but also as places for outdoor recreational activities. Even though some species are not affected by the presence of humans, there exist some concerns as to how the levels of human

recreation may affect the distribution and behaviour of wildlife (Boyle & Samson 1985; Boo 1990; Hill et al. 1997). At the individual level, disturbance from human activity may modify bird foraging behaviour (Burger & Gochfeld 1998; Fernández-Juricic & Tellería 2000), patch selection (Fernández-Juricic 2000a, b), and reproduction (Giese 1996). The effects of human disturbance at the population level should be evaluated in terms of the availability of alternative habitats and the fitness costs for the target species before stressing the species that deserve greater conservation concern (Gill et al. 2001). When human activity negatively affects bird populations, it may be necessary to consider appropriate indicators of tolerance, which would allow adjustments in minimum approaching distances in natural areas in relation to species' sensitivity to disturbance (Rodgers & Smith 1995, 1997).

Certain behavioural responses to human disturbance can be used to estimate tolerance, which can then guide management of natural areas at local and regional scales (Gill & Sutherland 2000). In this sense, the reaction of birds to pedestrians can be equated to the perceived threat of predation from humans (Lima & Dill 1990; Gill et al. 1996; Fox & Madsen 1997). Upon encountering pedestrians, birds usually increase the time devoted to vigilance and diminish feeding rates (Burger & Gochfeld 1998; Fernández-Juricic & Tellería 2000) or respond by fleeing (Gutzwiller et al. 1998; Miller et al. 1998). Generally, flight distances (the distance between an animal and an approaching human at which point the individual escapes from a visitor) have been used as a measure of bird tolerance (the larger the flight distance, the lower the tolerance; Burger & Gochfield 1991), and to determine minimum approaching distances, namely the minimal distance that a pedestrian may approach a bird before it is disturbed (Knight & Knight 1984; Rodgers & Smith 1995, 1997; Fox & Madsen 1997).

However, when used as a criteria to set up minimum approaching distances, flight distance may not be a good indicator of tolerance, since it may be greatly affected by other factors (Gill *et al.* 2001), and it may fail to decrease disturbance because it does not include a buffer area in which birds adapt their response to visitors. This may be the case for forest birds in highly visited areas, where people often diverge from pathways set for visitors. Rodgers and Smith (1997) have suggested that besides flight distances, alert distances (the distance between an animal and an

^{*}Correspondence: Dr Esteban Fernández-Juricic, Department of Zoology, Oxford University, Oxford OX1 3PS, UK e-mail: estebanfj@yahoo.com

approaching human at which point the animal begins to exhibit alert behaviours to the human) should also be evaluated in the determination of minimum approaching distances to obtain more conservative estimates of tolerance. Much of the research on bird tolerance to human disturbance has been devoted to waterbirds (Fox & Madsen 1997; Carney & Sydeman 1999), and there is comparatively little empirical evidence indicating whether alert distances of forest birds differ between species in relation to social and environmental factors (but see Riffell *et al.* 1996; Gutzwiller *et al.* 1998).

The goal of this paper is to evaluate alert distances of four differently-sized species relative to social factors (number of conspecifics and heterospecifics), location of human activity and cover (distance from pathway and to cover), and habitat structure (grass, shrub and tree cover, shrub and tree height). We also discuss the implications of employing alert distance as a measure of bird tolerance for park design. A previous study in this landscape showed inter-specific differences in flight distances in relation to species size and habitat structure (Fernández-Juricic et al. 2001). It may be expected that the number of conspecifics and heterospecifics in foraging flocks would reduce bird tolerance due to early warning (Ydenberg & Dill 1986), increasing alert distances (Knight & Cole 1995). Alert distance would diminish near cover, but would increase near pathways due to the proximity of disturbance (Hill et al. 1997; Fernández-Juricic & Tellería 2000). More complex habitat structure (higher vegetation cover and height) is expected to reduce alert distance as birds would have more available cover to hide from visitors (Knight & Temple 1995). Finally, controlling for the aforementioned factors, inter-specific differences in alert distances may be expected; for instance, large species should be less tolerant (larger alert distances) than small ones (Cooke 1980; Humphrey et al. 1987; Holmes et al. 1993).

