The Condor 105:316–326

TESTING THE RISK-DISTURBANCE HYPOTHESIS IN A FRAGMENTED LANDSCAPE: NONLINEAR RESPONSES OF HOUSE SPARROWS TO HUMANS

ESTEBAN FERNÁNDEZ-JURICIC[1,4], ANGEL SALLENT[2], RUBEN SANZ[3] AND IÑAKI RODRÍGUEZ-PRIETO[2]

[1]*Department of Ecology, Evolution, and Behavior, University of Minnesota, 100 Ecology Bldg., 1987 Upper Buford Circle, St. Paul, MN 55108-6097*

[2]*Grupo de Ecología Aplicada, C/ Bernardino García, 29, 1ero Izq., 28040 Madrid, Spain*

[3]*Departamento de Botánica, Facultad de Biología, Universidad Complutense de Madrid, Madrid E 28040, Spain*

Abstract. We used House Sparrows (*Passer domesticus*) as a model species to assess responses to different levels of human visitation in a fragmented urban landscape. Regionally, we analyzed linear and nonlinear variation in breeding densities in relation to observed pedestrian rates in forest fragments. Locally, we tested experimentally the resource-use–disturbance trade-off hypothesis, which suggests that an increase in the frequency of human visitation decreases the frequency of resource use by an animal, assuming that individuals react to humans as if they were potential predators, and that responses depend upon the probability of visually detecting humans. Breeding densities peaked at intermediate pedestrian rates in two consecutive years. Consumption rates of artificial food within fragments were higher at intermediate pedestrian rates, which may indicate that this species uses people as cues to find food. Consumption rates decreased at high pedestrian rates as a result of low tolerance to people and a reduction in the time devoted to foraging. Our results imply a balance between attraction to and avoidance of humans to account for these nonlinear responses, and that the resource-use–disturbance trade-off hypothesis can be a useful mechanistic explanation for understanding the responses to humans of species that may receive a direct or indirect benefit from human presence.

Key words: behavior, breeding density, human disturbance, human-wildlife interactions, nonlinearity, park design, recreation.

Probando la Hipótesis del Riesgo-Perturbación en un Paisaje Fragmentado: Respuestas No Lineales de *Passer domesticus* hacia Humanos

Resumen. Se escogió a *Passer domesticus* como especie modelo para analizar su respuesta a distintos niveles de perturbación humana en un ambiente urbano fragmentado. Regionalmente, se analizaron las variaciones lineales y no-lineales en las densidades reproductivas con relación a la tasa observada de visitantes a fragmentos forestales. Localmente, se comprobó experimentalmente la hipótesis del balance entre el uso del recurso y perturbación, la cual analiza la relación entre la frecuencia de visita y la frecuencia de uso del recurso, suponiendo que los animales reaccionan hacia los humanos como si fuesen depredadores, y que las respuestas dependen de las probabilidades de detección de humanos. Las densidades reproductivas en dos años consecutivos fueron más elevadas con tasas de visita intermedias. Las tasas de consumo dentro de fragmentos mostraron un pico cuando la frecuencia de visita fue intermedia, lo que sugiere que esta especie utiliza a los humanos como indicadores de alimento; pero la tasa de consumo disminuyó con frecuencias de visita mas elevadas como resultado de la baja tolerancia hacia humanos y la reducción del tiempo dedicado a la alimentación. Nuestros resultados indican que un balance entre atracción y repulsión hacia humanos está involucrado en las respuestas no lineales y que la hipótesis del balance entre el uso del recurso y el disturbio puede ser una explicación apropiada para comprender las respuestas de especies que reciben un beneficio directo o indirecto de la presencia humana.

INTRODUCTION

Wildlife responses to humans have caught the attention of managers and conservation biologists interested in the effects of human disturbance. The risk-disturbance hypothesis synthesizes this behavioral approach to explain and predict the responses of individuals and populations to humans on the grounds that animals seek a balance between avoiding disturbance and pursuing activities that may increase fitness, such as foraging, mating, and parental care (Frid and Dill 2002).

Manuscript received 27 June 2002; accepted 28 December 2002.

[4] E-mail: estebanfj@yahoo.com

Some studies that used this conceptual framework to explain patterns of habitat selection in relation to the presence of humans (e.g., Fox and Madsen 1997, Fernández-Juricic 2000a) have implicitly assumed linear negative responses to the number of people per unit time per unit area (hereafter, pedestrian rate) visiting a natural area (reserve, park, etc.). However, there are many other ways in which humans may interact with wildlife. For instance, pedestrian rate may not elicit any response (Gutzwiller and Anderson 1999, Marsden 2000, Gill et al. 2001a), or may positively affect species richness, breeding density, or habitat use (O'Connell et al. 2000, Fernández-Juricic 2001). Interestingly, human presence may also generate nonlinear responses (i.e., negative squared or negative cubic; Meents et al. 1983). In this scenario, the outcome of human-wildlife interactions would depend upon the range of disturbance levels considered. Previous studies have found such nonlinear relationships particularly at the community level (Blair 1996, Allen and O'Connor 2000), but comparatively little empirical evidence exists at the population and individual levels (but see Coppedge et al. 2001).

