Factors affecting intra- and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats

E. Fernández-Juricic, M.D. Jimenez, and E. Lucas

Abstract: Studies of escape from predators have usually focused on fleeing. We studied intra- and inter-specific variations in a previous level of decision-making during predator–prey encounters by determining the difference between the distance at which a predator is detected and the distance at which the prey flees from the predator (buffer distance). We measured buffer distances of four bird species (ground foragers) living in forested habitats (wooded recreational parks) to approaching humans. Buffer distances increased with group size and temperature, and this was probably related to dilution of the predation risk and a higher risk of heat stress, respectively. Buffer distances decreased with shrub and coniferous cover, probably because of increased visual obstruction, and increased with tree height, probably because of the increased security provided by taller trees. Grass cover increased buffer distances of wood pigeons (*Columba palumbus*) but decreased those of house sparrows (*Passer domesticus*) and magpies (*Pica pica*); this may be related to higher food availability, i.e., vegetation in grassy areas for wood pigeons and food left by humans in areas with bare ground for house sparrows and magpies. Buffer distances of blackbirds (*Turdus merula*) and house sparrows were greater in highly visited parks, which may be related to habituation. Finally, larger species showed greater buffer distances, landed farther away, used higher landing substrates (trees), and flew higher, probably because they need to ensure a certain margin of security from predators. Alternatively, the increased buffer distances of large species may be related to the increasing energy expenditure of flight. The buffer distance appears to be a good indicator of tolerance toward predators and (or) risk taken by prey after detecting predators.

Résumé : Les études sur les tactiques pour éviter les prédateurs mettent généralement l'accent sur la fuite. Nous avons examiné la variation interspécifique et la variation intraspécifique à un stade antérieur de décision lors des rencontres prédateur–proie, soit la distance entre le point de détection du prédateur et le point de fuite (distance tampon). Nous avons mesuré la distance tampon à l'approche d'humains chez quatre espèces d'oiseaux (qui cherchent leur nourriture au sol) vivant dans des habitats forestiers (parcs de récréation boisés). Les distances tampons augmentent en fonction de la taille du groupe et de la température, deux facteurs que l'on soupçonne être reliés, le premier à la dilution des risques de prédation et le second, à la probabilité accrue d'un stress thermique. Les distances tampons diminuent avec l'importance du couvert de buissons ou de conifères, probablement à cause des effets d'obstruction, et elles augmentent en fonction de la hauteur des arbres, probablement parce que les grands arbres offrent plus de sécurité. La couverture d'herbe au sol augmente la distance tampon chez les pigeons ramiers (*Columba palumbus*), mais la diminue chez le moineau domestique (*Passer domesticus*) et chez la pie (*Pica pica*), probablement parce qu'elle accroît la disponibilité de la nourriture, de la végétation pour les pigeons, et, sur les sols nus, des déchets laissés par les humains pour les moineaux et les pies. Les distances tampons chez les merles noirs (*Turdus merula*) et les moineaux domestiques sont plus grandes dans les parcs très fréquentés, peut-être en conséquence de l'habituation. Enfin, les espèces les plus grandes ont les distances tampons les plus grandes, elles se posent à des distances plus grandes, elles utilisent des substrats plus hauts (arbres) pour se poser et elles volent plus haut, probablement pour s'assurer une certaine marge de sécurité entre elles et les prédateurs. Les distances tampons plus grandes chez les grandes espèces peuvent aussi être reliées à l'augmentation de la dépense énergétique au cours du vol. La distance tampon semble constituer un bon indicateur de la tolérance des proies et (ou) des risques qu'elles prennent lorsqu'elles ont repéré des prédateurs.

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E. Fernández-Juricic.[1] Department of Ecology, Evolution and Behavior, University of Minnesota, 100 Ecology Building, 1987 Upper Buford Circle, St. Paul, MN 55108, U.S.A.
M.D. Jimenez. Centro de Investigaciones Ambientales de la Comunidad de Madrid "Fernando Gonzalez Bernaldez", Calle San Sebastián, 17, 28791, Soto del Real, Madrid, Spain.
E. Lucas. Departamento de Biología Animal I, Facultad de Biología, Universidad Complutense de Madrid, Madrid, E-28040, Spain.

[1] Corresponding author (e-mail: estebanfj@yahoo.com).