Methods

Study area and species

The study was conducted from May to July 1998 in five large wooded parks of Madrid, Spain (40.25 N; 03.43 W): Retiro (110 ha), Oeste (98 ha), Sur (29 ha), Dehesa de la Villa (25 ha), and Moro (18 ha). All parks had a high tree cover composed of a mix of deciduous and coniferous trees. The most common deciduous trees were *Populus* sp., *Platanus hybrida*, *Ulmus campestris*, and *Acer negundo*; coniferous tree species included mainly *Cedrus* sp., *Pinus* sp., and *Abies alba* (Bernis 1988). The parks also had areas of short irrigated grass, and shrubs, which included introduced and native species, such as *Ligustrum* sp., *Buxus* sp., *Viburnum* sp., and *Rubus* sp.

About 24 species of birds with different food and nesting requirements inhabit these parks (Fernández-Juricic 2000c). We selected four species, House Sparrow (*Passer domesticus*), Blackbird (*Turdus merula*), Woodpigeon (*Columba palumbus*), and Magpie (*Pica pica*) as representative model species. Following Cooke (1980), we used total length as an indicator of species size: House Sparrow (15 cm), Blackbird (24–25 cm), Woodpigeon (40–42 cm), and Magpie (44–48 cm) (Tellería *et al.* 1999).

Alert distances

Data were gathered between 0730 and 1800 hours, totalling 417 observation hours, on sunny or cloudy days, but never when raining or on windy days. Temperatures varied from 11°C to 32°C, but such variations did not affect alert distances of any species (Pearson product moment correlation; House Sparrows, r = 0.12, p = 0.19, power = 0.87; Blackbirds, r = 0.11, p = 0.18, power = 0.85; Woodpigeons, r = 0.07, p= 0.41, power = 0.78; Magpies, r = 0.16, p = 0.11, power =0.92; G-POWER, Version 2.0). Two observers (María Dolores Jimenez and Elena Lucas) gathered all the data. They were previously trained for three weeks in approaching birds in a 20-ha park not included in this study, to avoid conditioning birds in our five study sites. The order in which parks were visited was assigned randomly, with at most two parks per day and at least one-day interval between visits that had to be conducted in the same park. All data were gathered during weekdays.

In a preliminary study, we found that alert behaviours of the four species could be determined by an observer from at least 35 ± 1.6 m, nearly twice the greatest alert distance registered (Fig. 1). Therefore, we began our approaches from about 35 m away from the individuals upon which alert distances were recorded (focal individuals). We defined alert distance as the distance at which an individual raised its head up from the ground and moved it as if scanning (the bird's long axis was perpendicular to the ground; Slotow & Rothstein 1995; Fernández-Juricic & Tellería 2000) in response to an approaching visitor. Distance estimations (\pm 0.5 m) were based on measured paces, and controlled with a metre tape (Fernández-Juricic *et al.* 2001). We collected 25



Figure 1 Mean (\pm SE) alert and flight distances for four bird species in five parks in the city of Madrid (n = 125 samples per species). Species are ordered in relation to overall body length: house sparrow (15 cm), blackbird (24–25 cm), woodpigeon (40–42 cm), and magpie (44–48 cm). Flight distance data from Fernández-Juricic *et al.* (2001).

observations per species per park. For each species and park, observations were gathered from different locations in order to avoid disturbing the same individual more than once. Locations within parks were randomly selected. The observers never collected two observations from the same species consecutively from contiguous areas to circumvent any correlation between approaches.

Individual birds to be approached were selected following these criteria: no other person was within 30 m of the focal individual, the bird was not feeding (although it could be searching for food), and it did not show any type of alert behaviour before the approach. All individuals approached were on the ground, and we excluded birds looking for nest material. When the observer approached a group of birds, they focused on a single individual within the group chosen before the approach. Prior to the approach, the observer recorded the number of individuals of the same and different species around the focal bird in a 15-m radius circular plot as well as the distance of the focal individual to the nearest pathway and to the nearest cover (shrub or tree; Table 1). A focal individual was approached by a single observer at a steady speed (1 step/sec). During approaches, observers always wore light blue jeans and grey shirts to avoid differential bird reaction (Gutzwiller & Marcum 1997). The approach was linear without vegetation preventing the observer and bird seeing each other. Once the focal individual flew away, the observer continued up to the bird's original position, from which the following microhabitat variables were recorded in 25-m circular plots: grass cover (%), shrub cover (%), shrub height (m), coniferous cover (%), deciduous cover (%), and tree height (m) (Table 1). Cover variables corresponded to different vegetation substrates, and were estimated visually following Prodon and Lebreton (1981).

