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Frequency-dependent predation by birds at edges and interiors of woodland

ESTEBAN FERNÁNDEZ-JURICIC[1]*, RUBEN SANZ[2] and ANGEL SALLENT[3]

[1]*Departamento de Biología Animal I, Facultad de Biología, Universidad Complutense de Madrid, Madrid E 28040, Spain*
[2]*Departamento de Biología Vegetal I, Facultad de Biología, Universidad Complutense de Madrid, Madrid E 28040, Spain*
[3]*Grupo de Ecología Aplicada, C/Maudes 23 2°D. 28003, Madrid, Spain*

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Structural variations between edge and interior areas within forest fragments may bring about differences in food availability that may influence the selective behaviour of predators and prey population dynamics. The purpose of this paper was to assess patterns of artificial prey selection by wild birds (House Sparrow *Passer domesticus* and Rock Dove *Columba livia*) between edge and interior areas of woodland, taking into account differences in prey frequency (10% of one food type and 90% of the other) and density (30 baits/m^{-2} and 50 baits/m^{-2}). Experiments were conducted at 24 plots in 3 forest fragments in the city of Madrid, Spain. Selectivity did not vary among parks or between densities. However, selectivity did vary with the frequency and location of baits, showing an anti-apostatic trend (baits were preferred at low rather than at high frequencies) that was more pronounced at interiors than at edges. Two possible factors that may account for stronger anti-apostatic selection at edges are the higher densities of predators and pedestrians found there. However, there are many other possible explanations, and no specific conclusion can be supported with the current data. The results of this study also point out that site heterogeneity should be taken into account in the experimental design of future studies on frequency-dependent food selection by wild birds, particularly in fragmented landscapes.

ADDITIONAL KEYWORDS: frequency-dependent selection – birds – anti-apostatic selection – edge effects – fragmentation.

INTRODUCTION

Forest fragmentation increases habitat loss and formation of forest fragments, which above certain threshold sizes present two structurally and functionally different areas, usually known as edges and interiors (Faaborg *et al.*, 1995). Structurally, edges differ from interior areas due to vegetation structure and microclimatic variations (Saunders, Hobbs & Margules, 1991). Functionally, edges attract several species due to the higher availability of food in the surrounding matrix and of nesting sites in the fragment, at the expense of higher predation and parasitism (Murcia, 1995; McCollin, 1998). Comparatively little empirical evidence is available about how edge/interior areas affect individual behaviour and population dynamics, despite recent theoretical advances (Fagan, Cantrell & Cosner, 1999).

Structural variations between edge and interior areas may bring about differences in food availability (e.g. seed types) (Gates & Gysel, 1978; McCollin, 1998), which may be expected to influence the selective behaviour of predators and prey population dynamics (Murdoch & Oaten, 1975; Allen, 1988). One such behaviour is frequency-dependent predation, which refers to selection that is affected by the relative frequency of the food types (Greenwood, 1985; Allen, 1988). Pro-apostatic selection occurs when predators consume disproportionately more common prey types, whereas anti-apostatic selection implies that predators consume disproportionately more rare prey. Besides frequency, prey density may play an important role in the decision-making of predators, with pro-apostatic

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* Corresponding author. Present address: Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS. E-mail: estebanfj@yahoo.com.

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selection usually occurring at low prey densities, and anti-apostatic selection, at high prey densities (Allen, Raison & Weale, 1998; Weale *et al.*, 2000). Both types of selection have very different consequences for prey populations: pro-apostatic selection fosters diversity in populations or communities (Chesson, 1984), whereas anti-apostatic selection favours homogeneity (Allen, 1988).