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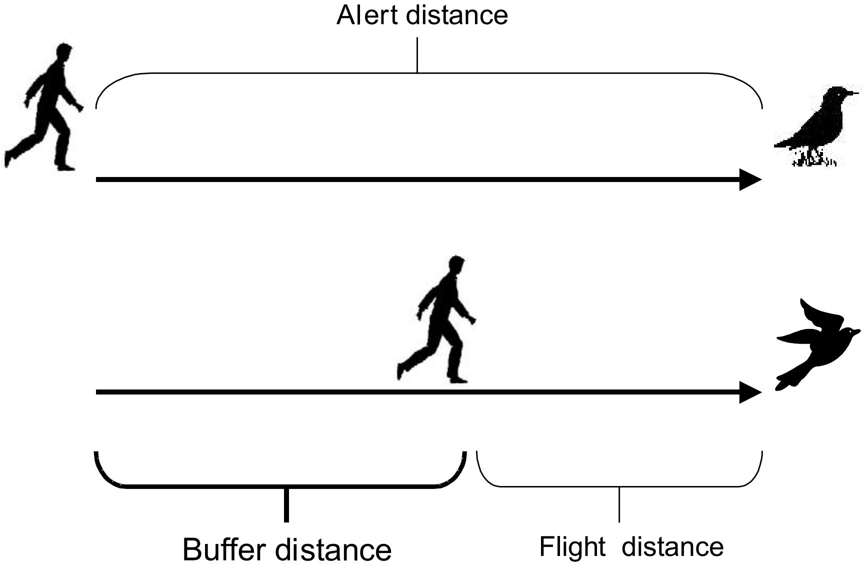
Fig. 1. Schematic representation of buffer distance, which is the difference between alert and flight distances. See the text for details.



Introduction

The decision to flee from predators entails benefits and costs (Ydenberg and Dill 1986). Animals benefit by reducing their chances of being predated, but they also incur costs by attracting predators, losing foraging opportunities, and expending energy in various escape tactics (Lima and Dill 1990; Lima 1993). The net result is that individuals trade access to food for safety (Lima 1985; Kotler and Blaustein 1995) by modifying their fleeing behavior (and ultimately habitat use) in relation to several factors: distance to refuge, predator speed, number of conspecifics, age, etc. (Lima et al. 1987; Dill 1990; Lima 1990; Cooper 1997; Kramer and Bonenfant 1997; Smith 1997; Randall et al. 2000; Swarthout and Steidl 2001). Upon detecting a predator, individuals may assess its position, velocity, and movement direction, so they remain in the same spot, monitoring its movements more closely while continuing to forage or holding still to maintain crypsis (Burger and Gochfeld 1990; Bonenfant and Kramer 1996). In the case of birds, if the predator approaches individuals directly, they should evaluate a potential refuge and the distance from the predator at which they would take off (Cooper 1999), which is usually known as the flight distance. After fleeing, birds are expected to choose a combination of escape tactics (e.g., flight speed and height, landing distance, and substrate) to keep a certain difference in time and distance from the predator and to reach cover (margin of safety, Dill 1990; Lima 1993; Bonenfant and Kramer 1996).

The costs and benefits associated with the decision to flee from predators have been extensively analyzed (Bonenfant and Kramer 1996; Blumstein et al. 1997; Randall et al. 2000). Studies have usually focused on the distance at which a predator is detected (alert distance; Fig. 1) and the distance from it at which prey flee (flight distance; Fig. 1). However, scant attention has been devoted to the difference between alert and flight distances, which entails a level of decision-making in predator–prey encounters that corresponds more closely to tolerance toward the predator or the risk taken by the prey during predator approaches. Actually, this “buffer distance” (Fig. 1) can be regarded as related to the margin of safety (Dill 1990; Kramer and Bonenfant 1997), as it is an indicator of the level of security prey need to avoid being caught. Our goals were (*i*) to assess the social factor (number of conspecifics) and environmental factors (temperature, distance to predator paths, availability of horizontal and vertical cover) affecting buffer distances, (*ii*) to determine whether the frequency of predator–prey encounters modifies buffer distances, and (*iii*) to analyze interspecific differences in buffer distances in relation to escape tactics. We studied buffer distances of four bird species (house sparrow, *Passer domesticus*; blackbird, *Turdus merula*; wood pigeon, *Columba palumbus*; and magpie, *Pica pica*) living in forested habitats (wooded recreational parks) to approaching humans, which have been used previously as surrogates for predation or disturbance (Blumstein et al. 1997; Martin and Lopez 1999; Fernández-Juricic and Tellería 2000; Harkin et al. 2000; Louis and Le Berre 2000; Cuadrado et al. 2001).

