Oecologia (2004) 140: 183–190
DOI 10.1007/s00442-004-1560-0

**Esteban Fernández-Juricic · Jukka Jokimäki ·
J. Chase McDonald · Francisco Melado ·
Adolfo Toledano · Carolina Mayo · Beatriz Martín ·
Isabel Fresneda · Verónica Martín**

Effects of opportunistic predation on anti-predator behavioural responses in a guild of ground foragers

Received: 9 September 2003 / Accepted: 19 March 2004 / Published online: 6 May 2004

Abstract We studied factors that affect prey selection by a generalist predator that opportunistically attacks prey species, and the associated inter- and intra-specific responses of prey to this type of predation. Our model system was a guild of ground-foraging birds that are preyed upon by magpies (*Pica pica*) during the breeding season. We found that magpies attacked up to 12 species during three consecutive breeding seasons. The overall capture success was estimated to be 4.9%. Magpies tended to attack from the air, targeting solitary prey, either on the ground or flying. Inter-specific prey responses to the risk of magpie predation included a reduction in the mean number of species occupying a foraging patch when magpies were present and a decrease in the distance between heterospecific neighbours. Intra-specific responses to magpie predation varied between species that were subject to different attack rates. Preferentially attacked prey enhanced their risk responses (increase in scanning time and scanning rate in the presence of magpies) relative to those species attacked in proportion to their abundance (increase only in scanning rate with magpies). Species attacked infrequently, relative to their abundance, showed no antipredator response. The probability of being attacked, rather than mortality rate, appears to be the factor to which prey species respond.

Keywords Anti-predator behaviour · Attack rate · Opportunistic predation · Prey selection · Vigilance

E. Fernández-Juricic (✉) · J. C. McDonald
Department of Biological Sciences, California State University,
Peterson Hall 1-109, 1250 Bellflower Blvd,
Long Beach, CA 90840, USA
e-mail: efernand@csulb.edu

J. Jokimäki
Arctic Centre, University of Lapland,
P.O. Box 122, 96101 Rovaniemi, Finland

F. Melado · A. Toledano · C. Mayo · B. Martín · I. Fresneda ·
V. Martín
Grupo de Ecología Aplicada, C/ Bernardino García,
29, 1ero Izq.,
28040 Madrid, Spain

Introduction

Predation risk may affect various fitness traits of individuals, the distribution and dynamics of populations, and the interactions within and between trophic levels (reviews in Lima and Dill 1990; Lima 1998a, b; Sih et al. 1998; Abrams 2000). Nevertheless, there is relatively little that is known about how predator behaviour modifies predator–prey interactions (Newton 1998; Lima 2002) and, particularly, how prey respond to opportunistic predation. Opportunistic predators can be defined as those whose attack on prey is conditioned by the spatial and temporal co-occurrence of both as well as by certain environmental or physiological conditions that trigger the use of alternative prey for survival and/or reproduction. This is relevant from an evolutionary standpoint because in many natural systems prey have evolved in multi-predator environments, in which anti-predator strategies should balance the risks posed by both specialized and non-specialized predators (Sih et al. 1998).

Our general goal is to study two aspects of opportunistic predation: (a) The factors that affect prey selection by a generalist predator that opportunistically attacks adult birds during a restricted time of the year; (b) The inter- and intra-specific responses of prey to such opportunistic predation. Our model system is a guild of ground-foraging birds inhabiting wooded parks in an urbanized landscape (e.g., Fernández-Juricic et al. 2001a, 2002). The opportunistic predator species is the magpie (*Pica pica*), which is an omnivorous species eating insects, cereals, fruit, carrion, household waste, plants, etc. mainly on the ground (Birkhead 1991; Cramp 1994). Ground-foraging birds and magpies overlap substantially in foraging patch use year round. Only during the breeding season may magpies occasionally prey on adult birds (Hochackka and Scharf 1986; Thomas 1982; Attridge 1997).

We first characterized the predatory behaviour of the magpies by assessing attack and capture rates, selection ratios (relationship between attack rate and prey abundance), and the relationship between type of predator attack, position of prey when attacked, and prey group size. These data were necessary to determine the prey species that were preferentially attacked or avoided. Second, we analysed prey patch use (mean number of prey species and mean abundance of individuals foraging on the ground and perching on trees) in relation to the presence/absence of predators. Third, we studied whether prey foraging on the ground modified inter-specific neighbour distances of prey species in relation to the presence/absence of predators in the same foraging patch. Fourth, we assessed variations in vigilance and foraging behaviour strategies of three prey species (one attacked in proportion to abundance, one preferred, and one avoided) in two foraging conditions: with and without predators present in the foraging patch.