Statistical analyses

Alert distances for each species did not differ between parks (ANOVA, House Sparrow, $F_{4,120} = 2.1$, p = 0.08, power= 0.92; Blackbird, $F_{4,120} = 1.55$, p = 0.19, power = 0.79; Woodpigeon, $F_{4,120} = 0.5$, p = 0.73, power = 0.81; Magpie, $F_{4,120} = 0.89$, p = 0.47, power = 0.87). Therefore, we

combined the data for all five parks to analyse the influence of the different factors (number of conspecifics and heterospecifics, location of human activity and cover, grass cover, shrub cover, shrub height, coniferous cover, deciduous cover, and tree height) on alert distances of each species. This procedure allowed us to test a wide range of social and structural conditions for which alert distances were recorded. A multiple regression analysis with forward stepwise selection procedures (p-value = 0.05) was used to identify the most significant factors, but controlling for their covariation (Nicholls 1989). The power of the tests varied from 92 to 84% (p = 0.05) with two and six factors per test, respectively; but when considering ten factors at the same time, power dropped to 65%. We then decided to test each set of factors (number of conspecifics and heterospecifics, location of human activity and cover, and the six habitat variables) separately to avoid a detrimental reduction in the power of each test. Consequently, tests were not completely independent, since the same dependent variable was employed three times per each species. We report the power of each test conducted; that is, the probability of rejecting an incorrect null hypothesis (Underwood 1997).

An ANCOVA test was employed to analyse inter-specific differences in alert distances in the five parks studied. Those factors previously identified as influencing alert distances were included as covariates to control for their effects on tolerance levels. Finally, we compared alert distances to previous estimations of flight distances (Fernández-Juricic *et al.* 2001) by means of an ANOVA test, to determine if these measures of tolerance differed significantly. We checked for normality and homoscedasticity of variables and of residuals before and after the analyses, respectively. Some variables were transformed with logarithmic (number of conspecifics, distance from pathway, distance to cover, shrub height) and arcsine (grass and shrub cover) transformations to meet normality assumptions. All statistical analyses were conducted with STATISTICA 5.5.

Results

Magpies and Woodpigeons' alert distances were greater than House Sparrows', with Blackbirds having intermediate

Table 1 Mean and range (minimum-maximum) of the ten independent factors included in the analyses.

Factors	House Sparrow	Blackbird	Woodpigeon	Magpie
Number of conspecifics	2.70 (1-27)	1.53 (1-11)	1.88 (1-8)	1.47 (1-6)
Number of heterospecifcs	0.37 (0-14)	0.46 (0-6)	0.43 (0-12)	0.49 (0-28)
Distance from pathway (m)	3.31 (0-30)	5.41 (0-25)	6.00 (0-30)	5.72 (0-30)
Distance to cover (m)	3.23 (0-12)	3.13 (0-11)	4.35 (0-20)	3.94 (0.2–17)
Grass cover (%)	53.94 (5-100)	66.29 (5-100)	65.34 (0-100)	69.68 (3-100)
Shrub cover (%)	10.49 (0-78)	12.75 (0-70)	10.50 (0-60)	10.41 (0-60)
Shrub height (m)	1.86 (0-6)	2.09 (0-8)	3.42 (0-16)	1.80(0-5)
Deciduous cover (%)	29.90 (0-95)	33.70 (0-99)	21.89 (0-95)	30.08 (0-95)
Coniferous cover (%)	26.96 (0-95)	24.58 (0-95)	26.27 (0-95)	26.66 (0-95)
Tree height (m)	9.58 (4-18)	9.84 (4-16)	8.77 (0-20)	9.90 (1-20)

Table 2 Relationship between alert distances and number of conspecifics (# Consp) and heterospecifics (# Heterosp). Results from multiple stepwise regressions. Shown in parentheses is the direction of the relationship for individual factors. NI = variable not included into the model because its contribution to R^2 was less than 1%.