Foraging in groups brings benefits in terms of safety from predation, usually through lower chances of being caught, owing to the dilution effect (Roberts 1996). We predicted, then, that a larger number of conspecifics would increase the buffer distance, as individuals in larger flocks would tolerate more risk. In forested habitats, an increase in the proportion of horizontal and vertical cover would increase buffer distances if individuals perceive it as protective cover (Lima et al. 1987; Lima 1990; White et al. 2001). Grass cover would also increase buffer distances, since it is a source of food (insects, vegetation, etc.) for ground foragers. Ambient temperature can affect tolerance toward predators through variation in metabolic requirements (Lens and Dhondt 1993; Haroldson et al. 1998; Carrascal et al. 2001); for instance, foraging activity and time spent in a patch may increase when energetic requirements are higher (e.g., at lower temperature). We expected, then, that a decrease in temperature would increase buffer distances. Moreover, since pathways are sources of disturbance (e.g., pedestrians passing by), the farther individuals were from pathways, the more buffer distances were expected to increase, because the individuals were less exposed to approaching humans (Fernández-Juricic and Tellería 2000). On the other hand, buffer distances would increase in areas with a higher frequency of human–bird interactions (e.g., highly visited areas) because of habituation effects (Labra and Leonard 1999; Louis and Le Berre 2000; Fernández-Juricic et al. 2001*b*; Lord et al. 2001). Finally, we expected that interspecific variation in buffer distances would be related to interspecific differences in escape strategies (Lima 1990, 1993) and body size (Marden 1987). Species with costly escape strategies (higher flight height, greater landing distance, and taller trees for landing) would have greater buffer distances in order to minimize missed foraging opportunities (Kramer and Bonenfant 1997). Similarly, large species would have increased buffer distances because of greater energy expenditure for flight (Witter and Cuthill 1993).

Methods

Study area and species

The study was carried out from April to June 1998 in four large wooded parks in Madrid (40.25°N, 03.43°W): Moro (18 ha), Dehesa (25 ha), Oeste (98 ha), and Retiro (110 ha). These parks were created >50 years ago and have a heterogeneous habitat structure with high tree cover composed of a mixture of deciduous and coniferous trees. The most common deciduous trees are *Populus* sp., *Platanus hybrida*, *Ulmus campestris*, and *Acer negundo*; coniferous tree species include mainly *Cedrus* sp., *Pinus* sp., and *Abies alba*. The parks also have extensive areas of short irrigated grass and shrubs, including introduced and native species such as *Ligustrum* sp., *Buxus* sp., *Viburnum* sp., and *Rubus* sp. All parks are recreational areas divided into patches by walking paths.

The four bird species selected for studying buffer distances can be considered ground foragers (Cramp 1992): house sparrows feed on seeds of wild plants, green shoots, buds, berries, and human refuse, blackbirds on insects, earthworms, and several cultivated and wild fruits, magpies on insects, snails, slugs, seeds, other birds, and human leftover food, and wood pigeons on vegetative material (seeds, small fruits, young green shoots, etc.).

Buffer distances

Data were gathered between 07:00 and 17:00, totaling 387 observation hours, on sunny or cloudy days, never on rainy or windy days. Temperatures varied from 10 to 38°C. Two observers (M.D.J. and E.L.) gathered all the data after intensive training. The parks were visited randomly during weekdays, two parks per day at most, and with at least a 1-day interval between visits that had to be conducted in the same park.