One of the mechanisms put forward to account for the modification of habitat use and breeding densities in fragmented landscapes is related to variation in the relationship between the frequency of human visitation and the frequency of resource use by the study animal (Fernández-Juricic 2000a, Fernández-Juricic and Tellería 2000). This resource-use–disturbance trade-off mechanism can be considered a special case of the risk-disturbance hypothesis (Frid and Dill 2002), as it holds that individuals react to humans as if they were potential predators (Fernández-Juricic and Tellería 2000), and that responses to people depend upon the probabilities of detecting pedestrians (Rodgers and Smith 1995, Fox and Madsen 1997, Fernández-Juricic, Jimenez, and Lucas 2001a, 2001b). Low pedestrian rates during the day may allow birds to cope with their breeding and feeding requirements. However, when pedestrian rate increases, individuals may face a sharp decrease in the temporal and spatial availability of resources due to human avoidance behaviors, thereby reducing the suitability and carrying capacity of fragments. The net outcome may reduce local breeding densities and the probability of fragment occupation (Fernández-Juricic 2000a, 2002). Therefore, assessing wildlife responses to people not only at the behavioral level but also at the population level (e.g., breeding density) is essential to comprehensively evaluating human disturbance (Newton 1998, Gill et al. 2001b).

The purpose of this study is twofold: to assess the linearity and nonlinearity of relationships between pedestrian rates and breeding densities in a fragmented landscape, and to test experimentally the hypothesis that the frequency of human visitation affects the frequency of resource use at a local scale. We studied House Sparrows (*Passer domesticus*) inhabiting forest fragments (wooded parks) in a fragmented urban habitat. Regionally (among fragments), we observed how House Sparrow breeding densities varied in 23 wooded parks scattered throughout Madrid, Spain, in relation to pedestrian rates during two consecutive breeding seasons, controlling for the effects of fragment size, habitat structure, and the density of predators and potential competitors. Locally (within fragments), we experimentally simulated three levels of pedestrian rates and analyzed the variation in consumption rates of artificial food, which can be a useful surrogate for resource use (Fernández-Juricic, Sanz, and Sallent 2001).

The House Sparrow is a good model to study nonlinear relationships because it may use people as clues to find food (Erz 1966, Blair 1996), but may not tolerate very high pedestrian rates (Fernández-Juricic, Jimenez, and Lucas 2001a), which would give rise to negative squared relationships. Despite being widespread throughout the world (Summers-Smith 1988), House Sparrow populations have decreased steadily in the last decade across several European countries, to the extent that local extinction has taken place in urban and rural habitats (Easterbrook 1999, Bezzel 2001, Hole et al. 2002).

METHODS

We conducted this study in the city of Madrid (40.25°N, 03.43°W), which has an extensive network of vegetation remnants (wooded parks) that harbor several forest bird species (Fernández-Juricic 2000a, 2000b). All parks studied had high tree cover, and were composed of a mix of deciduous and coniferous trees, introduced and native shrub species, and lawns.

BREEDING DENSITY SURVEYS

We estimated House Sparrow breeding densities in 23 wooded parks, ranging from 1 to 118 ha, during spring of 1997 and 1998 (April to June). We did not include parks <1 ha to avoid problems in the estimation of breeding densities in small areas (Haila 1988). Surveys were conducted four times within each wooded park every year by only one observer (EFJ). All parks were surveyed on weekday mornings (from 07:00 to 10:00). One problem with estimating breeding densities of House Sparrows is that the number of individuals in wooded parks is likely to be overrepresented by birds breeding in nearby buildings. We constrained the criteria for including individuals in our analyses to those that were seen using holes in trees and the typical globular nests with an entrance hole in one side that House Sparrows usually build in trees (Summers-Smith 1988). Another confounding factor is that females have a similar plumage to that of immatures; however, our sampling was concentrated when the number of immatures was supposed to be the lowest (Summers-Smith 1988). Furthermore, when identification was difficult, we concentrated on certain morphological traits (color of the beak, chin, and throat) to differentiate between females and immatures (Clement et al. 1993). Though conservative, these criteria would decrease the bias toward individuals not breeding in wooded parks.