	# Consp	# Heterosp
House Sparrow	NI	$R^2 = 0.01, (+), p = 0.27$
Blackbird	NI	NI
Woodpigeon	NI	$R^2 = 0.02, (+), p = 0.17$
Magpie	NI	NI

values (Fig. 1). Neither the number of conspecifics nor the number of heterospecifics was related to alert distances in any of the four species (Multiple regression models; House Sparrow, $F_{(2,123)} = 1.2$, $R^2 = 0.01$, p = 0.27, power = 0.50; Woodpigeon, $F_{(2,123)} = 1.9$, $R^2 = 0.02$, p = 0.17, power = 0.59; Table 2). Distance to cover was not associated with alert distances (Table 3); however, distance from pathway was negatively related to House Sparrow alert distance (Multiple regression models; House Sparrow, $F_{(2,122)} = 5.4$, $R^2 = 0.05$, p = 0.02, power = 0.72; Blackbird, $F_{(2,122)}^{(2,122)} = 1.2$, $R^2 = 0.01$, p = 0.27, power = 0.48; Woodpigeon, $F_{(2,123)} = 3.3$, $R^2 =$ 0.03, p = 0.07, power = 0.56; Magpie, $F_{(2,120)}^{(2,120)} = 2.04$, $R^2 =$ 0.03, p = 0.14, power = 0.48; Table 3). All vegetation structure factors but one, namely deciduous cover, were significantly associated with alert distances (Multiple regression models; House Sparrow, $F_{(2.117)} = 5.9$, $R^2 = 0.10$, p = 0.004, power = 0.91; Blackbird, $F_{(4,116)}^{(4,117)}$ = 9.4, R^2 = 0.25, p < 0.001, power = 0.99; Woodpigeon, $F_{(4,112)}$ = 9.9, R^2 = 0.26, p < 0.001, power = 0.99; Magpie, $F_{(3,117)} = 17.3$, $R^2 = 0.31$, p< 0.001, power= 0.99; Table 4). Increased alert distances of Woodpigeons and Magpies were associated with increased grass cover (Table 4). Reduced alert distances of Blackbirds and Woodpigeons were related to increased shrub and coniferous cover whereas shrub height was negatively related to alert distances of the four species (Table 4). Increased alert distances of House Sparrows, Blackbirds, and Magpies were associated with greater tree height (Table 4).

Controlling for the covariation of habitat structure (grass, shrub and coniferous cover, and shrub and tree height) and distance from pathway, alert distances varied significantly among species (ANCOVA test, $F_{(3.472)} = 27.27$, p < 0.001,

Table 3 Relationship between alert distances and distance from pathway (DP) and distance to cover (DC). Results from multiple stepwise regressions. Shown in parentheses is the direction of the relationship for individual factors. NI = variable not included into the model because its contribution to R^2 was less than 1%.

	DP	DC
House Sparrow	$R^2 = 0.05, (-), p = 0.02$	NI
Blackbird	NI	$R^2 = 0.01, (+), p = 0.27$
Woodpigeon	NI	$R^2 = 0.03, (+), p = 0.07$
Magpie	$R^2 = 0.02, (-), p = 0.08$	$R^2 = 0.01, (+), p = 0.31$

power = 0.99), being greater in the large species (Fig. 1). On the average, alert distances of the four species were 1.5 times higher than previous estimates of flight distances in the same parks (ANOVA, $F_{(3,92)} = 3.18$, p < 0.05, power = 0.96; Fig. 1).

Discussion

Alert distances for the four species studied show interspecific differences, may be modified by vegetation structure and the proximity of human activity, and differ significantly from flight distances measured for the same species in the same parks.

No relationship was found between the number of individuals (conspecifics or heterospecifics) and alert distances, which suggests that bird tolerance is similar irrespective of the benefits of foraging aggregations (e.g. increasing probabilities of predator detection, dilution effect; Roberts 1996; Beauchamp 1998). This lack of social effects on alert distances may stem from the large area (15 m-radius circular plots) in which measurements of the number of conspecifics and heterospecifics were made, which may have overestimated the number of individuals that form flocks. Hence, we may have failed to determine correctly the size of flocks. Furthermore, the low power of the tests may have resulted in a failure to observe a social effect (Table 2). The low power itself might be due to a low sample size of experimental approaches in which there were conspecifics or heterospecifics present.