We expected that magpies would launch attacks from the air rather than from the ground, to increase the surprise effect, and that they would attack solitary individuals on the ground, rather than perching or flying prey, to decrease the chances of detection or escape. As for inter-specific anti-predator responses, we expected that, on average, fewer prey species and individuals would tend to forage on the ground when magpies were present, and that individuals would hide in cover within patches (e.g., perching on trees/shrubs). For prey that remained in the foraging patch regardless of the presence of magpies, inter-specific neighbour distances would decrease, as a strategy to increase dilution and decrease the chances of being caught by magpies (Roberts 1996). Prey vigilance and foraging strategies would vary according to the potential danger of magpies for different species. Species that were attacked in greater proportion than their abundance were expected to increase their anti-predator responses (increase vigilance time and rate in the presence of magpies) relative to those attacked less (Lima 1992).

Materials and methods

Study area

The study was conducted in the city of Madrid, Spain (40°25’N, 03° 43’W) during the 1997–2000 breeding seasons. Madrid has an extensive network of vegetation remnants (wooded parks) that harbour several bird species. Parks were located in the city centre and most of them were managed. They had high tree cover, and were composed of a mix of deciduous and coniferous trees, introduced and native shrub species, and lawns. Internally, wooded parks were divided into patches limited by a series of pathways for people, who used them as recreational grounds. Different parks were used to assess predator and anti-predator behaviour; we describe them in each of the following sections.

Magpie predation

We systematically recorded magpie attacks on other bird species in 15 wooded parks, ranging from 1 to 118.2 ha. Recordings spanned three consecutive breeding seasons, with different observation hours per season: 253 in 1997, 202 in 1998, and 95 in 1999.

We defined an attack as a rapid directed flight at a clearly identifiable bird or a flock (Cresswell 1993), which resulted in the prey fleeing, being chased, or eventually being captured by magpies. We did not include in our analysis displacements by magpies (no prey chase involved, Birkhead 1991), which also occurred during the breeding season. During magpie attacks, we recorded: the number of individuals attacking, prey species attacked, whether or not a prey was captured, prey position when attacked (on the ground, flying, perching), prey aggregation (solitary, in group), and the type of magpie attack (magpies approached prey flying out from a perch or a different foraging patch or from the ground in the same foraging patch). After an attack, we followed the attacker for 10–15 min to assess whether it resumed attacking. In cases in which the same magpie attacked another individual we only considered its first attack in our analysis.

Prey availability

We recorded the density of prey species within each of the 15 parks. Surveys were done four times by only one observer (E.F.J.) in 1997–1999. All parks were surveyed on weekday mornings (from 0700 to

Table 1 Number of observed attacks by magpies and attack rate (observation hours between attacks), selection ratios (relationship between proportion of attacked individuals and the proportion of available individuals), and results of a Chi-square test to determine whether selection ratios differed significantly from 1. Data are classified by prey species and breeding season

Common name	Scientific name	Number of attacks	Intervals between attacks (h)	Selection ratio	χ^2 (p)	Number of attacks	Intervals between attacks (h)	Selection ratio	χ^2 (P)
Blackbird	*Turdus merula*	17	15	3.793	**14.42 (<0.001)**	11	18	3.095	**7.56 (0.006)**
House sparrow	*Passer domesticus*	10	25	0.389	**31.29 (< 0.001)**	4	51	0.249	**41.36 (<0.001)**
Spotless starling	*Sturnus unicolor*	7	36	3.046	3.71 (0.054)	8	25	3.601	**5.51 (0.018)**
Rock dove	*Columba livia*	5	51	0.631	1.91 (0.167)	2	101	0.376	**5.87 (0.015)**
Woodpigeon	*Columba palumbus*	2	127	0.989	0.01 (0.988)	5	40	1.611	0.85 (0.357)
Hoopoe	*Upupa epops*	1	253	4.443	0.61 (0.433)	–	–		
Treecreeper	*Certhia brachydactyla*	1	253	3.088	0.47 (0.494)	–	–		
Great tit	*Parus major*	1	253	2.773	0.42 (0.518)	–	–		
Serin	*Serinus serinus*	1	253	0.405	2.21 (0.137)	1	202	0.417	2.02 (0.155)
Greenfinch	*Carduelis chloris*	1	253	1.315	0.06 (0.809)	–	–		
Stock dove	*Columba oenas*	1	253	2.242	0.31 (0.575)	–	–		
Green woodpecker	*Picus viridis*	–	–			2	101	5.855	1.46 (0.226)

1000 hours) during April–June. For all parks >2 ha, we recorded the number of individuals seen or heard in 100 m long and 50 m wide transects (Järvinen and Väisänen 1975). We averaged the number of birds in each fixed transect (0.5 ha) throughout all visits. Transects were separated by 50–150 m to reduce spatial autocorrelation, and the same transects were used for each visit. The number of transects per wooded park was established in a logarithmic scale relation to the size of each park (range 1–95 transects). In parks <2 ha, we sampled the whole park employing a proportional amount of time to that used in line transects.