For all parks >2 ha, we recorded the number of individuals that met these criteria seen in 100-m-long and 50-m-wide transects (Järvinen and Väisänen 1977). We averaged the number of birds in each fixed transect (0.5 ha) throughout all visits; final values were expressed as number of individuals per ha. Transects were separated by 50–150 m to ensure their independence, and the same transects were used for each visit. The number of transects per wooded park was established in a logarithmic 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. Our surveys were designed to cover areas both at the interior and at the edges of fragments to assess the overall breeding density within parks. We did not consider differential observability to be a problem in our study system, because the sampled parks had similar habitat types (coniferous and deciduous cover with scattered shrubs), all surveys were conducted by the same person, and transects were small enough to detect individuals with high precision and accuracy.

FACTORS INFLUENCING BREEDING DENSITIES

To get an estimate that reflects how people could affect the frequency of resource use, we assessed the number of people using the parks per unit area and per unit time in 1997 and 1998, following Fernández-Juricic (2000a). Within each transect (0.5 ha), the number of pedestrians observed walking and sitting in 3-min periods was recorded at 08:00–09:00 and 13:00–14:00 by 1–3 observers. Sampling was repeated three times at each park, at 20-day intervals, with final values converted into number of pedestrians per min per ha.

We also measured park size, vegetation structure, availability of tree holes, and density of predators and potential competitors, because they may be relevant to the distribution of House Sparrows (Pogue and Schnell 1994). Measurements of park area were obtained from the official records of the Municipality of Madrid. Vegetation traits were measured in 25-m-radius circular plots distributed at 30-m intervals along transects in parks >2 ha, and randomly in parks <2 ha. The number of sample units per park was determined by its size (log-transformed; range 1–89 plots). Vegetation cover and height were visually estimated following Prodon and Lebreton (1981). Vegetation traits included grass cover, bare ground, shrub cover, coniferous cover, deciduous cover, tree height, number of stems <10 cm, 10–30 cm, 30–50 cm, and >50 cm diameter at breast height (dbh). To reduce the number of vegetation structure variables, we performed a principal components analysis (PCA) on the correlation matrix. Only those PCA factors with eigenvalues >1 were selected (Kaiser criterion), and factor loadings were rotated with a varimax raw transformation (StatSoft 2002).

In the same plots used to sample vegetation structure, we also measured the number of tree holes between 5 and 50 cm diameter. We analyzed the availability of tree holes separately, because House Sparrows prefer holes in trees as nesting substrates, although they build nests in trees as well (Summers-Smith 1988). The number of nest boxes was negligible, and was not included in analyses.

We estimated the density of Magpies (*Pica pica*) and domestic cats, because both are known to be predators of House Sparrows in this urban setting. We also assessed the density of four po-

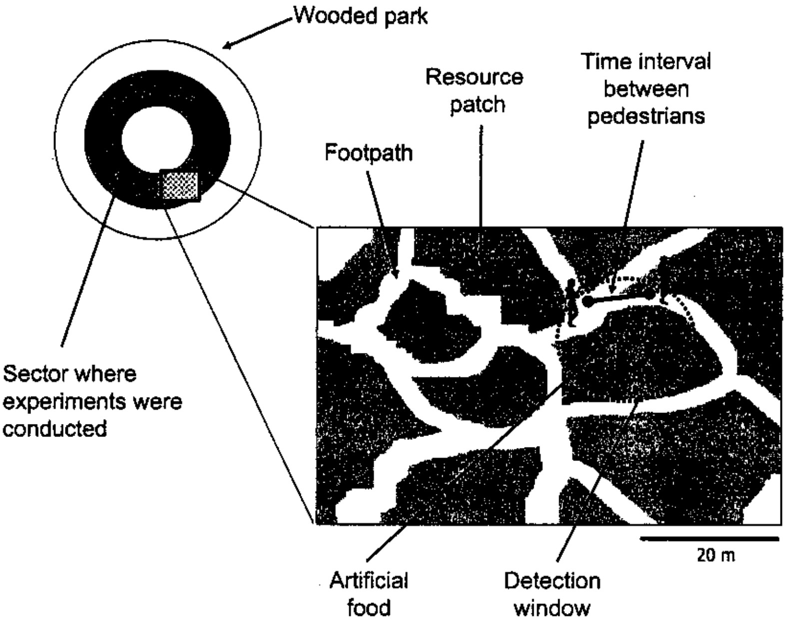

FIGURE 1. Design of experiments investigating consumption rate by House Sparrows in response to different pedestrian rates. Experiments were performed at 30–150 m from the edges of three Madrid parks. Artificial food was laid out within resource patches, 3 m from pathways along which pedestrians walked at three different rates (0 pedestrian per hr, 20 pedestrians per hr, 40 pedestrians per hr).

tential competitors for nesting holes: Tree Sparrow (*Passer montanus*), Great Tit (*Parus major*), Spotless Starling (*Sturnus unicolor*), and Stock Dove (*Columba oenas*). Density estimations of all these species were accomplished by means of line transects in the same spots in which House Sparrows were recorded and at the same time (as described for estimations of House Sparrow density); thus, sampling intensity was similar for all species.