The location of human activity affected only one species, House Sparrow, which increased alert distances in the proximity of pathways. This is an expected outcome as birds

Table 4 Relationship between alert distances and habitat structure factors (grass, shrub, deciduous and coniferous cover, shrub and tree height). Results from multiple stepwise regressions. Shown in parentheses is the direction of the relationship for individual factors. NI = variable not included into the model because its contribution to R^2 was less than 1%.

	House Sparrow	Blackbird	Woodpigeon	Magpie
Grass cover	NI	NI	$R^2 = 0.04, (+), p = 0.03$	$R^2 = 0.03, (+), p = 0.02$
Shrub cover	NI	$R^2 = 0.04, (-), p = 0.04$	$R^2 = 0.03, (-), p = 0.03$	NI
Shrub height	$R^2 = 0.05, (-), p = 0.03$	$R^2 = 0.15, (-), p < 0.001$	$R^2 = 0.16, (-), p < 0.001$	$R^2 = 0.14, (-), p < 0.001$
Deciduous cover	NI	NI	NI	NI
Coniferous cover	NI	$R^2 = 0.03, (-), p = 0.03$	$R^2 = 0.03, (-), p = 0.03$	NI
Tree height	$R^2 = 0.05, (+), p = 0.01$	$R^2 = 0.03, (+), p = 0.04$	NI	$R^2 = 0.14, (+), p < 0.001$

become more wary and less tolerant when feeding near areas in which human activity (and therefore potential disturbance) is greater (Fernández-Juricic & Tellería 2000).

The reaction of birds towards visitors is also modified by habitat structure; however, these results should be taken with care because the amount of variance explained was rather small (10-26%). Birds appear to modify their alert distances according to the availability of cover, as has been found for other species (Henson & Grant 1991; Skagen et al. 1991). The positive association of grass cover and Woodpigeon and Magpie alert distances may have to do with the perceived probability of detection by predators, which increases in open spaces where grass cover is higher than that of other substrates, such as shrub and tree (Lima & Dill 1990). Shrub and coniferous cover increases Blackbird and Woodpigeon tolerance of people, as does shrub height with Magpies, probably as a result of a higher availability of cover and consequently a lower perceived risk of predation (Ydenberg & Dill 1986; Martín & López 1995; Kramer & Bonenfant 1997), encouraging individuals to remain when people approach (Knight & Temple 1995). Finally, tree height increases the alert distances of House Sparrows, Blackbirds and Magpies. This may result from an increased perceived risk of predation (Ydenberg & Dill 1986), since individuals would need to fly longer distances to reach tree canopy, their preferred cover in which to hide from predators.

Larger species (Magpie and Woodpigeon) appear to be less tolerant (higher alert distances) to human approaches (Fig. 1). Although other studies found similar results (Cooke 1980; Humphrey et al. 1987; Skagen et al. 1991; Holmes et al. 1993; but see Gutzwiller et al. 1998), there is no clear explanation for this pattern. For raptors, it has been suggested that small species have higher energy expenditure than large ones due to greater area/body mass ratios, so small species are expected to be more tolerant of people to diminish energy costs associated with fleeing (Holmes et al. 1993). An alternative explanation is that larger species may have higher perceptual ranges (the ability to perceive landscape elements; Lima & Zollner 1996) than smaller ones (Kiltie 2000). This may be related to the increased visual acuity of larger species (Kiltie 2000), which would enable individuals to detect and react to human approaches at greater distances.

A recent study suggests that the reaction of bird populations to human approaches may depend on the availability of alternative habitats and the associated fitness costs (Gill *et al.* 2001). Therefore, differences in the behavioural responses of populations may be greatly affected by the benefits to the individual of responding by fleeing and the costs of not responding in that way (Gill *et al.* 2001). However, we think that such costs and benefits may not have a foremost influence on the distances at which birds become aware of the presence of pedestrians, because alert distances may be related to the probabilities of detecting a pedestrian approach, and, as a result, to the visual field of a species (Martin & Katzir 1994) and its visual acuity (Kiltie 2000).

