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LOCAL AND REGIONAL EFFECTS OF PEDESTRIANS ON FOREST BIRDS IN A FRAGMENTED LANDSCAPE¹

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Abstract. I assessed the effects of pedestrians on the distribution of forest bird species in wooded parks in the city of Madrid within and between fragments. Within fragments, increasing levels of pedestrians reduced species richness and overall abundance of individuals within circular plots. The abundance of foraging individuals of four species (Magpies Pica pica, Blackbirds Turdus merula, Starlings Sturnus unicolor, and Woodpigeon Columba palumbus) diminished when pedestrians walked near sampling plots, as well as their breeding densities in relation to increasing disturbance levels. Between fragments, after controlling for fragment size effects, pedestrian rate was negatively related to species richness in two breeding seasons. Species turnover was positively associated to mean pedestrian rate and inter-annual variability in pedestrian rate. At the species level, pedestrian rate negatively affected the probabilities of fragment occupation of 16 species beyond the effects of fragment size and isolation. Locally, the short-term behavioral responses to visitors may reduce the suitability of highly disturbed parks in such a way as to decrease breeding densities and the probabilities of fragment occupation and persistence. The effects of human disturbance in fragmented landscapes should be incorporated into management decisions as another relevant factor that may reduce habitat quality.

Key words: bird disturbance, conservation, fragmentation, human intrusion, pedestrians.

INTRODUCTION

Forest fragmentation is a negative influence on many bird species in forest habitats (Saunders et al. 1991, Wiens 1994). In general, the regional subdivision of formerly continuous habitats produces several isolated fragments, wherein local extinction, predation, and edge effects increase, whereas colonization and habitat suitability decrease (Andrén 1994, Simberloff 1994). Locally, isolated fragments could function as single habitats or as clusters of suitable resource patches for individual species depending on their coarseor fine-grained habitat selection process (Rolstad 1991).

Visitors to wildlife refuges could disturb bird species, with profound effects at the individual, population, and community levels (Skagen et al. 1991, Gill et al. 1996, Gutzwiller et al. 1998). Understanding how human disturbance modifies habitat selection processes is essential for managing natural fragmented landscapes, particularly those with high levels of visitors due to the recent popularity of outdoor recreational activities such as ecotourism and hiking. The essential issue for bird conservation is whether disturbance may decrease the probability of occupation or population levels in single fragments (Gill et al. 1996). If this response were widespread over a fragmented landscape, then human disturbance would be increasing the negative effects of forest fragmentation beyond the classical size and isolation effects.

I studied human disturbance effects upon forest birds in a fragmented landscape both within and between fragments. Within fragments, human disturbance is expected to reduce temporal access to food and nest resources, triggering a decline in species richness and abundance by re-

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ducing the carrying capacity and total suitable area of fragments. Between fragments, different disturbance levels would modify the probabilities of species occurrence according to their tolerance to people, controlling for area and isolation effects. An urban landscape was selected for the study because it has an extensive network of wooded parks imbedded in an urban matrix, with different degrees of visitor levels, area, and isolation. A previous study suggests that the patterns of community assembly of forest specialists in urban parks of Madrid are affected by area and regional pedestrian loads (Fernández-Juricic, in press), which makes this landscape suitable for the study of fragmentation and human disturbance effects at different scales.

Within fragments, I examined how resource patch selection and breeding densities could be modified by the number of pedestrians in three large parks with different disturbance levels. The following questions were addressed: (1) Do increasing levels of human disturbance reduce species richness (SR) and overall species abundance (OA) within resource patches? (2) Does the abundance of individual species feeding on the ground within resource patches decrease upon human presence? (3) Does the breeding density of individual species feeding on the ground decrease according to disturbance levels in the three parks?

Between fragments, I assessed whether human disturbance could modify spatial and temporal patterns of fragment occupation. The following questions were addressed: (1) Does human disturbance decrease species richness in this landscape, after controlling for the effects of area and isolation? (2) Does the temporal variability in human disturbance increase species turnover rates in fragments? (3) Besides area and isolation effects, could human disturbance decrease the probability of fragment occupation of individual species?