THE EFFECTS OF PEDESTRIAN RATE ON CONSUMPTION RATES

The resource-use–disturbance trade-off hypothesis predicts that intervals between pedestrians passing by a resource patch would affect the rate at which birds make use of that resource patch (Fernández-Juricic 2000a). We simulated different pedestrian rates and measured resource use (consumption rates) within patches during the morning in three large wooded parks: Retiro (110 ha), Oeste (98 ha), and Austria (30 ha) in March–May 2001. Patches were areas of lawn surrounded by footpaths within wooded parks (Fig. 1).

Because the density of House Sparrows tends to be higher at the edge (0–50 m) than at the interior (>70 m from the border) of wooded parks (Fernández-Juricic 2001), experiments were conducted in a strip that encompassed the transition between both areas (30–150 m from the border) so as to minimize sparrow density variation within parks (Fig. 1). At the edge of wooded parks, undisturbed resource patches did not exist in which to simulate different pedestrian rates, and interior areas contained few individuals.

To measure consumption rates, we prepared artificial food bait made of dry white bread cut into small cubes (1 cm^3). The size and color of bait made them clearly distinguishable from the background, at least to the human eye. Generally, visitors to parks supply white bread, and House Sparrows were used to feeding on it. However, it is unlikely that birds were overfed when experiments were conducted because (1) at morning, birds spent most of their time foraging, and did not rely on people, who began visiting parks (and thus feeding birds) after lunch; and (2) parks were cleaned up quite thoroughly before we started our experiments (07:00 to 07:30), with almost no leftovers remaining for birds to feed on. We then focused our sampling from 08:00 to 10:00.

To simulate different pedestrian rates around artificial food, we first defined a detection window as the circular area within which foraging sparrows could detect a pedestrian walking on a footpath (Fig. 1). A previous study estimated the alert distance (the distance at which an animal becomes alert to an approaching human) for House Sparrows in the three studied parks as being 11.9 ± 5.2 m (Fernández-Juricic, Jimenez, and Lucas 2001b). To be conservative, we considered the detection window as a circular area with 20-m radius (Fig. 1). With a group of volunteers, we varied the number of people walking per unit time on the footpaths within the detection window (Fig. 1) by keeping the interval between pedestrians constant. We simulated three pedestrian rates: 0 pedestrians per hr, 20 pedestrians per hr, and 40 pedestrians per hr. We kept occasional visitors away from the detection window by encouraging them to take alternative routes. When they would not take a different path, we repeated the trial the next sampling day.

At each wooded park, we conducted five trials per day, totaling 75 trials (25 per pedestrian rate) and 15 sampling days per park. All experiments were conducted during weekdays. Trials within wooded parks were separated from one another by 300 m to reduce the prospect of birds feeding in more than one artificial food patch in the same day. Each day, treatments were randomly distributed. In each trial, bait was scattered in a 1-m^2 area of lawn, 3 m away from the patch, at 50 pieces per m^2. At this distance, pedestrian rate was likely to affect the frequency of artificial food consumption by House Sparrows, because they generally escaped from pedestrians at 8.2 ± 4.1 m (Fernández-Juricic, Jimenez, and Lucas 2001a). Trials lasted 2 hr, with replenishment of food every 30 min by the pedestrian that walked along the footpath. However, we analyzed the results of only the first half-hour, because inclusion of other periods would render results not completely independent; they could have been influenced by the food present in each previous period. Trials were observed from a blind outside the detection window to assess the number of pieces left unconsumed by House Sparrows and the number of sparrows using the patch every minute. Trials in which people removed bait were repeated the next sampling day. We also repeated trials when more than 6% (3 out of 50 pieces) of food was consumed by other species (Rock Doves [*Columba livia*], Blackbirds [*Turdus merula*], Magpies). Pecked bait was considered consumed. We sampled every other day in each park. We used the percentage of food items consumed in 30 min in our analyses.

STATISTICAL ANALYSIS

In analyzing the relationship between House Sparrow breeding densities (y) and pedestrian rate (x), we used a polynomial regression (GLM procedures, McCullagh and Nelder 1989): $y = a + bx - cx^2$, where a is the intercept, and b and c are constants. This model allowed us to test for linear and nonlinear (negative squared) effects. We used a power link function, with the assumption that the response variable was normally distributed. The Wald test was used to evaluate the contribution of each factor to the overall model, and was tested against a χ^2 distribution (StatSoft 2002). Similar polynomial regressions were used to relate House Sparrow breeding densities to fragment size, habitat structure, tree-hole availability, and predator and competitor densities before assessing the effects of pedestrian rates. We calculated the retrospective (*post-hoc*) power of nonsignificant polynomial regressions with Power and Precision 1.2 (Biostat 1997), considering $\alpha = 0.05$. Each factor was examined separately instead of using a multiple regression approach, because recent evidence points out that these kinds of models are more accurate and powerful when using few independent factors (Pearce and Ferrier 2000).