Conservation implications

Wildlife conservation in urban areas is increasingly important because of its influence on urban dwellers' decisions on environmental issues at local and regional scales, not to mention its role in providing habitat for wildlife in an increasingly urbanized landscape (Michelson 1970; Katcher & Wilkins 1993; Vandruff et al. 1995; Fernández-Juricic & Jokimäki 2001). Many of the patches of native vegetation left by increasing urban sprawl have become refuges for bird species (Davis & Glick 1978; Soulé et al. 1988; Crooks & Soulé 1999; Cam et al. 2000). Hence, management of these wooded fragments is an important step towards the persistence of wildlife (Jokimäki 1999). The four studied species are suitable for modelling management strategies aimed at improving urban bird conservation. The goal of such strategies should be to allow people to enjoy urban parks (strolling, jogging, dogwalking, bird-watching, etc.) while maintaining bird diversity (Fernández-Juricic & Jokimäki 2001). The following recommendations apply mainly to ground foraging birds. First, alert distances can be a conservative indicator of bird tolerance to specific situations. Second, habitat complexity could increase tolerance levels of bird species by increasing the availability of cover to be used as refuges from disturbance, thereby decreasing the perceived risk of predation. Third, minimum approaching distances can be estimated from alert distances, and implemented to reduce human-wildlife conflicts. Fourth, because large species appear to be less tolerant of human approach than smaller species, the implementation of minimum approaching distances based on large species would allow smaller ones to use patches for feeding and breeding largely without being disturbed.

From a conservation perspective, a significant difference between alert and flight distances underscores the need to consider alert distance as a more conservative indicator of tolerance (Rodgers & Smith 1995), because it includes a buffer zone (the difference between alert and flight distance) in which birds may adapt their reaction to the behaviour of visitors. Minimum approaching areas can then be calculated by taking alert distances (AD) as the radius of a circle: $\Pi \times AD^2$ (van der Meer 1985; Fox & Madsen 1997). The resultant area could then be used to design the size of resource patches surrounded by pathways, which may lead the movement of pedestrians with minimal disturbance to birds.

Can the results of this study be applied to other landscapes? Obviously, the estimation of alert distances can only be used for conservation purposes in relation to the four species studied in this landscape. However, based on these results, we encourage the application of alert distances in other natural areas. Alert distances can be used to design footpaths for visitors with enough undisturbed areas for birds to forage and breed and for pedestrians to enjoy their visit.

Acknowledgements

We thank Jennifer Gill, Jean-Pierre Savard, Dave Dawson, Radha Nair, and an anonymous referee for their comments and suggestions, and Cesar Luis Alonso for fruitful discussions about human disturbance. Esteban Fernández-Juricic was funded by the Agencia Española de Cooperación Internacional (MUTIS Fellowship), la Caixa Foundation, and Consejo Nacional de Investigaciones Científicas y Técnicas.