METHODS

WITHIN-FRAGMENT PATTERNS

Resource patch utilization in relation to human disturbance was studied between May and July 1997 in three large parks of Madrid: Moro (18 ha), Oeste (98 ha), and Retiro (110 ha). Created >80 years ago, these parks are representative of the urban parks of this city, with extensive areas of watered grass, shrub cover, and a mix of de-

ciduous and coniferous trees. Shrub cover includes introduced and native species, such as *Ligustrum* sp., *Buxus* sp., *Viburnum* sp., *Rubus* sp., etc. The most common deciduous trees are *Populus* sp., *Platanus hybrida*, *Ulmus campestris*, and *Acer negundo*, whereas coniferous trees consist mainly of *Cedrus* sp., *Pinus* sp., and *Abies alba*. Internally, these parks are divided into patches limited by a series of pathways for people who use them as recreational grounds.

Within each park, I selected as sample units 30-m radius plots near internal pathways. The size of these plots approximated the mean size of patches divided by paths. These plots were separated from each other by at least 15 m and by the paths used by visitors. There was little movement of birds among patches due to visitors (Fernández-Juricic and Tellería, in press). These plots could be considered as resource patches, having approximately equal percentages of grass, tree, and shrub cover within and between parks (Fernández-Juricic and Tellería, in press). Food availability within plots, a possible confounding factor, was assumed to be roughly similar in the selected plots, because vegetation is sustained throughout the year by watering 3 days week⁻¹ and 4 hr day⁻¹ in each park, and differences in the slope of the terrain were negligible.

In the Oeste park, 60 plots were chosen, in the Retiro park, 60, and in the Moro park, 40 because it was smaller than the former two. In each plot, the following variables were measured during 3-min focal observations at morning (07:00-10:30) and midday (13:00-15:00): the number of individual pedestrians passing by the boundaries of each plot, species richness (SR; i.e., number of species per plot), overall abundance (OA), and abundance of Magpies Pica pica, Blackbirds Turdus merula, Starlings Sturnus unicolor, and Woodpigeons Columba palumbus, all of them being ground feeders. These species were selected because they were abundant enough to collect adequate sample size for comparisons. Measurements on each plot were repeated 4 times separated by 7 days in each park, so as to gather an adequate sample size. Count periods were short because the purpose was to detect a bird's reaction during pedestrians walking near sampling plots. Longer periods may not have detected such changes because some species returned to plots after people left the surroundings. I considered an individual bird disturbed when it reacted to human presence by stopping searching for food or foraging and by displaying vigilance behavior, such as movements against visitors and head-up postures. Observations of birds and people were conducted from 15–20 fixed observation areas (7.5 m radius) per park from which many selected plots could be covered by the observer, who stood near sampling plots and was out of sight of the focal bird. Thus, the observer conducted the observations hidden behind a large tree or shrub and separated from the plot by a distance that ranged from 0.5 to 3 m. In cases when birds detected the observer, the area was abandoned for 1 hr before resuming sampling.

A previous study showed that disturbance load in each park differed significantly; for a statistical treatment of these differences see Fernández-Juricic and Tellería (in press). The Moro park was the least disturbed, the Oeste park mildly disturbed, and the Retiro park the most disturbed. In the Moro park, 20 of the selected plots were always undisturbed during the study period and were later considered as controls for comparisons, and the other 20 received mild levels of pedestrians. In the Oeste and Retiro parks, all plots were disturbed at least once. Disturbance levels were higher at midday than at morning in the Retiro and Oeste parks; however, no such difference was detected in the Moro park.

Data analysis. The information gathered was pooled across visits for a single plot to obtain averaged values for different situations. To evaluate whether increasing levels of human disturbance within each park reduced SR and OA at morning and midday, an ANOVA test was performed. Three independent factors were included: park, time of the day, and three disturbance levels: undisturbed, disturbed with 1-2 pedestrians, and disturbed with >3 pedestrians. Sixty plots (30 with and 30 without disturbance) were included for the Retiro park, and 60 for the Oeste. The purpose of this analysis was to contrast these parks with an area not having been subject to visitors, so I included from the Moro park the 20 undisturbed plots as controls. All analyzed plots were different, ensuring the independence of the response variable, thereby avoiding pseudoreplication. Ten plots for each combination of treatments were selected. The following combinations of treatments were statistically evaluated by means of planned comparisons: (1) whether SR and OA varied between morning and midday in the control plots of the Moro park, (2) whether increasing disturbance levels produced a change in SR and OA in the Oeste and Retiro parks, (3) whether response (2) varied between the Oeste and Retiro parks, (4) whether response (2) varied between morning and midday in the Oeste and Retiro parks, and (5) whether SR and OA from undisturbed patches varied among the Moro, Oeste, and Retiro parks.