The effect of pedestrian rate on mean consumption rates within each wooded park was analyzed with a nested ANCOVA. Two confounding factors may have affected consumption rates: habituation to people walking around resource patches, and flock size. We analyzed their effects by including sampling day (ranging from 1 to 15) and flock size (mean size of House Sparrow foraging groups in 30 min) as covariates. This design included two independent factors tested simultaneously: wooded parks (Retiro, Oeste, Austria), and pedestrian rate (0, 20, and 40 pedestrians per hr). Pedestrian rate was considered a fixed factor and nested within parks, which was set as a random factor. We used a similar analysis to assess the effect of pedestrian rate and park on flock size. Because consumption rates among parks may also be related to the density of individuals, we evaluated

TABLE 1. Polynomial regressions ($y = a + bx - cx^2$) between House Sparrow breeding densities (y) and 11 independent variables: park area, habitat structure as measured by the first four principal components (PC) from a principal components analysis of 10 vegetation measurements, tree hole availability, and density of potential predators and competitors. Data were collected in two breeding seasons (1997–1998) in 23 wooded parks in Madrid. Density of one competitor, Tree Sparrow, was excluded from the model because it was found in <5 parks.

	1997				1998			
		P				P		
	r^2	x	x^2	Power	r^2	x	x^2	Power
Park size	0.02	0.91	0.92	0.08	0.04	0.34	0.33	0.11
PC1	0.05	0.35	0.48	0.13	0.09	0.09	0.86	0.20
PC2	0.18	0.12	0.08	0.41	0.21	0.09	0.12	0.48
PC3	0.06	0.39	0.66	0.15	0.02	0.81	0.70	0.08
PC4	0.11	0.29	0.16	0.24	0.09	0.52	0.16	0.20
Tree holes	0.05	0.36	0.32	0.13	0.14	0.49	0.40	0.31
Magpie density	0.11	0.48	0.38	0.24	0.16	0.20	0.33	0.36
Cat density	0.07	0.80	0.76	0.16	0.03	0.90	0.84	0.09
Great Tit density	0.16	0.75	0.85	0.36	0.16	0.83	0.94	0.36
Spotless Starling density	0.02	0.82	0.92	0.08	0.12	0.84	0.40	0.20
Stock Dove density	0.17	0.61	0.57	0.38	0.08	0.64	0.65	0.18

differences in breeding densities (see above) among the three parks with a one-way ANOVA. We further analyzed differences between levels of significant factors with linear contrasts. All analyses were conducted with Statistica 6.1 (StatSoft 2002). Values reported in the Results section are means ± SE. We set our significance level at $P < 0.05$.

RESULTS

BREEDING DENSITIES

Vegetation structure variables were reduced to four significant components (% total variance explained: PC1, 19%; PC2, 19%; PC3, 19%; PC4, 20%). PC1 could be considered a gradient from thin trees (number of stems <10 cm dbh, factor loading = −0.9) to taller (tree height, factor loading = 0.8) trees. PC2 correlated negatively with grass cover (factor loading = −0.8), and positively with bare-ground cover (factor loading = 0.8). PC3 was positively related to deciduous cover (factor loading = 0.9) and negatively to coniferous cover (factor loading = 0.7). PC4 was positively associated with the number of stems 30–50 cm dbh (factor loading = 0.8) and >50 cm dbh (factor loading = −0.8).

House Sparrow breeding densities were normally distributed in both years (Shapiro-Wilk test: both $W < 1.0$, $P > 0.35$), and so were PC1, PC2, PC3, PC4, tree hole availability, and predator density (W varied from 0.87 to 0.98, all $P > 0.05$). However, fragment size and pedestrian rate did not follow a normal distribution. Despite these differences, results were similar with and without transformation of the original data. Some explanatory variables were correlated: fragment size and pedestrian rate (1997, $r = -0.46$, $n = 23$, $P < 0.05$; 1998, $r = -0.44$, $n = 23$, $P < 0.05$), and pedestrian rate in 1997 and pedestrian rate in 1998 ($r = 0.89$, $n = 23$, $P < 0.001$). The other correlations were not significant (r varied from −0.35 to 0.32, all $P > 0.05$, $n = 23$).

None of the possible confounding factors (fragment size, habitat structure, tree-hole availability, predator and competitor densities) affected House Sparrow breeding densities in 1997 or 1998 (Table 1). The power of these tests, however, was rather low, varying from 0.08 to 0.41 in 1997, and from 0.09 to 0.48 in 1998, with fragment size having, on average, the lowest power in both years (Table 1).