There is little empirical evidence as to how frequency dependent predation varies between edges and interiors of woodland. Determination of a predator's food selectivity in both areas would allow us to deepen our understanding of how fragmentation conditions may affect the behaviour of predators within fragments, and the possible consequences for prey population stability. The purpose of this paper is to compare patterns of prey-selection by wild birds (seed-predators) in edge vs. interior areas of woodland. The study was conducted in three large forest fragments in the city of Madrid, Spain. Urban ecosystems are interesting arenas for studying ecological patterns and processes at community, population and individual levels (Crooks & Soulé, 1999; Niemelä, 1999; Grim *et al.*, 2000). Urban landscapes usually consist of a set of newly created fragments (different-sized urban parks) isolated from one another by an urban matrix that may restrain wildlife movements (Fernández-Juricic, 2000a). Within urban parks some species are concentrated in the interior areas (forest specialists), whereas others are at the edges (generalists) (Adams & Dove, 1989). That was the case with wooded parks in Madrid, where some generalist species (mainly the House Sparrow *Passer domesticus* and the Rock Dove *Columba livia*) show a preference for edges, apparently affected by higher human activity in the edges, which may increase their foraging opportunities due to the availability of refuse, food-leftovers, etc. (Fernández-Juricic, 2001). We tested the effects of prey frequency and density on predation by these species at edges and interior areas.

METHODS

STUDY AREA

Urban parks in the city of Madrid harbour several bird species whose patterns of distribution and abundance are similar to those in other fragmented landscapes (Fernández-Juricic, 2000a–c). We conducted experiments in July 1999 in the Oeste (98 ha) and Retiro (110 ha) parks, and in March 2000 in the Austria (30 ha) park. All of the parks were created more than 40 years ago, and are structurally representative of the other parks in Madrid, with extensive areas of grass, shrub cover, and a mix of deciduous and coniferous trees. We considered an edge to be the 60-m wide belt that constituted the border of the wooded park, to reduce the confounding effects of park size (Brawn & Robinson, 1996). Forest interior areas were sampled at least 100 m away from the border. A previous study in Madrid analysing six wooded parks (including the ones sampled in this study) showed that habitat structure was not different between edge and interior areas within each park, taking into account several measures of vegetation cover (grass, shrub, and tree), number of shrub and tree species, and number of stems <10, 10–50, and >50 cm diameter at breast height (DBH) (Fernández-Juricic, 2001).

PREDATOR SPECIES

Although other species were occasionally seen consuming baits (see below), the experiments were designed for House Sparrows and Rock Doves, since their presence was widespread in this landscape. These model species have been used in many frequency dependent predation studies (reviewed in Allen, 1988; Allen *et al.*, 1998), as in other food selection studies (e.g. Elcavage & Caraco, 1983; Elgar, 1987; Breitwisch & Hudak, 1989). The densities of sparrows and doves are higher at edges than at interior areas in wooded parks of Madrid (Fernández-Juricic, 2001).

PREY ITEMS

In a preliminary study, we tested during two-week periods how birds reacted to seeds, pastry baits, coloured bread, and brown and white bread; the latter being the most effective bait for attracting birds. Brown and white bread were approximately equivalent in energetic terms, but they differed slightly in composition (mean values per 100 g; white bread, energetic value = 285 kcal, proteins = 9 g., carbohydrates = 51 g, and lipids = 5 g; brown bread, energetic value = 256 kcal, protein = 8 g, carbohydrates = 49 g, lipids = 4 g, saturated acid oils = 0.5 g, fibre = 7 gr, and sodium = 0.5 g.; R.S.I. Company, Madrid). Baits were then made of brown and white dry bread cut into small cubes (1 cm^3). The size and colour of both types of baits made them clearly distinguishable from the background, at least to the human eye. Visitors to parks usually supply white and brown bread, and both species were accustomed to feeding on it. However, it is unlikely that birds were overfed when experiments were conducted on the following grounds. Early in the morning, birds spent most of their time searching for food and feeding, and did not rely on people, as they began visiting parks (and thus feeding birds) after lunch. We thus focused our sampling at morning (8:00 to 12:00 a.m.). Second, parks were cleaned quite thoroughly before we started our experiments, so no leftovers of any kind remained for birds to feed on.