I evaluated whether there was a change in the abundance within plots of ground foraging individuals of four species (Magpie, Blackbird, Starling, and Woodpigeon) in the three studied parks by means of a nested ANOVA design. This analysis allows testing the effects of disturbance separately within each park (McKonne and Lively 1993). I included two independent factors: parks and disturbance, with 20 different plots in each combination of factors. Disturbance was considered a fixed factor and nested within parks, which was set as a random factor. To determine whether these short-term responses toward human presence could produce a decrease in the breeding densities of these four species according to the level of disturbance, I analyzed their densities in the three studied parks with one-way ANOVA tests. Density estimations in these analyses included only those park sectors in which I conducted measurements of SR and OA within plots.

BETWEEN-FRAGMENT PATTERNS

Thirty parks, ranging from 0.4 to 100 ha, were surveyed in the city of Madrid during spring, May to September, in 1997 and 1998. Parks were sampled 4-5 times per year at morning from 07:00 to 11:00 in order to determine species richness and the density of individual species. Individuals seen or heard vocalizing in 100 \times 50-m fixed strip-transects were recorded in large parks; whereas in small ones, birds were surveyed across the whole park (Tellería and Santos 1997). To avoid studying species that were not breeding in urban parks and that use them as alternative habitats for feeding, I included in the analyses only those species that were present for at least 25% of the visits, observed on at least two consecutive visits, and recorded when singing, building a nest, or carrying food. Species belonging to the Anatidae and Apodidae families were excluded from the analysis, as their distribution is mainly determined by water sources and breeding sites in buildings, respectively. Such resources were not homogeneously distributed over the urban landscape and could have biased the results. House Sparrows (*Passer domesticus*) and Rock Doves (*Columba livia*) were not included because they are widespread species in urban habitats, highly associated with human activities (Adams and Dove 1989).

Park areas were obtained from the official records of the Municipality of Madrid. The degree of isolation was evaluated on a 1:20,000 map by estimating three types of distances between parks: D1 (distance to the nearest park), D2 (distance to the nearest park harboring at least one more species), D3 (distance to the mainland, Casa de Campo, a 1,722-ha plot in the northwest of Madrid, which can be regarded as representative of the regional pool of species; unpubl. data).

Vegetation structure in these urban parks was highly correlated with park size; thus, the effects of vegetation were not taken into account in later analyses, assuming that park area would roughly encompass habitat structure effects. Although this assumption could somewhat simplify the effect of subtle variations in habitat structure, the purpose of the study was not to determine the role of structural factors in shaping community structure but to assess human disturbance effects after controlling for other confounding variables, and in this case, area could control for vegetation structure. I considered this assumption appropriate to analyze how disturbance profiles affected species richness and single species distribution.

In determining the amount of pedestrians in each park, a team of observers recorded simultaneously the number of pedestrians, at morning and midday, in 3-min periods in the same locations of the line transects used to sample bird species. In small parks, a single observer was enough to cover the whole area. This procedure was repeated three times at each park with an interval of 25 days. Final figures were averaged and turned into pedestrians min⁻¹ 10-ha-park⁻¹.

Data analysis. At the community level, calculations were based on the number of species and the turnover rate per fragment, the latter being assessed as the total number of local extinction and colonization events/total number of species observed in both years (Clark and Rosenzweig 1994). Mean disturbance was assessed as (pedestrian rate 1997 + pedestrian rate 1998)/2. The inter-annual variability in disturbance was calculated as (pedestrian rate 1997 - pedestrian rate 1998)². I first used stepwise linear regressions to relate the number of species in each year to park area and isolation (D1, D2, and D3) to determine the main explanatory variables. The residuals were then regressed to pedestrian rate to assess the effect of visitors, controlling for area and isolation effects. Variables that explained turnover rates were evaluated in two analyses, one considering mean disturbance, and the other, inter-annual variation in disturbance, including in both cases the effects of area and isolation (D1, D2, and D3). All regression models were obtained with forward selection procedures, F to enter = 3.5.