Buffer distance was defined as the distance between the point where a bird raised its head from the ground (the long axis of the body was perpendicular to the ground) in response to the approach of a human and the point where the bird flushed (Fig. 1). We assumed that predator detection was positively correlated with the display of alert behaviors, which has been shown previously (Powell 1974; Rodgers and Smith 1995; Swarthout and Steidl 2001; E. Fernández-Juricic and N. Shroeder, unpublished data). In a previous study we determined the variation in vigilance bout length and vigilance rate in the presence and absence of humans (E. Fernández-Juricic and F. Melado, unpublished data). Having determined the threshold vigilance which would indicate that the bird was scanning for humans, we were able to record the distance at which it switched from foraging to monitoring the observer's approach (Fig. 1), which corresponded to longer vigilance bouts and higher vigilance rates in all species. A similar procedure for estimating alert distance has been reported elsewhere (Swarthout and Steidl 2001). Previous estimations of alert distance showed no variation *within* species, given similar habitat complexity (Fernández-Juricic et al. 2001*a*), therefore we assumed a similar ability to detect approaching humans within each species.

We began our approach about 35 m from the individuals whose buffer distances were to be recorded (focal individuals) because individuals became alert at 14.1 ± 6.1 m (mean ± SE). Distance estimates (±0.05 m) were based on measured paces and controlled with a meter tape (Fernández-Juricic et al. 2001*b*). Twenty-five observations were gathered per species in each park. For each species and park, observations were recorded at different locations to avoid disturbing the same individual more than once. Locations were randomly selected within parks. Observers never collected two observations from the same species consecutively from contiguous areas to avoid affecting responses between approaches.

All individuals approached were on the ground, and birds looking for nest material were not considered. When the observer approached a group of birds, she focused on a single individual within the group, chosen at random before the approach was made. Previously, the observer recorded the number of conspecifics around the focal bird, the distance from the focal individual to the nearest pathway, and ambient temperature. When birds were in groups, alert and flight distances could be highly dependent on the presence of conspecifics. Our experimental approach did not allow us to separate that effect, so we included the number of conspecifics as an explanatory variable in our analyses. Observers approached birds at a steady speed (1 step/s) and wearing similar clothing to preclude differential reaction (Gutzwiller and Marcum 1997). The approach was linear, with no vegetation to prevent the observer and bird from seeing each other (Fig. 1). Once the focal individual had flown away, the observer continued to approach the bird's original position, where the following microhabitat variables were recorded in circular plots with a 25-m radius: grass cover (%), shrub cover (%), coniferous cover (%), deciduous cover (%), shrub height (m), and tree height (m). Cover variables were visually estimated following Prodon and Lebreton (1981). We also followed the flushed individual until it landed in a different location and recorded its flight height (<1 or >1 m), landing distance from the point where it flushed (0–10, 11–20, 21–30, or >30 m), and landing substrate (grass, shrub, tree, or other).

We assumed that the frequency of predator–prey encounters would be directly related to the density of predators: in our case, visitors to the parks. Our approach was to evaluate behavioral changes in different populations associated with different degrees of exposure to humans. This has proved to be useful for assessing variation in tolerance of predators (Berger et al. 1983) despite the existence of possible confounding factors (Mitani et al. 1991). We measured human visitation in each park by recording the number of pedestrians

Table 1. Relationship between buffer distances and social and environmental factors for four bird species.

	House sparrow	Blackbird	Magpie	Wood pigeon
No. of conspecifics	$R^2 = 0.05$ (+), $P < 0.05$			$R^2 = 0.04$ (+), $P < 0.05$
Temperature	$R^2 = 0.08$ (+), $P < 0.01$			$R^2 = 0.05$ (+), $P < 0.05$
Grass cover	$R^2 = 0.04$ (–), $P < 0.05$		$R^2 = 0.04$ (–), $P < 0.05$	$R^2 = 0.07$ (+), $P < 0.05$
Shrub cover		$R^2 = 0.08$ (–), $P < 0.05$		
Coniferous cover		$R^2 = 0.04$ (–), $P < 0.05$		
Tree height	$R^2 = 0.04$ (+), $P < 0.05$	$R^2 = 0.07$ (+), $P < 0.05$	$R^2 = 0.16$ (+), $P < 0.001$	

Note: The results are from multiple stepwise regressions. The direction of the relationship for individual factors is shown in parentheses. We present only those factors whose contribution to R^2 was more than 1%.

in the morning (7:30–11:00) and at midday (12:00–14:30) during 5-min periods in circular plots with a 25-m radius in those areas of the wooded parks where birds were experimentally approached. We performed 10 counts in the morning and 10 at midday. Each park was sampled on 2 workdays and on 1 day at weekends to compare visitor loads among parks. Final figures were averaged for each park as the number of pedestrians per minute per plot. The most important confounding factor was the variability in habitat complexity among parks, Moro Park being the most diverse (in terms of grass, shrub, coniferous, and deciduous cover), followed in order by Oeste, Retiro, and Dehesa parks (Fernández-Juricic et al. 2001*a*). Therefore, we included vegetation structure as covariate in the analyses of buffer distances among parks.