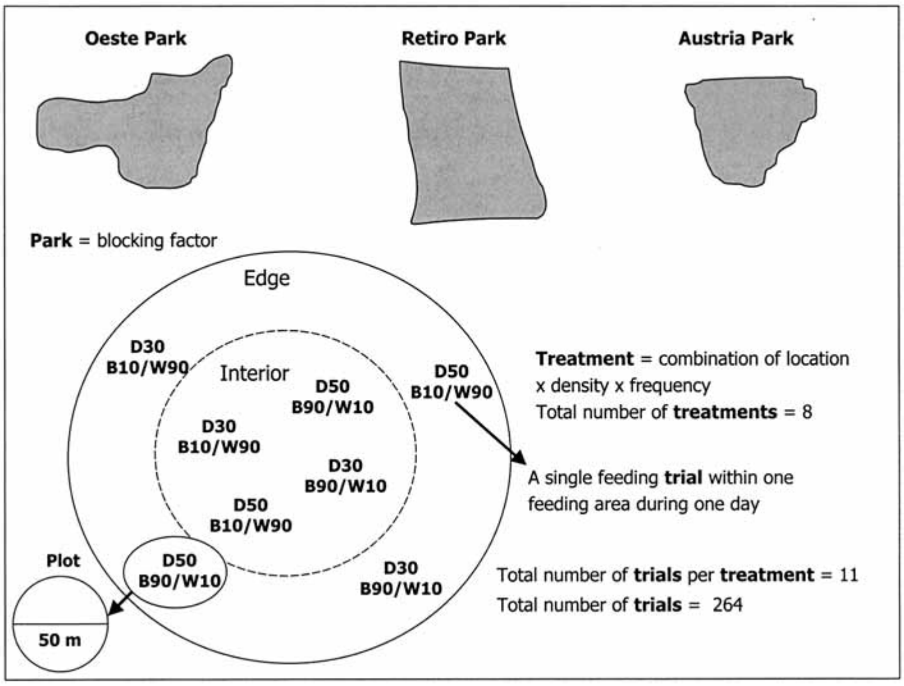

Figure 1. Schematic representation of the experimental design. Three factors were examined simultaneously: location (edge, interior), density (30 baits/m^{-2} and 50 baits/m^{-2}), and frequency (10% and 90%). Park (Oeste, Retiro, Austria) was considered a blocking factor. Trials were conducted in 25-m radius circular plots. See details on the text. D, density; B, brown baits; W, white baits.

EXPERIMENTAL DESIGN

Our sampling design consisted of three factors tested simultaneously: location within park (edge/interior), frequency of baits, and density of baits. Park was considered a blocking factor. At each park, we conducted eight trials per day, totalling four combinations of frequency × density in each area (four at edge and four at interior areas, Fig. 1). Trials were conducted on 25-m radius circular plots (Fig. 1). Plots within parks were separated from one another by at least 250–500 m (and parks were separated by 3247 ± 912 m) so as to reduce the prospect that birds fed in more than one plot.

In each trial, baits were presented at two frequencies: 10% of one type of bread and 90% of the other. Baits were randomly scattered in a 1 m^2 area at two densities: low, 30 baits/m^{-2}, and high, 50 baits/m$^-$2 (Fig. 1). We totalled 264 trials, with 11 trials per treatment (each of the 8 location × frequency × density combinations) in each park. Baits were laid out on a grass lawn, at least 3 m away from pathways. Trials lasted 4 hours, and were checked every hour to determine whether people removed baits. If so, such trials were not taken into account, and were repeated the next day. Pecked baits were considered predated. We sampled every other day in each park, totalling 41 sampling days.