Anti-predator responses

We conducted three different studies with similar designs (see also Fernández-Juricic and Tellería 2000). In the first study, we assessed whether the mean number of ground-foraging prey species (Table 1) per patch and the mean number of individuals (including all species) per patch varied when magpies were present or absent from patches. The study was conducted in the 1998 breeding season in three wooded parks: Retiro (118.2 ha), Oeste (98.60 ha), and Moro (18.86 ha). Within each wooded park, we chose 25-m radius sample plots near internal pathways. The size of these plots reflected the mean size of patches divided by pathways. Sampling plots were separated from each other by at least 15 m and by the pathways used by visitors. Sampling plots had similar habitat configuration within parks, and were considered as resource patches. Our design was balanced, with 25 samples per treatment in different sampling plots.

We surveyed each sampling plot from observation points for 6–8 min, focusing on the selected plots but remaining out of sight and out of the sampling plot. Whenever birds detected an observer, their behaviour changed substantially (Fernández-Juricic and Tellería 2000). In such cases, the point was abandoned for 1 h before resuming sampling. We recorded the number of ground-foraging prey species and their abundance both on the ground and perching in bushes/trees based on sightings and vocalizations. We recorded prey perching because hiding in cover could be a strategy to avoid predation while magpies were present in a patch.

In the second study, we assessed whether prey species modified the distances to their nearest heterospecific neighbours while foraging on the ground with and without magpies. We carried out the study in the 1997 breeding season in three wooded parks: Retiro, Oeste, and Austria (29.39 ha). We recorded as many samples as possible per park, with at least 18, and at most 50, samples per treatment. We also measured the distance between magpies and prey when one or more than one prey species were present in the sampling plot to determine whether magpies modified the distance to prey with variations in the number of prey species present per patch foraging on the ground. The number of samples per treatment varied among parks, with at least 16, and at most 25.

Distance to the nearest heterospecific neighbour was measured from hidden observation points to minimize human disturbance. Samples in which birds may have been affected by the presence of the observer were not considered. We used high resolution maps to record the location of magpies and different prey species when first observed. After the birds left the plot, the observer measured the distance to the nearest neighbour with a meter tape (±0.05 m). In those occasions when three prey species were foraging in the same sampling plot, we measured first and second nearest neighbour distances of each species (Krebs 1998), but averaged these values to get a single estimate. When foraging in groups, neighbour distances were recorded by taking into account the distance from the centre of the flock.

In the third study, we assessed the vigilance and foraging behaviour of three model species (house sparrows *Passer domesticus*, avoided by magpies; blackbirds *Turdus merula*, preferred by magpies; and woodpigeons *Columba palumbus*, attacked in proportion to their density, see Results) under two scenarios while foraging on the ground: with and without magpies present in the sampling plot. The size of the sampling plots was larger than in the two previous studies (35-m radius). This study was conducted during two breeding seasons (1999–2000) in three wooded parks: Retiro, Oeste, and Moro. We pooled the data of both breeding seasons due to the similarity of results. Sample size varied between species, but we gathered at least 16 samples and at most 25 samples per combination of factors (scenario and park).

Sampling was conducted from fixed observation points that were out of sight of focal individuals. If a focal individual detected the observer, the sampling plot was temporarily abandoned. If prey species were foraging in flocks, the observer chose the focal individual at random before starting behavioural observations. Samples lasted 1–5 min (see also Fernández-Juricic and Tellería 2000). Feeding (head-down) and scanning (head-up) were treated as mutually exclusive activities. We recorded the number and duration of scanning events and the number of times the focal individual pecked on the ground searching for food, and calculated scanning rate (number of head-up's per min), total time spent scanning (s/min), and food searching rate (number of pecks per min). All measurements were tape-recorded. We also measured some confounding factors that might have affected scanning and foraging behaviour: group size, grass cover (%), shrub cover (%), and tree cover (%).

Statistical analyses

To describe magpie attacks and to assess the association among type of magpie attack, prey position, and prey group size we pooled the data of the three breeding seasons because general predation patterns did not differ among years. However, to assess variations in attack rates and selection ratios, we analysed separately the 1997 and 1998 breeding seasons. Pearson product moment correlations were used to analyse the relationship between attack rate and prey density.

Because of the low number of captures (see Results), we decided to assess whether magpies showed any preference when *attacking* different prey species. Hence, we estimated selection ratios at the population level (following Krebs 1998 and Manly et al. 2002) considering prey attacked rather than killed. Our experimental design can be considered as type I (Manly et al. 2002), with determination of prey being attacked and prey availability (prey density) across all the studied parks and no individual recognition of magpies. For a given prey species, we calculated the selection ratio (w_I) as the proportion of the sample of attacked individuals divided by the proportion of available individuals. Selection ratios that did not differ from 1 suggest that prey were attacked in proportion to their abundance, above 1 indicated preference, and below 1 indicated avoidance. To determine whether a selection ratio was significantly different from 1, we first estimated the standard error of w_I and then calculated the significance using a Chi-square test with one degree of freedom following Manly et al. (2002).