Statistical analyses

Several variables were transformed using logarithmic and arcsine transformation to meet normality: buffer distance, number of conspecifics, distance to pathway, grass cover, shrub cover, and shrub height. To assess the influence of social and environmental factors on buffer distance and identify the most significant factors, we performed multiple regressions with forward stepwise selection procedures ($p = 0.05$; Nicholls 1989). A one-way ANOVA was employed to assess variation in the level of human visitation among parks. We analyzed the effect of frequency of predator–prey interactions on buffer distance for each species with an analysis of covariance (ANCOVA), including park as a fixed factor and the social and environmental factors affecting buffer distances for each species as covariates. A similar analysis was used to evaluate interspecific differences in buffer distance. We used Tukey's tests to assess differences between levels of a factor, and we only report significant variations. Interspecific variations in escape tactics were analyzed with χ^2 tests.

Because of the high number of probability estimations, we conducted a correction to avoid increasing the probability of Type I error. Many of the corrections available (Wright 1992) are so stringent that Type II errors can increase substantially, decreasing the power of individual tests (Chandler 1995). We minimized this problem with a two-tier approach. We first identified groups of related tests (following Chandler 1995) and then performed a less conservative correction (Sidák's correction; Wright 1992) over each of them. Within each group, P values (P_1) were first ordered so that $P_1 < P_2 < \ldots < P_n$, and then each value was sequentially adjusted to $P_{i(\text{Sidák})} = 1 - (1 - P_i)^{(n-i+1)}$, where n is the number of P values in each group of tests (see Wright 1992). Finally, we report transformed P values.

Results

Social and environmental factors

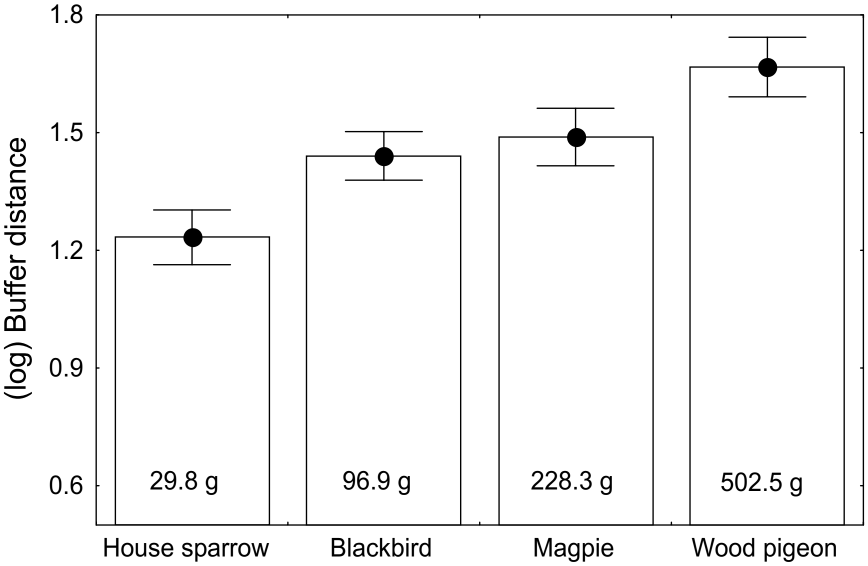
Six out of nine factors are considered to have affected buffer distances of the four species. For house sparrows, buffer distance increased with temperature, number of conspecifics, and tree height but decreased with grass cover ($F_{[4,95]} = 5.56$, $R^2 = 0.21$, $P < 0.003$; Table 1). For blackbirds, buffer distance was negatively related to shrub and coniferous tree cover and positively to tree height ($F_{[3,96]} = 5.11$, $R^2 = 0.19$, $P < 0.02$; Table 1). Increasing buffer distances of magpies were positively associated with tree height and negatively with grass cover ($F_{[2,97]} = 12.81$, $R^2 = 0.20$, $P < 0.001$; Table 1). Finally, increasing buffer distances of wood pigeons were associated with increases in numbers of conspecifics, temperature, and grass cover ($F_{[3,96]} = 5.11$, $R^2 = 0.16$, $P < 0.02$; Table 1). All factors had similar effects on buffer distances of the four species, except one, grass cover, which decreased rather than increased buffer distances of house sparrows and magpies (Table 1).