In 1997 and 1998, we found linear and quadratic (negative squared) effects (Table 2), whereby breeding densities initially increased with pedestrian rates, but declined after pedestrian rates reached 20 pedestrians per ha per hr (Fig. 2). The net result is that breeding densities peaked at intermediate pedestrian rates.

CONSUMPTION RATES

Consumption rate was normally distributed (Shapiro-Wilk: $W = 0.95$, $P = 0.35$). Sampling day did not affect consumption rates (β =

TABLE 2. Generalized linear models of the relationship between House Sparrow breeding densities and pedestrian rate in 23 wooded parks in the city of Madrid, 1997–1998.

	Parameter	SE	χ^{2a}	P
1997 ($r^2 = 0.42$)				
Intercept	64.6	27.4	2.7	0.10
Pedestrian rate	102.8	51.9	5.1	0.02
Pedestrian rate^2	−34.1	16.5	8.3	<0.01
1998 ($r^2 = 0.37$)				
Intercept	48.2	13.8	8.8	<0.01
Pedestrian rate	74.6	29.9	5.8	0.02
Pedestrian rate^2	−21.3	9.3	7.0	<0.01

[a] Wald statistic, df = 1 for all parameters; $n = 23$ parks.

-0.05, $t_{214} = -0.7$, $P = 0.46$), suggesting that House Sparrows did not habituate to the experimental conditions. Flock size appeared to increase consumption rates, with a relationship that was close to significance ($\beta = 0.09$, $t_{214} = 1.5$, $P = 0.07$). However, flock size did not vary among trials of varying pedestrian rates ($F_{2,216} = 0.5$, $P = 0.58$), nor among wooded parks ($F_{2,216} = 0.1$, $P = 0.87$). After controlling for sampling day and flock size, consumption rates differed among parks ($F_{2,214} = 21.3$, $P < 0.001$; Fig. 3), and among pedestrian rates within parks ($F_{6,214} = 22.9$, $P < 0.001$; Fig. 3).

Consumption rates were higher in the Retiro than in the Oeste ($F_{1,214} = 34.5$, $P < 0.001$) and Austria parks ($F_{1,214} = 29.3$, $P < 0.001$). However, there were no differences in consumption rates between the Oeste and Austria parks ($F_{1,214} = 0.2$, $P = 0.64$). Taking into account human visitation levels, we found greater consumption at intermediate pedestrian rates (20 vs. 0 pedestrians per hr, $F_{1,214} = 106.3$, $P < 0.001$; 20 vs. 40 pedestrians per hr, $F_{1,214} = 87.9$, $P < 0.001$; Fig. 3). No significant differences were found between extreme pedestrian rates (0 vs. 40 pedestrians per hr, $F_{1,214} = 0.8$, $P = 0.36$).

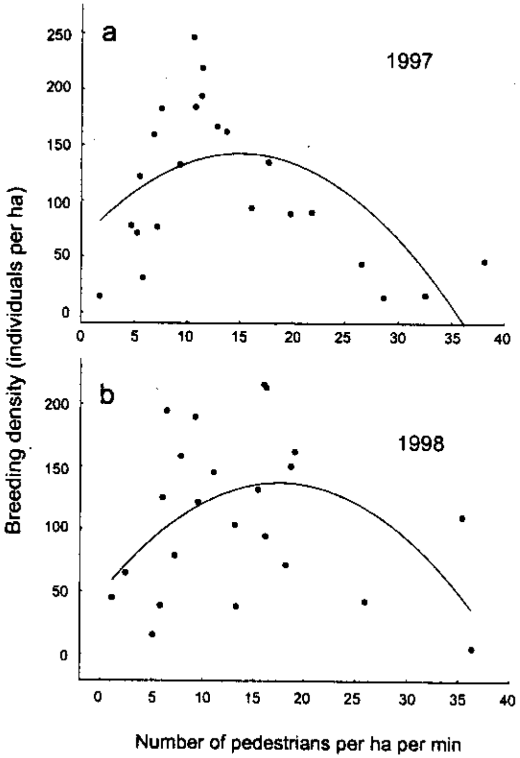

FIGURE 2. Relationships between House Sparrow breeding densities in 23 wooded parks in Madrid and observed pedestrian rate in (a) 1997 and (b) 1998.

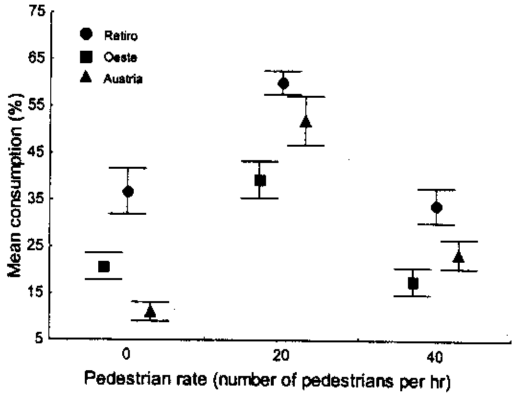

FIGURE 3. Relationship between mean consumption rate (expressed as percentage of food items consumed in 30 min) by House Sparrows and three assigned levels of pedestrian rates (0, 20, and 40 pedestrians per hr) at three parks in Madrid.