References

- Beauchamp, G. (1998) The effect of group size on mean food intake rate in birds. *Biological Review* 73: 449–472.
- Boo, E. (1990) *Ecotourism: the Potentials and Pitfalls.*. Washington, DC, USA: World Wildlife Fund.
- Boyle, S.A. & Samson, F.B. (1985) Effects of nonconsumptive recreation on wildlife: a review. *Wildlife Society Bulletin* 13: 110–116.
- Burger, J. & Gochfield, M. (1991) Human distance and birds: tolerance and response distances of resident and migrant species in India. *Environmental Conservation* 18: 158–165.
- Burger, J. & Gochfield, M. (1998) Effects of ecotourists on bird behaviour at Loxahatchee National Wildlife Refuge, Florida. *Environmental Conservation* 25: 13–21.
- Cam, E., Nichols, J.D., Sauer, J.R., Hines, J.E. & Flather, C.H. (2000) Relative species richness and community completeness: birds and urbanization in the Mid-Atlantic States. *Ecological Applications* 10: 1196–1210.
- Carney, K.M. & Sydeman, W.J. (1999) A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds* 22: 68–79.
- Cooke, A.S. (1980) Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. *Biological Conservation* 18: 85–88.
- Crooks, K.R. & Soulé, M.E. (1999) Mesopredator release and avifaunal extinction in a fragmented system. *Nature* 400: 563–566.
- Davis, A.M. & Glick, T.F. (1978) Urban ecosystems and island biogeography. *Environmental Conservation* 5: 299–304.
- Fernández-Juricic, E. (2000a) Avifaunal use of wooded streets in an urban landscape. *Conservation Biology* 14: 513–521.
- Fernández-Juricic, E. (2000b) Local and regional effects of human disturbance in a fragmented landscape. *Condor* 102: 247–255.
- Fernández-Juricic, E. (2000c) Bird community composition patterns in urban parks of Madrid: the role of age, size and isolation. *Ecological Research* 15: 373–383.
- Fernández-Juricic, E. & Tellería, J.L. (2000) Effects of human disturbance on Blackbird *Turdus merula* spatial and temporal feeding patterns in urban parks of Madrid, Spain. *Bird Study* 47: 13–21.
- Fernández-Juricic, E. & Jokimäki, J. (2001) A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. *Biodiversity and Conservation*, in press.
- Fernández-Juricic, E., Jimenez, M.D. & Lucas, E. (2001) Bird tolerance to human disturbance in urban parks of Madrid (Spain). Management implications. In: Avian Ecology and Conservation in an Urbanizing World, ed. J.M. Marzluff, R. Bowman & R.

Donnelly. Dordrecht, the Netherlands: Kluwer Academic Press, in press.

- Fox, A.D. & Madsen, J. (1997) Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. *Journal of Applied Ecology* 34: 1–13.
- Giese, M. (1996) Effects of human activity on adelie penguin *Pygoscelis adeliae* breeding success. *Biological Conservation* 75: 157–164.
- Gill, J.A., Sutherland, W.J. & Watkinson, A.R. (1996) A method to quantify the effects of human disturbance on animal populations. *Journal of Applied Ecology* 33: 786–792.
- Gill, J.A. & Sutherland, W.J. (2000) Predicting the consequences of human disturbance from behavioural decisions. In: *Behaviour and Conservation*, ed. L.M. Gossling & W. Sutherland, pp. 51–64. Cambridge, UK: Cambridge University Press.
- Gill, J.A., Norris, K. & Sutherland, W.J. (2001) Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation* 97: 265–268.
- Gutzwiller, K.J. & Marcum, H.A. (1997) Bird reactions to observer clothing color: implications for distance-sampling techniques. *Journal of Wildlife Management* 61: 935–947.
- Gutzwiller, K.J., Marcum, H.A., Harvey, H.B., Roth, J. & Anderson, S.H. (1998) Bird tolerance to human intrusion in Wyoming Montane Forests. *Condor* 100: 519–527.
- Henson, P. & Grant, T.A. (1991) The effects of human disturbance on trumpeter swan breeding behavior. *Wildlife Society Bulletin* 19: 248–257.
- Hill, D., Hockin, D., Price, D., Tucker, P., Morris, R. & Treweek, J. (1997) Bird disturbance: improving the quality and utility of disturbance research. *Journal of Applied Ecology* 34: 275–288.
- Holmes, T.L., Knight, R.L., Stegall, L. & Craig, G.R. (1993) Responses of wintering grassland raptors to human disturbance. *Wildlife Society Bulletin* 21: 461–468.
- Humphrey, P.S., Livezey, B.C. & Siegel-Causey, D. (1987) Tameness of birds of the Falkland Islands: an index of preliminary results. *Bird Behaviour* 7: 67–72.
- Jokimäki, J. (1999) Occurrence of breeding bird species in urban parks: effects of park structure and broad-scale variables. Urban Ecosystems 3: 21–34.
- Katcher, A. & Wilkins, G. (1993) Dialogue with animals: its nature and culture. In: *Biophilia Hypothesis*, ed. S.R. Kellert & E.O. Wilson, pp. 173–197. Washington, DC, USA: Island Press.
- Kiltie, R.A. (2000) Scaling of visual acuity with body size in mammals and birds. *Functional Ecology* 14: 226–234.
- Knight, R.L. & Knight, S.N. (1984) Responses of wintering bald eagles to boating activity. *Journal of Wildlife Management* 48: 999–1004.
- Knight, R.L. & Cole, D.N. (1995) Factors that influence wildlife responses to recreationists. In: *Wildlife and Recreationists: Coexistence Through Management and Research*, ed. R.L. Knight & K.J. Gutzwiller, pp. 71–79. Washington, DC, USA: Island Press.
- Knight, R.L. & Temple, S.A. (1995) Wildlife and recreationists: coexistence through management. In: Wildlife and Recreationists: Coexistence Through Management and Research, ed. R.L. Knight & K.J. Gutzwiller, pp. 327–333. Washington, DC, USA: Island Press.
- Kramer, D.L. & Bonenfant, M. (1997) Direction of predator approach and the decision to flee to a refuge. *Animal Behaviour* 54: 289–295.
- Lima, S.L. & Dill, L.M. (1990) Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal* of Zoology 68: 619–640.