Exposure to visitors

Human visitation levels varied significantly among parks, Moro and Retiro parks being the least and most visited, respectively, and Oeste and Dehesa parks having intermediate visitation levels (Moro Park, 0.64 ± 0.59 pedestrians/min/plot (mean ± SD); Oeste Park, 1.03 ± 0.86 pedestrians/min/plot; Dehesa Park, 1.6 ± 1.97 pedestrians/min/plot; Retiro Park, 3.59 ± 5.25 pedestrians/min/plot; $F_{[3,316]} = 16.93$, $P < 0.001$). However, post-hoc analyses indicated that human visitation levels were only significantly higher in Retiro Park in relation to Moro Park (Tukey's test, $P < 0.001$), Oeste Park (Tukey's test, $P < 0.001$), and Dehesa Park (Tukey's test, $P < 0.001$).

Controlling for the social and environmental factors that affected each species, we found that buffer distances of house sparrows ($F_{[3,92]} = 0.75$, $P = 0.67$) and magpies ($F_{[3,94]} = 0.48$, $P = 0.83$) did not vary among parks. However, blackbirds' buffer distances did vary among parks (Moro Park, 3.3 ± 3.0 m; Oeste Park, 3.6 ± 3.0 m; Dehesa Park, 3.8 ± 2.2 m; Retiro Park, 5.5 ± 3.1 m; analysis on log $_{(x+1)}$ buffer distance, $F_{[3,93]} = 3.55$, $P < 0.05$). Buffer distances in Retiro Park were significantly greater than in Moro Park (Tukey's test, $P < 0.05$). Furthermore, wood pigeons' buffer distances also varied among parks (Moro Park, 4.0 ± 3.5 m; Oeste Park, 8.5 ± 8.4 m; Dehesa Park, 5.2 ± 2.9 m; Retiro Park, 5.7 ± 3.3 m; analysis on log $_{(x+1)}$ buffer distance, $F_{[3,93]} = 3.55$, $P < 0.05$), with a significant increase in buffer distance

Fig. 2. Buffer distances (mean ± SE) for four bird species in four wooded parks in Madrid. Body mass, based on Cramp (1992), is shown at the bottom of each bar.



only in Oeste Park relative to Moro Park (Tukey's test, $P < 0.05$).

Interspecific differences in buffer distances and escape tactics

In analyzing differences in buffer distances among species, we also considered a park effect due to the differences among parks that were detected in some species. Setting aside the effects of social and environmental factors, we found that buffer distances varied among species ($F_{[3,378]} = 9.51$, $P < 0.001$; Fig. 2), with larger species showing more tolerance toward predators. Wood pigeons' buffer distances were significantly greater than those of house sparrows (Tukey's test, $P < 0.01$) and blackbirds (Tukey's test, $P < 0.05$). After Sidák's correction was used, the park effect was not significant ($F_{[3,378]} = 2.92$, $P = 0.11$), nor was the interaction between species and park ($F_{[9,378]} = 1.71$, $P = 0.31$).

As for escape tactics, flying heights differed among species ($\chi^2_{[3]} = 29.36$, $P < 0.001$, Table 2). After taking off, wood pigeons tended to fly at heights of >1 m, whereas magpies, house sparrows, and particularly blackbirds flew at lower heights as well (Table 2). Landing distances also varied among species ($\chi^2_{[9]} = 26.21$, $P < 0.05$; Table 2), with house sparrows and blackbirds generally landing in substrates within 10 m of the fleeing point and magpies and wood pigeons landing farther from it. Finally, species tended to land on different substrates ($\chi^2_{[9]} = 63.22$, $P < 0.001$; Table 2); house sparrows and blackbirds chose all substrates (ground, shrub, and tree) in similar proportions, magpies usually landed in trees but sometimes on the ground, and wood pigeons landed primarily in trees.