The relationship between type of magpie attack, prey position, and prey group size was assessed with a log-linear analysis. We included the three factors in the model and presented results of partial and marginal associations (StatSoft 2003).

We used a factorial ANOVA to analyse the effect of the presence of magpies within sampling plots on the number and overall abundance of prey species. Two factors were included: scenario and park. We used an ANCOVA to analyse variation in heterospecific nearest neighbour distance. Two analyses were conducted with two independent factors each: (a) neighbour distance between prey species with and without magpies in three parks, and (b) neighbour distance between magpies and prey with one and more than one prey species in three parks. Magpie and prey group sizes were included as co-variates in both analyses to control for potential relationships with neighbour distance. The following variables were normalized by log-transformation: neighbour distances, magpie group size, and prey group size. To analyse the effects of magpies on the scanning and foraging behaviour of prey species, we used an ANCOVA analysis, with two factors: scenario and park. Four co-variates were incorporated in the models to control for potential confounding factors: group size, grass cover, shrub cover, and tree cover. Scanning time and rate, and food searching rate were logtransformed to meet normality assumptions. In all ANCOVA analysis, the park was considered a random factor.

Reported throughout Results are means ± SE. Statistical analyses were conducted with STATISTICA 6.1.

Results

General patterns of magpie predation

During three consecutive breeding seasons (1997–1999), we recorded 101 attacks by magpies on 12 bird species (Table 1). Only 5 of 101 attacks resulted in successful prey capture: (4.9% success): house sparrow (2 of 14 attacks, 14.3% success), greenfinch (1 of 1 attack, 100% success), rock dove (1 of 7 attacks, 14.3% success), and woodpigeon (1 of 7 attacks, 14.3% success). Magpies attacked alone in 94 of the observed cases (93.1%), 6 times in pairs (5.9%), and only once in a group of 6 individuals (1%).

Attack rate varied from as low as one attack per 253 observation hours in 1997 to as high as one attack per 15 observation hours in 1998 (Table 1). We did not find a significant relationship between attack rate and prey density in either breeding season (1997, r=0.504, P=0.114, n=11; 1998, r=−0.05, P=0.922, n=7).

Selection ratios varied among prey species (Table 1). In 1997, one species was preferred (blackbird), one was avoided (house sparrow), and 9 species were selected in proportion to their abundance (starling, rock dove, woodpigeon, hoopoe, treecreeper, great tit, serin, greenfinch, stock dove; Table 1). In 1998, two species were preferred (blackbird, starling), two were avoided (house sparrow, rock dove), and three were selected in proportion to their abundance (woodpigeon, serin, green woodpecker; Table 1). The selection ratios did not change when our analyses were based on availability of flocks instead of availability of individuals (available from the authors upon request).

We found a relationship among the type of magpie attack, position of prey when attacked, and prey group size. The model that best fitted the observed frequencies included two effects (partial association, χ^2=2.72, df=5, P=0.742) that could be interpreted as follows. Magpies usually launched an attack from the air rather than from the ground. They selectively attacked prey flying or on the ground rather than prey perching (marginal association, χ^2=7.95, df=2, P=0.018, Table 2). Also, magpies usually attacked solitary prey rather than prey in groups (marginal association, χ^2=21.22, df=1, P<0.001, Table 3). When excluding either effect, the model fit became significantly worse than with the two effects considered simultaneously (partial association, χ^2 > 20, df=1–5, P<0.001).

Table 2 Marginal frequency for the effects included in the log-linear model that fitted the observed frequencies showing association between type of magpie attack and position of the target individuals

Type of attack	Position of target individuals			Total
	Flying	Perching	Ground	
Flying	38	9	37	84
Ground	0	0	9	9
Total	38	9	46	93

Table 3 Marginal frequency for the effects included in the log-linear model that fitted the observed frequencies showing group size of the target individuals

Group size of target individuals		Total
Alone	Group	
69	24	93

Number and abundance of prey species per patch

The mean number of prey species foraging on the ground decreased significantly when magpies were present within the sampled patches ($F_{1,2}$=31.39, P<0.03, Fig. 1). However, the number of ground-foraging species perching in trees/bushes did not vary significantly with and without the presence of magpies within patches ($F_{1,2}$=1.15, P=0.465, Fig. 1). Mean abundance of all prey species on the ground did not vary significantly with the presence or absence of magpies (without magpies, 3.45±0.44; with magpies, 3.12±0.45; $F_{1,2}$=0.63, P=0.509), and neither did the mean abundance of all prey species perching in trees/bushes (without magpies, 2.82±0.31; with magpies, 2.41 ±0.32; $F_{1,2}$=0.99, P=0.423). The effects of park and the interaction between park and the presence of magpies were not significant (P>0.05).