STATISTICAL ANALYSES

We analysed the selectivity of predators with the β index (Manly, 1974), following the procedures of Church, Jowers & Allen (1997). The preference for brown prey was assessed as: $\beta_{brown} = [\log (b/B)/\log (b/B) + \log (w/W)]$; where B and W represent the number of brown and white prey items presented, and b and w the number of brown and white prey items left at the end of a trial. β_{brown} ranges from 0 (total rejection of brown baits) to 1 (exclusive preference for brown baits). When one type of prey was completely consumed, β values were calculated by setting the number of remaining prey as 0.0001, following Church *et al.* (1997).

To analyse the effect of location, frequency, and density on β values, we used a mixed-effect ANOVA with variance component analysis, using a two-tiered approach: first, by analysing the relative importance of variation among days versus variation among parks; and second, by testing treatment effects based on error among parks. We defined σ^2 as the error term among days, σ^2_P as the additional error among parks, σ^2_{TP} as the error among treatments, and σ^2_{TP} as the error due to the interaction between parks and treatments (Table 2A). In this first analysis, we considered park as a random factor, and treatment (all eight location × density × frequency combinations) as one single fixed

Table 1. Means (±SD) of the selectivity index (β_{brown}) corresponding to park, location, density, and frequency effects

Effect	B_{brown}	SD
Park		
Retiro	0.49	0.18
Oeste	0.54	0.27
Austria	0.56	0.27
Location		
Edge	0.49	0.19
Interior	0.56	0.29
Density		
30 baits/m^{-2}	0.54	0.24
50 baits/m^{-2}	0.52	0.26
Frequency		
10%	0.59	0.21
90%	0.47	0.26

factor. We did not deem necessary to include density and frequency as nested factors within location, because we assumed that the variability of plots within locations (within edges and interiors) was similar to that between locations (between edges and interiors). Such an assumption was based upon the fact that plots within locations were as far apart from each other as they were from plots in other locations (see above), and that habitat structure did not differ between edges and interiors (Fernández-Juricic, 2001). In the second part of the analysis, we tested for location, frequency, and density effects and their interactions using MS_{TP} as the denominator of the F-ratio (Table 3).

RESULTS

Of the baits consumed, 97% were predated by House Sparrows and Rock Doves. Occasionally, we registered Blackbirds (*Turdus merula*) and Magpies (*Pica pica*).

Selectivity for brown baits did not vary among parks (Tables 1, and 2A), and the interaction between park and treatment was not significant (Table 2A). The only significant effect was treatment (the combination of location, frequency, and density) (Table 2A); however, it accounted for a low proportion (nearly 10%) of the overall variability (Table 2B).

Breaking down treatment effects, we found that selectivity was higher at interiors than at edges, although density of baits did not affect selectivity (Tables 1 and 3). Selectivity varied significantly with the frequency of baits, showing an anti-apostatic trend: brown baits were preferred at low rather than at high frequencies (Tables 1 and 3). This anti-apostatic trend was significantly more pronounced at interior than at edge areas (location × frequency interaction, Table 3, Fig. 2). All other interactions (location × density, frequency × density, location × frequency × density) were not significant (Table 3).

DISCUSSION

Our results indicate that selection by wild birds feeding at edge and interior areas of forest fragments was frequency dependent. The behaviour of individuals differed at edge and interior areas in such a way as to determine anti-apostatic preferences for food: birds selected rare rather than common food items (Allen, 1988). Anti-apostatic selection has been found in several studies involving other types of baits, and with bird species similar to those considered in this study (Horsley *et al.*, 1979; Allen & Anderson, 1984; Wilson, Allen & Anderson, 1990; Church *et al.*, 1997; Allen *et al.*, 1998; Weale *et al.*, 2000).