Discussion

Our results point out that (*i*) buffer distances of four different species were similarly affected by social and environmental factors, (*ii*) populations of blackbirds and wood pigeons exposed to frequent predator–prey interactions decreased their buffer distances, and (*iii*) buffer distances and escape tactics varied among species.

When house sparrows and wood pigeons foraged in increasingly larger groups, they delayed fleeing after detecting approaching humans. It is expected that observers were detected earlier by large flocks (reviewed in Roberts 1996), and that increasing buffer distance may be related to the dilution effects of groups (Turner and Pitcher 1986) whereby an individual in a large group reduces its chances of being caught when an attack occurs (Bertram 1978; Lazarus 1979; Cresswell 1994; Bednekoff and Lima 1998). Thus, foraging in groups increases buffer distances, owing to a lower perceived predation risk and an increased probability of escaping attacks. Unexpectedly, a higher ambient temperature increased buffer distances of house sparrows and wood pigeons. The high temperatures (10–38°C) experienced by birds during spring may have triggered a different thermal problem: heat stress (Schleucher et al. 1991; Petrie and Rogers 1997; Weathers 1997; Schleucher and Eckhart 2001). Fleeing from the observer sooner can increase muscle activity and heat production, and this may have led to an increase in buffer distances at high ambient temperatures to prevent hyperthermia.

The relationship between buffer distance and available cover varied among species, and this may be related to the differential quality of substrates (protective or obstructive) that is typical of heterogeneous habitats (Lima et al. 1987; Lima 1990; Lazarus and Symonds 1992; Kunkel and Pletscher 2000). For blackbirds, an increase in the proportion of horizontal cover (shrub and coniferous) decreased buffer distances, probably because closed cover may diminish the chances of detecting the approach of other humans (or predators), owing to obstruction caused by the surroundings, thus reducing tolerance of potential threats (Lima et al. 1987; Lima 1990; Harkin et al. 2000). This may also explain the spatial and temporal restrictions on habitat use encountered previously when blackbirds experienced a high number of visitors per unit time (Fernández-Juricic and Tellería 2000). Vertical cover (tree height), on the other hand, increased buffer distances of house sparrows, blackbirds, and magpies, a response that is

Table 2. Percentages of individuals of each species that used different escape tactics, i.e., different flying heights, landing distances, and landing substrates.

	Flying height		Landing distance				Landing substrate			
	<1 m	>1 m	0–10 m	11–20 m	21–30 m	>30 m	Tree	Shrub	Ground	Other
House sparrow	21 (0.12)	79 (0.03)	63 (0.86)	22 (0.41)	5 (2.13)	10 (0.06)	44 (3.07)	21 (4.16)	30 (1.36)	5 (0)
Blackbird	36 (13.96)	64 (3.38)	69 (3.02)	21 (0.71)	4 (3.18)	6 (1.14)	38 (6.47)	25 (9.79)	32 (2.47)	5 (0)
Magpie	14 (1.55)	86 (0.38)	42 (3.50)	34 (3.03)	16 (4.45)	8 (0.17)	63 (0.57)	6 (4.16)	24 (0.01)	7 (0.8)
Wood pigeon	7 (8.01)	93 (1.94)	50 (0.64)	24 (0.06)	13 (1.28)	13 (1.52)	84 (12.49)	2 (9.79)	11 (7.24)	3 (0.8)

Note: Values in parentheses are χ^2 values.

probably related to the increased level of security, and therefore refuge, that higher trees may provide, thereby reducing accessibility for pedestrians. Finally, grass cover exerted different effects, increasing buffer distances of wood pigeons and decreasing those of house sparrows and magpies. Wood pigeons feed mainly on vegetal material, so a longer delay in fleeing as grass cover increases may reflect greater availability of food, suggesting that birds would tolerate an increased risk of capture (Ydenberg and Dill 1986). The response of house sparrows and magpies may also be related to greater food availability, as they usually feed on human refuse and leftover food, which happened to be more abundant in areas that were more frequented by visitors, and, as a result, related to decreasing grass cover.