At the species level, the presence/absence of individual species within parks was analyzed by means of stepwise logistic regressions. I assessed the probabilities of park occupation in both years, including the effects of area, isolation (D1, D2, and D3), and human disturbance in the same analysis. All species occurring in less than five parks were not included in this analysis because of low sample size.

Park area, pedestrian rate, mean pedestrian rate, and interannual variation in pedestrian rate were log-transformed (log x + 1) to meet the requirements of normality and homoscedasticity (Underwood 1997). STATISTICA 5.1 software was used for all statistical analyses except for logistic regressions, which were conducted with SPSS 7.5.

RESULTS

WITHIN-FRAGMENT PATTERNS

Increasing levels of pedestrians within plots in each park were associated with decreasing species richness (SR) as well as overall abundance (OA). In the control park (Moro), no differences in SR and OA were detected between morning and midday in undisturbed plots (SR, $F_{1,126} = 0$, P = 1.0; OA, $F_{1,126} = 0.57$, P = 0.45). Higher disturbance levels were related to reduced SR and OA within plots in the Oeste and Retiro parks (SR, $F_{2,126} = 115.3$, P < 0.001; OA, $F_{2,126}$ = 103.5, P < 0.001; Fig. 1). Such reduction in SR and OA did not vary either between Oeste and Retiro parks (SR, $F_{2,126} = 0.63$, P = 0.53; OA, $F_{2,126} = 0.16$, P = 0.85), or between morning and midday (SR, $F_{2,126} = 0.48$, P = 0.62;

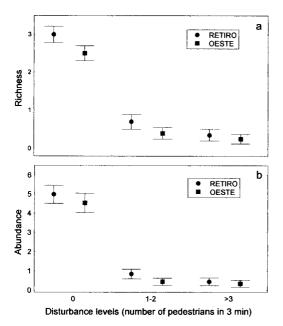


FIGURE 1. Species richness (a) and overall abundance (b) within 30-m radius sample plots in two parks of Madrid (Oeste, Retiro) under three levels of pedestrians in 3-min intervals (undisturbed plots, plots with 1-2 pedestrians, and plots with >3 pedestrians).

OA, $F_{2,126} = 1.14$, P = 0.32). No differences were detected in undisturbed plots among the three parks (SR, $F_{1,126} = 0.43$, P = 0.52; OA, $F_{1,126} = 0.49$, P = 0.49).

At the species level, Magpies, Blackbirds, Starlings, and Woodpigeons showed a consistent pattern of significantly reduced abundance of foraging individuals when pedestrians were walking by sample plots in each of the three sampled parks (Magpie, $F_{3,114} = 15.8$, P < 0.001; Blackbird, $F_{3,114} = 7.7$, P < 0.001; Star-

ling, $F_{3,114} = 10.0$, P < 0.001; Woodpigeon, $F_{3,114} = 3.1$, P < 0.03; Table 1). Concomitant with abundance reductions, a park effect was detected for one species only (Starling, $F_{2,114} = 6.9$, P < 0.002; Table 1); the other species followed the same patterns of abundance reductions in the three parks (Magpie, $F_{3,114} = 1.7$, P = 0.22; Blackbird, $F_{3,114} = 0.9$, P = 0.4; Woodpigeon, $F_{3,114} = 1.5$, P = 0.24; Table 1).

Patterns of breeding density confirmed that in parks with higher disturbance levels (Retiro and Oeste), densities were significantly lower (AN-OVA tests; Magpie, $F_{2.58} = 3.51$, P < 0.29; Blackbird, $F_{2.58} = 3.76$, P < 0.05; Starling, $F_{2.58} = 5.58$, P < 0.01; Woodpigeon, $F_{2.58} = 4.11$, P < 0.02; Table 1). Only Woodpigeon densities in the Moro and Oeste parks appeared to be similar (Table 1).