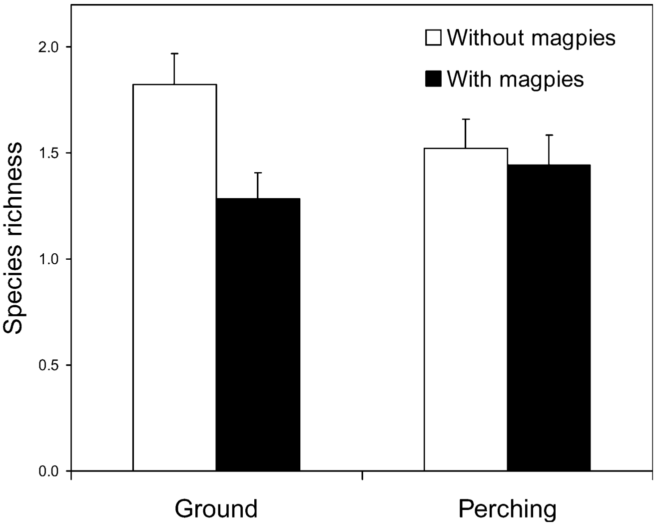

Fig. 1 Mean prey species richness when foraging on the ground and perching on trees/bushes without and with magpies present within resource patches

Heterospecific neighbour distances

The distance between magpies and prey species did not vary significantly when there was one or more than one prey species present in the patch (one, 12.46±0.84; more than one, 11.02±0.88; $F_{1,2}$=0.23, P=0.671). The effects of park, interaction between park and number of prey species, magpie group size, and prey group size were not significant (P>0.05). However, after controlling for prey group size ($F_{1,160}$=12.05, P<0.001), mean neighbour distance between species decreased significantly when magpies were present in the patches (magpie absent, 2.93 ±0.18; magpie present, 0.82±0.29; $F_{1,4}$=32.62, P<0.01). This effect did not differ significantly between the three parks studied (P>0.05). Finally, the effects of magpie group size and the interaction between the presence/absence of magpies and parks were not significant (P>0.05).

Prey scanning and foraging behaviour

Avoided prey species

The foraging behaviour of house sparrows was not statistically different when magpies were present or absent (scanning time, $F_{1,2}$=0.23, P=0.679; scanning rate, $F_{1,2}$=0.02, P=0.901; food searching rate, $F_{1,2}$=0.26, P=0.658; Fig. 2). We found a group size effect, whereby scanning time ($F_{1,60}$=5.15, P<0.03) and scanning rate ($F_{1,60}$=4.51, P<0.05) decreased with the number of conspecifics. All other studied effects (park, interaction between park and presence/absence of magpies, grass cover, shrub cover, and tree cover) were not significant (P>0.05).

Preferred prey species

Blackbirds increased the amount of time allocated to scanning with the presence of magpies ($F_{1,2}$=26.74, P<0.03, Fig. 2a). Scanning rate increased when magpies were present in the sampling plot ($F_{1,2}$=34.95, P<0.03, Fig. 2b). Controlling for variations in grass cover ($F_{1,93}$=6.01, P<0.02), food searching rate decreased when magpies were in the sampling plot ($F_{1,2}$=21.91, P<0.05, Fig. 2c), probably as a result of more time invested in scanning. All other studied effects (park, interaction between park and presence/absence of magpies, group size, shrub cover, and tree cover) were not significant (P>0.05).

Prey attacked in proportion to its availability

Woodpigeons did not show significant differences in their scanning time with the presence or absence of magpies ($F_{1,2}$=0.19, P=0.699, Fig. 2a). However, scanning rate did increase when magpies were present in the sampling plot ($F_{1,2}$=44.52, P<0.03, Fig. 2b). Finally, food searching rate was not affected significantly by the presence of magpies ($F_{1,2}$=1.39, P=0.350, Fig. 2c); however, it did increase with group size ($F_{1,78}$=7.11, P<0.01). All other studied effects (park, interaction between park and presence/absence of magpies, grass cover, shrub cover, and tree cover) were not significant (P>0.05).