According to our results, the strength of anti-apostatic selection increased at interior areas. Such a pattern is expected to be related to differences between edge and interior areas. A previous study showed that in large wooded parks of Madrid (including those used in this study) densities of sparrows and Rock Doves as well as pedestrian rates were higher at edges than in interior areas (Fernández-Juricic, 2001). On the one hand, competition for food would increase at edges since more individuals have to cope with their energetic requirements. Individual birds would have less opportunities to take many food items as they are quickly consumed, which would modify their food choice in direct response to competitors (Plowright & Landry, 2000). On the other hand, pedestrians affect the feeding behaviour of these species, restraining the time devoted to searching and consuming food (Fernández-Juricic, 2000b; Fernández-Juricic & Tellería, 2000). Thus, it might be possible that at edges feeding bouts were shorter than in interior areas. Both factors may have led individuals to forage more randomly at edges (Church *et al.*, 1997), reducing the strength of anti-apostatic selection in relation to interior areas. Even though these are two possible explanations, other reasons may be proposed to account for strong anti-apostatic selection at interiors, such as variation in food preference among individuals (Allen & Anderson, 1984; Chesson, 1984), microclimate differences between edges and interiors of forest fragments (Saunders *et al.*, 1991; McCollin, 1998), the influence of landscape composition (Fagan *et al.*, 1999), etc. Nevertheless, no conclusive explanation can be reached with our data.

Previous studies pointed out that at low prey densities selection is pro-apostatic, and as prey density increases, it becomes anti-apostatic (Allen, 1988; Allen *et al.*, 1998; Weale *et al.*, 2000). Despite our prey density variations, we did not find such an effect. The most

Table 2. Mixed-effect ANOVA for β_{brown}, considering park as a random factor, and treatment (combining location × density × frequency) as one single fixed factor. (A) General results showing the degrees of freedom (df), mean squares (MS), expected mean squares E[MS], F-ratios, and the associated probability. Significant results are marked in bold. (B) Percentage contribution of each factor to the overall variability

(A)

Source of variation	df	MS	E[MS]	*F*	*P*
Treatment	7	$MS_T=0.249$	$\sigma^2+n\ \sigma^2_{TP}+3n$	$MS_T/MS_{TP}=3.917$	**0.014**
Parks	2	$MS_P=0.154$	$\sigma^2+8n\ \sigma^2_P$	$MS_P/MS_D=2.84$	0.063
Treatment × Parks	14	$MS_{TP}=0.064$	$\sigma^2+n\ \sigma^2_{TP}$	$MS_{TP}/MS_D=1.177$	0.293
Within plots (days)	240	$MS_D=0.054$	σ^2		
Total	263				

(B)

Variance component	Variance	Contribution (%)
σ^2_T	$(MS_T/MS_{TP})/(3n)=0.0056$	9.13
σ^2_P	$(MS_P/MS_D)/(8n)=0.0011$	1.83
σ^2_{TP}	$(MS_{TP}/MS_D)/(n)=0.0008$	1.41
σ^2	$MS_D=0.0541$	87.63
Total	$MS_D=0.0617$	100

Table 3. Mixed-effect ANOVA for β_{brown}, analysing individual effects (location, density, and frequency) and their interactions. Significant results are marked in bold; df, degrees of freedom; MS, mean squares

Source of variation	df	MS	*F*	*P*
Location	1	$MS_L=0.4307$	$MS_L/MS_{TP}=6.7626$	**0.021**
Density	1	$MS_D=0.0256$	$MS_D/MS_{TP}=0.4030$	0.536
Frequency	1	$MS_F=0.9433$	$MS_F/MS_{TP}=14.8103$	**0.002**
Location × Density	1	$MS_{L\times D}=0.0017$	$MS_{L\times D}/MS_{TP}=0.0267$	0.873
Location × Frequency	1	$MS_{L\times F}=0.3461$	$MS_{L\times F}/MS_{TP}=5.4341$	**0.035**
Density × Frequency	1	$MS_{D\times F}=0.0002$	$MS_{D\times F}/MS_{TP}=0.0028$	0.959
Location × Frequency × Density	1	$MS_{L\times F\times D}=0.1941$	$MS_{L\times F\times D}/MS_{TP}=3.0476$	0.102
Treatment × Parks	14	$MS_{TP}=0.0637$	$MS_{TP}/MS_D=1.177$	0.293
Within plots (days)	240	$MS_D=0.0541$		