BETWEEN-FRAGMENT PATTERNS

Twenty-five species in 1997 and 29 in 1998 were recorded in 30 urban parks of Madrid. Park area, but not distance (D1, D2, and D3), significantly accounted for species richness in 1997 and 1998 (Table 2). After controlling for fragment-size effects, pedestrian rate was negatively related to species richness in both years [residuals species richness 1997 vs. park area = 0.99- 0.47 log (pedestrian rate 1997); residuals species richness 1998 vs. park area = 1.32 - 0.69log (pedestrian rate 1998); Table 2]. Species turnover in both years was accounted for by mean pedestrian rate and inter-annual variability in pedestrian rate, independently [species turnover = $0.21 + 0.13 \log$ (mean pedestrian rate 1997–1998); species turnover $= 0.3 + 0.06 \log$ (interannual change in pedestrian rate); Table 2]. Neither fragment size nor distance was included

TABLE 1. Abundance within 30-m radius plots of four species foraging on the ground upon presence (D) or absence (UD) of pedestrians walking near plots, and their breeding densities (individuals/0.5 ha) in three urban parks, Retiro, Oeste, and Moro, in Madrid, Spain.

		Magpie	Blackbird	Starling	Woodpigeon
Retiro	Plot Abundance UD	0.9 ± 0.7	1.2 ± 1.3	0.9 ± 1.3	0.8 ± 0.8
	Plot Abundance D	0.3 ± 0.5	0.7 ± 0.7	0.2 ± 0.4	0.3 ± 0.4
Oeste	Plot Abundance UD	1.3 ± 0.9	1.1 ± 0.8	1.6 ± 1.7	0.6 ± 0.9
	Plot Abundance D	0.1 ± 0.3	0.4 ± 0.6	0.2 ± 0.5	0.3 ± 0.7
Moro	Plot Abundance UD	0.6 ± 0.6	1.5 ± 1.1	0.2 ± 0.4	0.4 ± 0.6
	Plot Abundance D	0.2 ± 0.4	0.4 ± 0.6	0	0.2 ± 0.6
Retiro	Breeding density	0.8 ± 1.2	2.3 ± 1.7	0.8 ± 1.3	0.9 ± 1.1
Oeste	Breeding density	1.1 ± 0.9	3.3 ± 2.3	1.7 ± 1.9	1.8 ± 1.2
Moro	Breeding density	1.2 ± 1.7	3.9 ± 2.3	2.8 ± 2.6	1.8 ± 1.2

	$F_{1,28}$	Р	Adjusted R ²
Species richness 1997			
Log (area)	144.31	< 0.001	0.83
Log (pedestrian rate 1997) (+)	10.39	< 0.003	0.13
Species richness 1998			
Log (area)	75.13	< 0.001	0.73
Log (pedestrian rate 1998) (+)	7.49	< 0.011	0.06
Species turnover			
Log (mean pedestrian Rate 1997–1998)	78.25	< 0.001	0.73
Log (inter annual change in pedestrian rate)	64.09	< 0.001	0.69

TABLE 2. Relationships between species richness/turnover and pedestrian rate obtained through linear and multiple stepwise regression. (+) = after controlling for area effects.

in the two separate multiple stepwise regression models for explaining turnover.

At the species level, pedestrian rate affected the probabilities of fragment occupation beyond the effects of fragment size and isolation. Thirtyfour models were obtained, corresponding to 17 species (data are available from the author upon request). The variables selected were highly consistent between years for each species. Park area positively influenced the probabilities of occupation of 14 species; distance to the nearest park (D1) negatively affected 14 species; distance to the nearest park harboring at least one more species (D2), 5 species; and distance to mainland (D3), 2 species. In only one species, Robin Erithacus rubecula, distance to the nearest park (D1) positively affected its fragment occupation probabilities. The negative influence of pedestrian rate was prevalent, affecting 16 of 17 species. Only one species, Blue Tit Parus caeruleus, was not affected by human disturbance in either year.

DISCUSSION

The results of this study support the view that the rate of visitors in an urban fragmented landscape modifies patterns of species distribution within fragments by changing resource patch selection and breeding density patterns, and between fragments by modifying the likelihood of fragment occupation and persistence during breeding seasons.