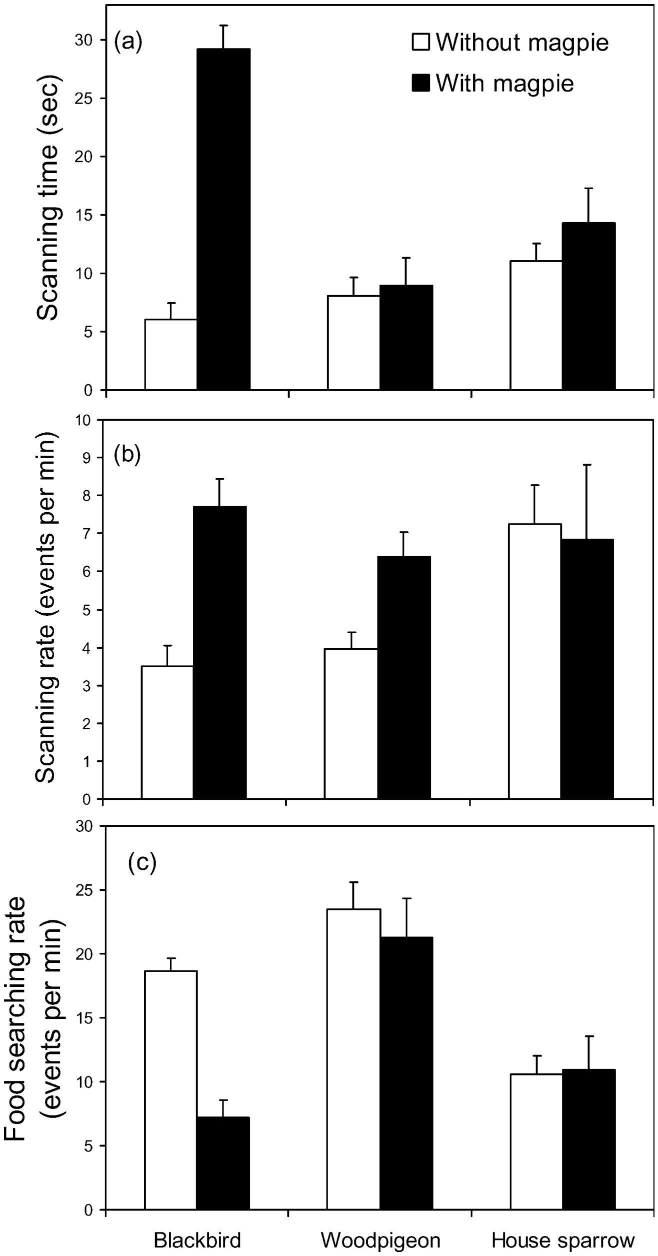

Fig. 2a–c Variations in **a** scanning time, **b** scanning rate, and **c** food searching rate among three species (blackbirds *Turdus merula*, woodpigeons *Columba palumbus*, and house sparrows *Passer domesticus*) in two scenarios: individuals foraging without and with magpies

Discussion

Predation patterns

Magpies prey on adult birds only during the breeding season. Capture success appears to be low (4.9%) compared to other raptor systems that were studied using similar methodology (e.g., Cresswell 1996: *Accipiter nisus*, 9.9%; *Falco columbarius* 8.8%; *F. peregrinus*, 5.7%). This may be related to the fact that magpies are non-specialized predators and that adult bird hunting may be a secondary, rather than a primary, source of protein to feed chicks (Birkhead 1991).

Magpies mainly targeted prey on the ground or flying between patches. This may increase the surprise factor because magpies launched their attacks from perching positions reducing the time exposed to prey. Moreover, magpie tendency to attack solitary individuals, instead of those foraging in groups, may be explained by several factors. Solitary individuals may have lower probability of detecting attacking predator than those foraging in flocks (e.g., Neill and Cullen 1974, Powell 1974; Cresswell 1994, but see Fernández-Juricic and Schroeder 2003). Singling out solitary prey may be easier than when prey forage in groups (confusion effect, e.g., Krakauer 1995). Finally, solitary individuals may be in worse body conditions than individuals in groups (e.g., Kenward 1978).

Inter- and intra-specific prey responses to opportunistic predation

Inter-specifically, the decrease in the mean number of prey species foraging near magpies can be considered a common response to increased predation risk (reviewed in Lima and Dill 1990). However, we did not find a similar effect on prey abundance, probably because of restricted patch profitability that limited the number of individuals per patch. Our results suggest that prey may have moved towards predator-free patches, where the time available to foraging would be higher due to lower predation risk, rather than hiding within patches (e.g., perching in trees/ bushes) in high risk situations.

Different prey species also increased aggregation when magpies were present in a foraging patch. We cannot regard these tighter aggregations as flocks, because heterospecifics did not co-ordinate movements in and out of patches. Nevertheless, it is an interesting effect taking into account that the prey species studied are not considered to form inter-specific aggregations during the breeding season. Similar seasonal responses were found in forest passerines, which clumped their breeding territories when the perceived risk of predation increased (Forsman et al. 1998). The tendency to form aggregations in our system may be accounted for by the lower probabilities of magpies attacking groups, and the lower chances of prey being caught if an attack occurred due to dilution effects (e.g., Whitfield 2003).

There are relatively few theoretical and empirical studies on the intra-specific responses to opportunistic predation (e.g., Lima 1992; Matsuda et al. 1993; Stanford 1995; Ward et al. 1997; Bshary and Noë 1997). For instance, hedgehogs (*Erinaceus europaeus*) avoided patches and reduced foraging effort in response to the odours of its opportunistic predator, the badger (*Meles meles*); but these reactions vanished within a couple of days in experimental conditions and after a few minutes in natural situations (Ward et al. 1997). Red colobus monkeys (*Colobus badius tephrosceles*) responded to opportunistic predation by chimpanzees (*Pan troglodytes schweinfurthii*) by moving to the upper canopy, reducing neighbour distance, emitting specific vocalizations and varying vocal rates with the distance to predators (Stanford 1995).