Buffer distances of blackbirds and wood pigeons were greater in highly visited wooded areas. Although we cannot ascribe causal relationships, owing to the large number of possible confounding factors (such as the variation in habitat complexity among the parks), this pattern may be related to the frequency of predator–prey interactions. Previous studies showed that antipredator behavior can change significantly after the reintroduction or extirpation of predators (reviewed in Berger 1998); for instance, scanning time and rate can increase as predation levels increase (Hunter and Skinner 1997). Despite the similarities in responses to humans and predators (Berger et al. 1983), humans do not usually cause mortality, only fitness-related effects such as a decrease in foraging time (Fernández-Juricic and Tellería 2000) or displacement from suitable foraging areas (Fernández-Juricic 2000). Therefore, individuals may have learnt to tolerate human intrusions in highly visited areas as a strategy for reducing the energy costs associated with loss of foraging opportunities (Labra and Leonard 1999). This change in the direction of antipredator responses according to the frequency of predator–prey interactions due to habituation to humans appears to be common not only in birds (Cooke 1980; Riffell et al. 1996; Lord et al. 2001) but also in other taxa such as lizards (Labra and Leonard 1999) and mammals (Mainini et al. 1993; Neuhaus and Mainini 1998; Louis and Le Berre 2000).

Buffer distances varied among species after confounding factors were controlled for. This could have been due to variation in one of the components of buffer distance (alert or flight distance) while the other remained constant (e.g., no interspecific differences in alert distance, only in flight distance). This is not the case in the present study because we had previously found interspecific variations in alert distance as well as flight distance among the same species (Fernández-Juricic et al. 2001*a*, 2001*b*). Differences in buffer distance could be accounted for by interspecific variations in escape tactics and body size (see Lima 1993), these two explanations not being mutually exclusive. On the one hand, based on our results it could be suggested that the greater the difference between alert and flight distances (e.g., greater tolerance toward predators), the farther the landing distance and the higher the landing substrate, as prey need to ensure a certain margin of security (landing close to an approaching predator after showing high tolerance levels may increase the predation risk because the predator might follow the prey). For example, wood pigeons showed greater buffer distances than house sparrows and blackbirds, and concurrently landed farther away, used higher landing substrates (trees), and flew higher. For these species, each trip to a refuge may be long and costly, and as a result, such escape strategies may reduce the chances of using the same foraging patch again (Kramer and Bonenfant 1997). Actually, recent experimental evidence suggests that for magpies, the farther the landing distance, the longer the time taken to resume feeding and the lower the probability of returning to the same patch (E. Fernández-Juricic and M.D. Jiminez, unpublished data). Consequently, species with a higher probability of losing foraging opportunities when spatially and temporally displaced from suitable patches may be more tolerant of approaching predators or more prone to take risks than species that can quickly return to and make use of these patches after the potential threat is removed (Dill 1990; Lima and Dill 1990). On the other hand, body size may have played an important role in the variation in buffer distances, as increasing body mass is expected to reduce aerial manoeuvrability and take-off ability (Marden 1987; Witter et al. 1994; Metcalfe and Ure 1995; but see Kullberg 1998), which could increase energy expenditure for flight (Witter and Cuthill 1993). Larger species (such as the wood pigeon) might face increased metabolic costs, and hence augment their tolerance toward approaching predators or humans in order to optimize foraging time (Ydenberg and Dill 1986). Therefore, behavioral and morphological variations in escape tactics may be affecting interspecific differences in the perception of risk, and, as a result, buffer distances.

Many theoretical models assume that prey flee as soon as predators are detected after breaking cover (e.g., Hart and Lendrem 1984), which makes flight distance the main indicator of tolerance toward predators. However, predator detection depends upon the visual perception of different species (e.g., Smith and Litvaitis 1999), and as a result alert distances should also be taken into consideration when studying tolerance. Our results underscore the fact that the difference between alert and flight distances (buffer distance) is a good indicator of tolerance and (or) risk taken by prey, since individuals do not usually flee as soon as potential predators are detected, but delay their decision until marginal benefits equal marginal costs (Ydenberg and Dill 1986). Furthermore, buffer distance can have implications for habitat use in areas with high levels of human visitation (natural areas, parks, reserves). As the frequency of visitors increases, so does the area where potential human–bird interactions occur, which could affect habitat-use patterns of different species (e.g., Fernández-Juricic 2000; Fernández-Juricic and Tellería 2000). Therefore, understanding interspecific differences in tolerance could help minimize the effects of human disturbance by allowing the factors that increase buffer distances at local scales to be managed.

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