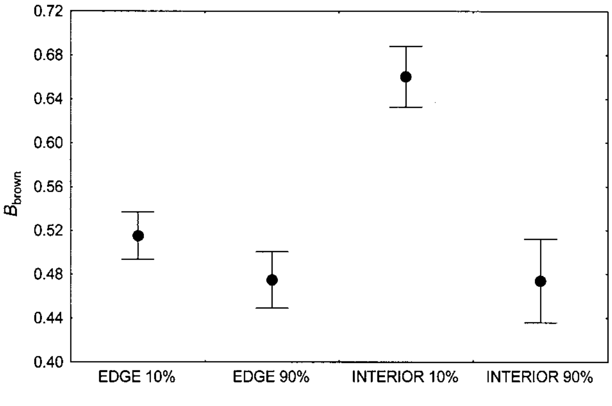

Figure 2. Effects of edge/interior areas and frequency of brown baits (10% and 90%) on selectivity by avian predators ($\beta_{brown}\pm SE$).

likely explanation may be related to the limited range of densities employed (30–50 baits/m^{-2}), as birds may have not distinguished between such variations. Indeed, studies in which density effects were apparent used greater ranges; for instance, 10 200 baits/m^{-2} (Horsley *et al.*, 1979), and 9990 baits/m^{-2} (Allen *et al.*, 1998), even though such huge prey densities are not generally found in natural conditions. Another alternative to explain the lack of density effects may come from our experimental design, which analysed density variations without changing plot size, and thus concentrated all baits in small patches. Church *et al.* (1997) explained that in this situation most baits can be easily detected in such small feeding patches, for birds have all necessary information clues about prey availability, and therefore frequency dependent effects may be lessened.

Two implications can be drawn from our results. First, the between-site variability in bird selection that has characterized many previous studies (e.g. Greenwood, 1985; Church *et al.*, 1997; Allen *et al.*, 1998) should be taken into account in the design of future prey selection experiments, as prey selectivity could differ markedly between areas, even within the same type of habitat. This may turn out to be the case when sampling in different-sized forest fragments, as the proportion of edges and interiors differs greatly, and so do the factors that could affect predator selectivity. Second, it may be suggested that populations of House Sparrows and Rock Doves follow different patterns of foraging behaviour between edge and interior areas within forest fragments. Such differential foraging specialization is likely to affect consumer-resource dynamics (Janzen, 1983; Santos & Tellería, 1994). For instance, House Sparrows and Rock Doves may favour or restrain the penetration to fragments of certain plant species, which can be expected to modify dispersal and establishment rates of different types of seeds (e.g. native vs. non-native). It can be expected that homogenization effects by means of local extinction of rare prey with anti-apostatic selection would be stronger in interior areas. Further study would be necessary to assess the role of seed-predator behaviour in the success of non-native vs. native species between edges and interiors of forest fragments.

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REFERENCES

Adams LW, Dove LE. 1989. *Wildlife reserves and corridors in the urban environment: a guide to ecological landscape planning and resource conservation.* Maryland: National Institute of Urban Wildlife, Columbia.

Allen JA. 1988. Frequency-dependent selection by predators. *Philosophical Transactions of the Royal Society of London B* **319:** 485–503.

Allen JA, Anderson KP. 1984. Selection by passerine birds is anti-apostatic at high prey density. *Biological Journal of the Linnean Society* **23:** 237–246.

Allen JA, Raison HE, Weale ME. 1998. The influence of density on frequency-dependent selection by wild birds feeding on artificial prey. *Proceedings of the Royal Society of London B* **265:** 1031–1035.

Brawn JD, Robinson SK. 1996. Source-sink population dynamics may complicate interpretation of long-term census data. *Ecology* **77:** 3–12.