We found differential responses to opportunistic predation. Species that were preferentially attacked (blackbird) or attacked in proportion to their abundance (woodpigeon) showed some anti-predator responses; whereas the species that was attacked less than in proportion to its abundance (house sparrow) did not show any behavioural adjustment to the presence of magpies. These responses are akin to the predictions of Lima's (1992) model concerning prey facing non-dangerous predators. This model entails a two-predator system with varying risk to prey, which exhibit nonspecific defences (e.g., those effective for both predators). The model predicts that as attack rate increases, so does anti-predator behaviour (e.g., proportion of time vigilant), but only when predators are easy to detect in order to escape successfully. However, species in which the chances of detecting predators successfully are much lower may not modify anti-predator behaviour in the presence of predators. This is because their best strategy to reduce mortality may be minimizing time exposed to predators rather than increasing vigilance. This might be the case of house sparrows whose probability of detecting disturbances has been shown to be much lower than blackbirds and woodpigeons (Fernández-Juricic et al. 2001b). The lack of house sparrow responses to magpies could be related to conflicting anti-predator strategies. If house sparrows have different responses to different predators (e.g., aerial, ground), they would tend to ignore predation from rare or occasional ones (Matsuda et al. 1993), as spending time in preventing opportunistic predation may be too costly.

Species that did respond to opportunistic predation showed different strategies, which may be related to the frequency of predator–prey interactions (e.g., magpie attack rates). As blackbirds are preferentially attacked, they may need to deploy more responses (increasing both scanning time and scanning rate) to ensure they would detect an attack. The pass-along effect may be also implicated (Lima 1990), as blackbirds that successfully evaded an attack may have increased the chances of an attack to other individuals. Woodpigeons, on the other hand, had fewer attacks relative to blackbirds, and displayed only one anti-predator strategy (increasing scanning rates). By interrupting foraging more often, woodpigeon inter-scan intervals would shorten (Hart and Lendrem 1984), enhancing the chances of keeping track of magpie movements.

We conclude that magpie predation can be considered opportunistic in the sense that it may be an occasional foraging strategy. However, magpies do not attack at random. They differentially attack several prey species with different relative abundances. As a result, prey tended to invest more in anti-predator responses when relative predation risk (e.g., attack rates in relation to abundance) was higher (Cresswell et al. 2003).

Implications for the ecology of predator–prey interactions

A recent study (Lima 2002) pointed out that understanding predator behaviour will bring more insights into the theory of predator–prey interactions. Along these lines, our results suggest that opportunistic predators show targeting behaviour under circumstances that may increase capture probabilities (e.g., prey alone rather than in groups). However, Cresswell et al. (2003) found that opportunistic predators may not be selective on the basis of body posture (e.g., preferentially targeting head-down foraging individuals). Therefore, we extend Lima's (2002) suggestion and call for a theoretical reassessment of the role of opportunistic, as opposed to specialized, predation, as many prey species deploying anti-predator behaviour face multi-predator environments (Lima 1990; Sih et al. 1998). This task will require more empirical studies in systems other than avian.

Given the relatively low levels of capture success detected in our system, our data support the view that mortality per se may not be a good indicator of predation risk (Lima 1990, 2002). Instead, anti-predator behaviour appears to be regulated by the probability of being attacked. Therefore, capture rates would have more to do with anti-predator strategies of different species than with the number of available prey of those species (Abrams 1993). This may be particularly relevant for opportunistic predators, because of the wide variety of potential prey species. It follows that functional and numerical responses of *opportunistic* predators should be estimated considering not only predator and prey abundances (Abrams and Ginzburg 2000; Vucetich et al. 2002), but also the composition of prey communities and the complex relationship between predator targeting behaviour and inter- and intra-specific anti-predator responses. For instance, when opportunistic predators show no preference and prey show non-specialized anti-predator responses, functional responses may be a function of prey density alone. However, functional responses may also be affected by prey behaviour when prey show different types of specialized anti-predator responses.

Acknowledgements We thank Patrick Zollner, Vanessa Quinn, Brian Sturtevant, and two anonymous referees for comments and feedback.