DISTURBANCE PATTERNS WITHIN FRAGMENTS

Individual birds appear to restrain the space and time of foraging opportunities, as if people were potential predators (Gill et al. 1996, Fernández-Juricic and Tellería, in press). Undisturbed control plots harbor similar SR and OA of individuals from morning to midday. This fact undermines the role of temperature fluctuations in shaping the patterns of patch exploitation (Walsberg 1993), at least in the conditions under which this study was conducted. Even though other factors (territoriality, food and cover availability, microclimate variations, etc.) could have played a significant role, it seems plausible that the observed responses in disturbed patches were due to pedestrians. When pedestrian levels increase, individuals stop their foraging activities and hide in protective cover within resource patches, or move to other ones. Thus, human disturbance decreases the probabilities of using resource patches, such that individuals track the temporal fluctuations of disturbance to increase their foraging opportunities (Fernández-Juricic and Tellería, in press).

Considering individual species, similar abundance reductions in sampled plots due to disturbance were observed, with Magpies, Blackbirds, and Starlings being the most affected species (Table 2). Such response has been found in other birds inhabiting wildlife refuges, particularly those foraging on the ground which are more vulnerable to pedestrian disturbance (Burger and Gochfeld 1991, Rodgers and Smith 1997). On the other hand, breeding densities of the four species studied decreased considerably in disturbed parks, which could have been brought about by many factors (low availability of foraging and breeding substrates, predation, etc.); however, there are grounds for suggesting that disturbance may also have played a role.

LINKING WITHIN-FRAGMENT PATTERNS TO HIGHER SCALES

Pedestrians could increase within-fragment heterogeneity, having sites with different amounts of disturbance. This could modify the scale over which birds perceive a single fragment (Lima and Zollner 1996): from a continuous (coarsegrained) habitat to a cluster of separated resource patches (fine-grained) with varying quality. The key to linking such local responses to regional scales may be the frequency of disturbance. Disturbance fluctuations within fragments could be low enough during the day to allow birds to cope effectively with food and breeding requirements, occupying and flushing from resource patches at similar rates in relation to the temporal distribution of disturbance. However, if disturbance becomes more prevalent in space and time, individuals would face a decrease in the temporal and spatial availability of resources (Lima and Dill 1990). The short-term behavioral response to pedestrians can reduce the suitability of highly disturbed fragments. Such local response toward disturbance could turn out to be another decision trade-off that influences the probabilities of fragment occupation at a landscape scale. For an individual to occupy a highly disturbed patch, it might contend with higher perceived predation costs stemming from the number of pedestrians.

DISTURBANCE PATTERNS BETWEEN FRAGMENTS

In this landscape, the classical effects of fragment size and isolation are modified by the number of visitors to each fragment. Fragment size, along with the associated effects of higher habitat complexity, is the foremost factor affecting species richness and the probabilities of occupation of individual species. Large fragments decrease the likelihood of population extinction, enhance the temporal persistence of populations, and harbor a greater diversity of habitats (Hinsley et al. 1995, Tellería and Santos 1997). In this urban environment, isolation effects were more apparent in explaining individual species distributions rather than in accounting for overall species richness patterns. The distance separating parks restrains fragment colonization, particularly of low perceptual-range species (e.g., short dispersal species, such as Parus sp.), probably as a result of the harshness of the urban matrix separating suitable fragments (Keitt et al. 1997).

The regional effect of human disturbance strengthens the way in which species accrue in increasingly large fragments. On a given fragment size, fewer species tend to occupy fragments with higher pedestrian levels. Thus, human disturbance appears to intensify the effects of habitat fragmentation, reducing landscape suitability (Soulé et al. 1992). Similar conclusions have been drawn from modeling approaches (Caswell and Cohen 1993, Sutherland and Anderson 1993) by which the slope of the species-area curve becomes an increasing function of disturbance levels. Such regional patterns brought about by local disturbance loads should be examined in other habitats as well, in order to assess whether the negative effects of visitors would exert similar consequences.

Many studies have addressed how human disturbance accounts for decreasing winter densities of several bird species on local and regional scales, by diminishing the availability of foraging cover and the carrying capacity of highly disturbed patches (Madsen 1994, Klein et al. 1995, Hill et al. 1997). Such effects usually lead to lower densities, which may ultimately trigger local extinctions (Goss-Custard et al. 1994). The results of the present study underscore how such mechanisms could also influence the temporal distribution of breeding species in a fragmented landscape. Low disturbed parks in both years had lower species turnover, suggesting that they were more suitable for enhancing site-fidelity of individuals that bred in previous years (Willard et al. 1995). By the same token, if disturbance decreases between years, the persistence of individual species increases. Low turnover rates can be understood as an indication of high fragment quality, with territories being filled more quickly, and with less tendency for adults to abandon breeding territories after the reproductive period (Newton 1998).