House Sparrow breeding densities varied among the three wooded parks ($F_{2,66} = 6.5$, $P < 0.003$), with the highest densities in Retiro (74 ± 41 individuals per ha), followed by Austria (31 ± 15 individuals per ha) and Oeste (25 ± 19 individuals per ha).

DISCUSSION

Our results suggest that House Sparrows benefit from environments with intermediate levels of human visitation, and that pedestrians affect resource use as well as breeding density patterns. Interestingly, we found consistent support for a nonlinear response at local and regional scales, which suggests that this species interacts with humans in complex ways.

Breeding densities of House Sparrows were not modified by fragment size, habitat structure, tree-hole availability, or predator and competitor densities. This may have resulted from the scale of our measurements (Fernández-Juricic, Jimenez, and Lucas 2001b), from environmental and stochastic variability not considered in this study (Sæther et al. 1999), or from the low power of the tests. In the case of fragment size, the lack of response may be related to the fact that generalist species do not tend to be affected by the area of fragments (Connor et al. 2000). Future studies should consider other variables (e.g., food availability, nest-site quality, distance between nests, etc.) at different portions of the response curve, as these factors may be correlated with the positive and negative aspects of the response. However, we failed to detect such relationships.

Only pedestrian rate modified breeding densities, with consistent nonlinear patterns found in two consecutive breeding seasons; although one must be cautious to generalize this pattern due to the moderate amount of variability explained (37–42%, Table 2). The nonlinear pattern was negative squared, with higher densities at intermediate pedestrian rates. Even though we did not study other important population-level responses (breeding success, juvenile survival), there is evidence for this species that sites with high breeding densities also show high breeding success (Sæther et al. 1999), probably as a result of their tendency to breed in aggregations (Summers-Smith 1988). Nevertheless, these nonlinear variations do not mean that regional population trends are affected likewise by pedestrian rates, because the regional population (particularly individuals that breed in the urban matrix) may still be large enough to buffer local variations in House Sparrow abundance (Newton 1998).

The experimental assessment of the relationship between the frequency of resource use (estimated as consumption rates) and the frequency of human visitation (estimated as pedestrian rates) also yielded a negative-squared response, which appears to be the result of human-approaching and avoidance behaviors at different pedestrian rates. When no pedestrians were passing through the detection window, consumption rates were lower than at intermediate frequencies (20 pedestrians per hr), probably because House Sparrows normally use people as cues to find food in wooded parks (Erz 1966, Fernández-Juricic 2001), and the benefits surpass the risks. Yet, with increasing pedestrian rates (40 pedestrians per hr), consumption rates decreased. This response may be mediated by a temporal reduction in opportunities to consume food, because (1) food was located close enough to paths that humans disturbed feeding House Sparrows, and (2) the intervals between passing pedestrians (e.g., feeding bouts) decreased at 40 pedestrians per hr. One explanation for the higher consumption rates in the Retiro park may be the high density of House Sparrows in relation to the Oeste and Austria parks. This higher density may have increased competition for food, thereby raising individual feeding rates (Clark and Mangel 1986). Nonetheless, during our observations we did not find interference (e.g., prey stealing) to be an important factor within flocks.

Previous studies suggested that the resource-use–disturbance trade-off mechanism could explain negative responses of different species to humans at regional scales (Fernández-Juricic 2000a, 2002, Fernández-Juricic and Tellería 2000). Hence, one possibility is that the nonlinear variations in breeding densities of House Sparrows may be related to their nonlinear variation in resource use within fragments. The key to understanding this effect is to consider how foraging and breeding behavior can vary as the effect of humans becomes widespread spatially (within the whole fragment) and temporally (during the whole season). Within certain ranges of pedestrian rates, House Sparrows may prefer to settle in highly visited wooded parks, as humans may be sources of refuse and leftovers, thereby increasing food availability

(Fernández-Juricic 2001). However, constant, extremely high pedestrian rates within fragments may also increase the chances of disruption of foraging and nesting activities in such a way that it may pay individuals to find alternative nesting sites (e.g., buildings), with the resultant reduction in local breeding densities (Fernández-Juricic 2000a, Fernández-Juricic and Tellería 2000). Such a variation in breeding behavior owing to pedestrians has been documented in eagles (Steidl and Anthony 2000), penguins (Giese 1996), and skimmers (Safina and Burger 1983). For this process to be possible, the amount of suitable area affected by pedestrians within fragments should be large, and the levels of human visitation should remain high during the day. Both conditions are met in highly visited wooded parks in Madrid (Fernández-Juricic 2000a). Although this explanation is suggestive, direct evidence has yet to be gathered linking this mechanism with other demographic variables not analyzed in this study (e.g., breeding success, survival, mortality), since responses to people at the individual level may not affect trends at the population level (Gill et al. 2001b).