References

Abrams PA (1993) Why predation rate should not be proportional to predator density. Ecology 73: 726-733

Abrams PA (2000) The evolution of predator–prey interactions: theory and evidence. Annu Rev Ecol Syst 31:79–105

Abrams PA, Ginzburg LR (2000) The nature of predation: prey dependent, ratio dependent or neither? Trends Ecol Evol 15:337–341

Attridge W (1997) Magpie catching house martin. Br Birds 90:191–192

Birkhead T (1991) The magpies: the ecology and behavior of black-billed and yellow-billed magpies. Poyser, London

Bshary R, Noë R (1997) Anti-predation behaviour of red colobus monkeys in the presence of chimpanzees. Behav Ecol Sociobiol 41:321–333

Cramp S (ed) (1994) Handbook of the birds of Europe, the Middle East and North Africa. The birds of the western Palearctic, vol VIII, Crows to finches. Oxford University Press, Oxford

Cresswell W (1993) Escape responses by redshanks, *Tringa tetanus*, on attack by avian predators. Anim Behav 46:609–611

Cresswell W (1994) Flocking as an effective anti-predation strategy in redshanks, *Tringa totanus*. Anim Behav 47:433–442

Cresswell W (1996) Surprise as a winter hunting strategy in Sparrowhawks *Accipiter nisus*, Peregrines *Falco peregrinus* and Merlins *F. columbarius*. Ibis 138:684–692

Cresswell W, Lind J, Kaby U, Quinn JL, Jakobsson S (2003) Does an opportunistic predator preferentially attack nonvigilant prey? Anim Behav 66:643–648

Fernández-Juricic E, Tellería JL (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, Sanz R, Sallent EA (2001a) Frequency-dependent predation by wild birds at edges and interiors of woodland. Biol J Linn Soc 73:43–49

Fernández-Juricic E, Jimenez MD, Lucas E (2001b) Alert distance as an alternative measure of bird tolerance to human disturbance. Implications for park design. Environ Conserv 28:263–269

Fernández-Juricic E, Jimenez MD, Lucas E (2002) Factors affecting intra- and inter-specific variations in the difference between alert and flight distances in forested habitats. Can J Zool 80:1212–1220

Fernández-Juricic E, Schroeder N (2003) Do variations in scanning behaviour affect tolerance to human disturbance? Appl Anim Behav Sci 84:219–234

Forsman JT, Mönkkönen M, Inkeröinen J, Reunanen P (1998) Aggregate dispersion of birds after encountering a predator: experimental evidence. J Avian Biol 29:44–48

Hart A, Lendrem DW (1984) Vigilance and scanning patterns in birds. Anim Behav 32:1216–1224

Hochackka WM, Scharf CS (1986) Black-billed Magpie, *Pica pica*, predation on bats. Can Field Nat 100:121–122

Järvinen O, Väisänen RA (1975) Estimating relative densities of breeding birds by the line transect method. Oikos 29:225–228

Kenward RE (1978) Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. J Anim Ecol 47:449–460

Krakauer DC (1995) Groups confuse predators by exploiting perceptual bottlenecks: a connectionist model of the confusion effect. Behav Ecol Sociobiol 36:421–429

Krebs CJ (1998) Ecological methodology. Benjamin Cummings, New York

Lima SL (1990) Evolutionary stable antipredator behavior among isolated foragers: on the consequences of successful escape. J Theor Biol 143:77–89

Lima SL (1992) Life in a multi-predator environment: some considerations for anti-predatory vigilance. Ann Zool Fenn 29:217–226

Lima SL (1998a) Nonlethal effects in the ecology of predator–prey interactions. Bioscience 48:25–34

Lima SL (1998b) Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Adv Study Behav 27:215–290

Lima SL (2002) Putting predators back into behavioral predator–prey interactions. Trends Ecol Evol 17:70–75

Lima SL, Dill ML (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Matsuda H, Abrams PA, Hori M (1993) The effect of adaptive anti-predator behaviour on exploitative competition and mutualism between predators. Oikos 68:549–559

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies. Kluwer, Dordrecht

Neill SRStJ, Cullen JM (1974) Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. J Zool 172:549–569

Newton I (1998) Population limitation in birds. Academic, San Diego

Powell GVN (1974) Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. Anim Behav 22:501–505

Roberts G (1996) Why individual vigilance declines as group size increases? Anim Behav 51:1077–1086

Sih A, Englund G, Wooster D (1998) Emergent impacts of multiple predators on prey. Trends Ecol Evol 13:350–355

Stanford CB (1995) The influence of chimpanzee predation on group size and anti-predator behaviour in red colobus monkeys. Anim Behav 49:577–587

StatSoft, Inc. (2003) Electronic Statistics Textbook. Tulsa, Okla. Available at: http://www.statsoft.com/textbook/stathome.html

Thomas M (1982) Magpie chasing and probably catching House sparrow. Br Birds 75:36–37

Vucetich JA, Peterson RO, Schaefer CL (2002) The effect of prey and predator densities on wolf predation. Ecology 83:3003–3013

Ward JF, MacDonald DW, Doncaster CP (1997) Responses of foraging hedgehogs to badger odour. Anim Behav 53:709–720

Whitfield DP (2003) Redshank *Tringa totanus* flocking behaviour, distance from cover and vulnerability to sparrowhawk *Accipiter nisus* predation. J Avian Biol 34:163–169