CONSERVATION IMPLICATIONS

Could the rationale proposed in this study be applied to other landscapes? Even though pedestrian levels in urban areas could be regarded as high, it is worth considering how human presence could disrupt bird patch-selection and fragment occupation in other habitats, particularly those which are of conservation value. Because of the interest of people in visiting wildlife refuges, human disturbance effects turn out to be particularly relevant in highly endangered habitats (namely wetlands) and outdoor recreational areas (national parks, reserves, etc.) that harbor threatened species. From the current results, I suggest that higher disturbance loads could decrease fragment densities, increasing local extinction probabilities. This may be related to tolerance levels to people as well as biological traits of each species (Stacey and Taper 1992, Saether et al. 1996). Preliminary data suggest that large species with low tolerance levels are more prone to suffer local extinction in this urban landscape (unpubl. data). Further studies should address the combination of habitat structure and disturbance on a local scale, and how this interaction could bring about changes in different landscapes.

Irrespective of the relatively independent effects of area, isolation, and disturbance, interactions among them could trigger synergistic effects (McCollin 1998). For instance, area could interact with disturbance increasing its negative effects in small fragments. Because small fragments have higher edge/area ratios than large ones, applying similar disturbance loads could decrease the proportion of suitable area of small fragments beyond that in large ones. Such interactions argue in favor of implementing single large, instead of several small, protected areas (Doak and Scott Millis 1994), at least in highly disturbed landscapes.

Human disturbance loads ought to be incorporated in management decisions at local and regional scales. Wildlife managers are encouraged to carefully evaluate whether visitor presence could disrupt bird behavior and breeding densities, and then seek short and long term solutions, such as restriction of overall visitor levels, re-distribution of disturbance loads, setting buffer zones for visitors, seasonal limitation of tourism, and restricting access to areas with high diversity value.

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LITERATURE CITED

- ADAMS, L. W., AND L. E. DOVE. 1989. Wildlife reserves and corridors in the urban environment: a guide to ecological landscape planning and resource conservation. Natl. Inst. Urban Wildl., Columbia, MD.
- ANDRÉN, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different

proportions of suitable habitat: a review. Oikos 71:355-366.

- BURGER, J., AND M. GOCHFELD. 1991. Human disturbance and birds: tolerance and response differences of resident and migrant species in India. Environ. Conserv. 18:158–165.
- CASWELL, H., AND J. E. COHEN. 1993. Local and regional regulation of species-area relations: a patch occupancy model, p. 99–107. *In* R. E. Ricklefs and D. Schluter [EDS.], Species diversity in ecological communities. Historical and geographical perspectives. Univ. Chicago Press, Chicago.
- CLARK, C. W., AND M. L. ROSENZWEIG. 1994. Extinction and colonization processes: parameter estimates from sporadic surveys. Am. Nat. 143:583– 596.
- DOAK, D. F., AND L. SCOTT MILLIS. 1994. A useful role for theory in conservation. Ecology 75:615–626.
- FERNÁNDEZ-JURICIC, E. In press. Spatial and temporal distribution of bird forest species in wooded parks in the city of Madrid (Spain). Conservation implications. Proc. 4th Int. Symp. Urban Wildl. Conserv.
- FERNÁNDEZ-JURICIC, E., AND J. L. TELLERÍA. In press. Effects of human disturbance on Blackbird *Turdus merula* spatial and temporal feeding patterns in urban parks of Madrid, Spain. Bird Study.
- GILL, J. A., W. J. SUTHERLAND, AND A. R. WATKINSON. 1996. A method to quantify the effects of human disturbance on animal populations. J. Appl. Ecol. 33:786–792.
- GOSS-CUSTARD, J. D., R. W. G. CALDOW, R. T. CLARKE, S. E. A. LE V. DIT DURELL, J. URFI, AND A. D. WEST. 1994. Consequences of habitat loss and change to populations of wintering migratory birds: predicting the local and global effects from studies of individuals. Ibis 137:S56–S66.
- GUTZWILLER, K. J., H. A. MARCUM, H. B. HARVEY, J. D. ROTH, AND S. H. ANDERSON. 1998. Bird tolerance to human intrusion in Wyoming montane forests. Condor 100:519–527.
- HILL, D., D. HOCKIN, D. PRICE, P. TUCKER, R. MORRIS, AND J. TREWEEK. 1997. Bird disturbance: improving the quality and utility of disturbance research. J. Appl. Ecol. 34:275–288.
- HINSLEY, S. A., P. E. BELLAMY, AND I. NEWTON. 1995. Bird species turnover and stochastic extinction in woodland fragments. Ecography 18:41–50.
- KEITT, T. H., D. L. URBAN, AND B. T. MILNE. 1997. Detecting critical scales in fragmented landscapes. Conserv. Ecol. [online] Vol. 1 No. 4. Available from the Internet. URL: http://www.consecol.org/ vol1/iss1/art4
- KLEIN, M. L., S. R. HUMPHREY, AND H. FRANKLIN PER-CIVAL. 1995. Effects of ecotourism on distribution of waterbirds in a wildlife refugee. Conserv. Biol. 6:1454–1465.
- LIMA, S. L., AND L. M. DILL. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68:619–640.
- LIMA, S. L., AND P. A. ZOLLNER. 1996. Towards a behavioural ecology of ecological landscapes. Trends Ecol. Evol. 11:131–135.