Breitwisch R, Hudak J. 1989. Sex differences in risk-taking behavior in foraging flocks of House sparrow. *Auk* **106:** 150–153.

Chesson PL. 1984. Variable predators and switching behaviour. *Theoretical Population Biology* **26:** 1–26.

Church SC, Jowers M, Allen JA. 1997. Does prey dispersion affect frequency-dependent predation by wild birds? *Oecologia* **111:** 292–296.

Crooks KR, Soulé ME. 1999. Mesopredator release and avifaunal extinction in a fragmented system. *Nature* **400:** 563–566.

Elcavage P, Caraco T. 1983. Vigilance behaviour in house sparrow flocks. *Animal Behaviour* **31:** 303–304.

Elgar MA. 1987. Food intake rate and resource availability: flocking decision in house sparrows. *Animal Behaviour* **35:** 1168–1176.

Faaborg J, Brittingham MC, Donovan TM, Blake J. 1995. Habitat fragmentation in the temperate zone. In: Martin TE, Finch DM, eds. *Ecology and management of neotropical migratory birds.* Oxford: Oxford University Press, 357–380.

Fagan WF, Cantrell RS, Cosner C. 1999. How habitat edges change species interactions. *American Naturalist* **153:** 165–182.

Fernández-Juricic E. 2000a. Avifaunal use of linear strips in an urban landscape. *Conservation Biology* **14:** 513–521.

Fernández-Juricic E. 2000b. Local and regional effects of pedestrians on forest birds 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. 2001. Avian spatial segregation at edges and interiors of urban parks in Madrid, Spain. *Biodiversity and Conservation* (in press).

Fernández-Juricic E, Tellería JL. 2000. Effects of human disturbance on Blackbirds *Turdus merula* spatial and temporal feeding patterns in urban parks of Madrid, Spain. *Bird Study* **47:** 13–21.

Grimm NB, Grove JM, Pickett STA, Redman CL. 2000. Integrated approaches to long-term studies of urban ecological systems. *Bioscience* **50:** 571–584.

Gates JE, Gysel LW. 1978. Avian nest dispersion and avian fledging success in field forest ecotones. *Ecology* **59:** 871–883.

Greenwood JJD. 1985. Frequency-dependent selection by seed predators. *Oikos* **44:** 195–210.

Horsley DT, Lynch BM, Greenwood JJD, Hardman B, Mosely S. 1979. Frequency-dependent selection by birds when the density of prey is high. *Journal of Animal Ecology* **48:** 483–490.

Janzen DH. 1983. No park is an island: increase in interference from outside as park size decreases. *Oikos* **41:** 402–410.

Manly BFJ. 1974. A model for certain types of selection experiments. *Biometrica* **30:** 281–294.

McCollin D. 1998. Forest edges and habitat selection in birds: a functional approach. *Ecography* **21:** 247–260.

Murcia C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* **10:** 58–62.

Murdoch WW, Oaten AS. 1975. Predation and population stability. *Advances in Ecological Research* **9:** 1–131.

Niemelä J. 1999. Ecology and urban planning. *Biodiversity and Conservation* **8:** 119–131.

Plowright CMS, Landry F. 2000. A direct effect of competition on food choice by pidgeos. *Behavioural Processes* **50:** 59–64.

Santos T, Tellería JL. 1994. Influence of forest fragmentation on seed consumption and dispersal of Spanish Juniper *Juniperus thurifera. Biological Conservation* **70:** 129–134.

Saunders DA, Hobbs RJ, Margules C. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **5:** 18–32.

Weale ME, Whitwell D, Raison HE, Raymond DL, Allen JA. 2000. The influence of density on frequency-dependent food selection: a comparison of four experiments with wild birds. *Oecologia* **124:** 391–395.

Wilson SE, Allen JA, Anderson KP. 1990. Fast movement of densily aggregated prey increases the strength of anti-apostatic selection by wild birds. *Biological Journal of the Linnean Society* **41:** 375–380.