- Lima, S.L. & Zollner, P.A. (1996) Towards a behavioural ecology of ecological landscapes. *Trends in Ecology and Evolution* 11: 131–135.
- Martin, G.R. & Katzir, G. (1994) Visual fields and eye movements in herons (Ardeidae). *Brain, Behaviour, and Evolution* 44: 74–85.
- Martín, J. & López, P. (1995) Influence of habitat structure on the escape tactics of the lizard *Psammodromus algirus*. Canadian Journal of Zoology 73: 129–132.
- Michelson, W. (1970) Man and his Urban Environment: a Sociological Approach. Reading, MA, USA: Addison-Wesley: 242 pp.
- Miller, S.G., Knight, R.L. & Miller, C.K. (1998) Influence of recreational trails on breeding bird communities. *Ecological Applications* 8: 162–169.
- Nicholls, A.O. (1989) How to make biological surveys go further with generalised linear models. *Biological Conservation* 50: 51–75.
- Prodon, R. & Lebreton, J.D. (1981) Breeding avifauna of a Mediterranean succession: the holm oak and cork oak series in the eastern Pyrenees, 1. Analysis and modelling of the structure gradient. *Oikos* 37: 21–38.
- Riffell, S.K., Gutzwiller, K.J. & Anderson, S.H. (1996) Does repeated human intrusion cause cumulative declines in avian richness and abundance? *Ecological Applications* 6: 492–505.
- Roberts, G. (1996) Why individual vigilance declines as group size increases. *Animal Behaviour* 51: 1077–1086.
- Rodgers, J.A. & Smith, H.T. (1995) Set-back distances to protect nesting bird colonies from human disturbance in Florida. *Conservation Biology* 9: 89–99.

- Rodgers, J.A. & Smith, H.T. (1997) Buffer zone distances to protect foraging and loafing waterbirds from human disturbance in Florida. *Wildlife Society Bulletin* 25: 139–145.
- Skagen, S.K., Knight, R.L. & Orians, G. (1991) Human disturbance of an avian scavenging guild. *Ecological Applications* 1: 215–225.
- Slotow, R. & Rothstein, S.I. (1995) Influence of social status, distance from cover, and group size on feeding and vigilance in White-crowned Sparrows. *The Auk* 112: 1024–1031.
- Soulé, M.E., Bolger, D.T., Alberts, A.C., Wright, J., Sorice, M. & Hill, S. (1988) Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* 2: 75–92.
- Tellería, J.L., Asensio, B. & Díaz, M. (1999) Aves Ibéricas. II. Paseriformes. Madrid, Spain: J.M. Reyero.
- Underwood, A.J. (1997) *Experiments in Ecology. Their Logical Design* and Implementation Using Analysis of Variance. Cambridge, UK: Cambridge University Press.
- van der Meer, J. (1985) De verstoring van vogels op de slikken van de Oosterschelde. Unpublished report 85.09, Deltadienst Milieu en Inrichting, Middelburg, Germany.
- Vandruff, L.W., Leedy, D.L. & Stearns, F.W. (1995) Urban wildlife and human well-being. In: Urban Ecology as the Basis for Urban Planning, ed. H. Sukopp, M. Numata & A. Huber, pp. 203–211. The Hague, the Netherlands: SPB, Academic Publishing.
- Ydenberg, R.C. & Dill, L.M. (1986) The economics of fleeing from predators. Advances in the Study of Behaviour 16: 229–249.