- MADSEN, J. 1994. Impacts of disturbance on migratory waterfowl. Ibis 137:S67–S74.
- MCCOLLIN, D. 1998. Forest edges and habitat selection in birds: a functional approach. Ecography 21: 247–260.
- MCKONNE, M. J., AND C. M. LIVELY. 1993. Statistical analysis of experiments conducted at multiple sites. Oikos 67:184–186.
- NEWTON, I. 1998. Population limitation in birds. Academic Press, London.
- RODGERS, J. A., JR., AND H. T. SMITH. 1997. Buffer zone distances to protect foraging and loafing waterbirds from human disturbance in Florida. Wildl. Soc. Bull. 25:139–145.
- ROLSTAD, J. 1991. Consequences of forest fragmentation for the dynamics of bird populations: conceptual issues and the evidence. Biol. J. Linn. Soc. 42:149–163.
- SAETHER, B. E., T. H. RINGSBY, AND E. ROSKAFT. 1996. Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. Oikos 77:217–226.
- SAUNDERS, D. A., R. J. HOBBS, AND C. R. MARGULES. 1991. Biological consequences of ecosystem fragmentation: a review. Conserv. Biol. 5:18–32.
- SIMBERLOFF, D. 1994. Habitat fragmentation and population extinction of birds. Ibis 137:S105–S111.
- SKAGEN, S. K., R. L. KNIGHT, AND G. H. ORIANS. 1991.

Human disturbances of an avian scavenging guild. Ecol. Appl. 1:215–225.

- Soulé, M. E., A. C. Alberts, AND D. T. Bolger. 1992 The effects of habitat fragmentation on chaparral plants and vertebrates. Oikos 63:39–47.
- STACEY, P. B., AND M. TAPER. 1992. Environmental variation and the persistence of small populations. Ecol. Appl. 2:18–29.
- SUTHERLAND, W. J., AND C. W. ANDERSON. 1993. Predicting the distribution of individuals and the consequences of habitat loss: the role of prey depletion. J. theor. Biol. 160:223–230.
- TELLERÍA, J. L., AND T. SANTOS. 1997. Seasonal and interannual occupation of a forest archipelago by insectivorous passerines. Oikos 78:239–248.
- UNDERWOOD, A. J. 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge Univ. Press, Cambridge.
- WALSBERG, G. E. 1993. Thermal consequences of diurnal microhabitat selection in a small bird. Ornis Scand. 24:174–182.
- WIENS, J. A. 1994. Habitat fragmentation: island vs. landscape perspectives on bird conservation. Ibis 137:S97–S104.
- WILLARD, M., G. MERRIAM, AND B. A. MAURER. 1995. Dynamics in subdivided populations of Neotropical migratory birds in a fragmented temperate forest. Ecology 76:27–40.