IMPLICATIONS FOR HUMAN-WILDLIFE INTERACTIONS

The behavioral mechanisms underlying wildlife responses to humans can be useful for developing models that predict the outcome of human-wildlife interactions. Nonlinear responses may be common in other species that are attracted directly (sources of food and breeding substrates, Blair 1996) or indirectly (attraction of potential prey species, Vierling 2000) by humans but whose tolerance levels may decrease with increasing human visitation levels. Actually, nonlinear responses have received scant attention, and may be more widespread than previously thought. For instance, they may account for reductions in predation risk in areas with high levels of human visitation (Osborne and Osborne 1980), increased exploitation of resources close to people avoided by competing species (Skagen et al. 1991), and variations in bird density with microhabitat features (Meents et al. 1983, Coppedge et al. 2001, Vanhinsbergh and Chamberlain 2001).

Nonlinear patterns between pedestrian rates and the performance of a species ought to be assessed in the future in areas with different degrees of human visitation, for they can change management policies radically. In our case, at intermediate pedestrian rates, sparrow control measures could be appropriate to reduce the impacts (aesthetic, health, etc.) of superabundant species to human life in cities; but at high pedestrian rates, sparrow populations may need protection to avoid local extinction. Nonlinear responses can also affect the development of models explaining the distribution of a species at the landscape scale (Milsom et al. 2000). Such models usually assume linear interactions, drawing conclusions that may not consider the entire range of response of a given species (Meents et al. 1983). Consequently, models with only linear terms could produce overly restrictive management alternatives (namely, unnecessary closure of areas of conservation interest).

ACKNOWLEDGMENTS

We thank Jennifer Gill, Ken Norris, Jukka Jokimäki, and two anonymous referees for constructive comments, and all the volunteers (particularly Beatriz González, Francisco Casado, and Jesús Rodriguez) for valuable help during the experiments. EFJ was funded by "la Caixa" Foundation and Consejo Nacional de Investigaciones Científicas y Técnicas.

LITERATURE CITED

ALLEN, A. P., AND R. J. O'CONNOR. 2000. Interactive effects of land use and other factors on regional bird distributions. Journal of Biogeography 27: 889–900.

BEZZEL, E. 2001. Does only the sparrow survive? Birds in the exploited landscape 2000. Journal für Ornithologie 142:160–171.

BIOSTAT. 1997. Power and Precision, version 1.2. Biostat, Teaneck, NJ.

BLAIR, R. B. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6:506–519.

CLARK, C. W., AND M. MANGEL. 1986. The evolutionary advantages of group foraging. Theoretical Population Biology 30:45–75.

CLEMENT, P., A. HARRIS, AND J. DAVIS. 1993. Finches and sparrows. Christopher Helm, A and C Black, London.

CONNOR, E. F., A. C. COURTNEY, AND J. M. YODER. 2000. Individual-area relationships: the relationship between animal population density and area. Ecology 81:734–748.

COPPEDGE, B. R., D. M. ENGLE, S. D. FUHLENDORF, R. E. MASTERS, AND M. S. GREGORY. 2001. Urban sprawl and juniper encroachment effects on abundance of wintering passerines in Oklahoma, p. 225–242. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [EDS.], Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Norwell, MA.

EASTERBROOK, T. G. 1999. Population trends of wintering birds around Banbury, Oxfordshire 1975–96. Bird Study 46:16–24.

ERZ, W. 1966. Ecological principles in the urbanization of birds. Ostrich Supplement 6:357–364.

FERNÁNDEZ-JURICIC, E. 2000a. Local and regional effects of pedestrians on forest birds in a fragmented landscape. Condor 102:247–255.

FERNÁNDEZ-JURICIC, E. 2000b. Avifaunal use of linear strips in an urban landscape. Conservation Biology 14:513–521.

FERNÁNDEZ-JURICIC, E. 2001. Avian spatial segregation at edges and interiors of urban parks in Madrid, Spain. Biodiversity and Conservation 10:1303–1316.

FERNÁNDEZ-JURICIC, E. 2002. Can human disturbance promote nestedness? A case study with breeding birds in urban habitat fragments. Oecologia 131: 269–278.

FERNÁNDEZ-JURICIC, E., M. D. JIMENEZ, AND E. LUCAS. 2001a. Bird tolerance to human disturbance in urban parks of Madrid, Spain. Management implications, p. 261–275. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [EDS.], Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Norwell, MA.

FERNÁNDEZ-JURICIC, E., M. D. JIMENEZ, AND E. LUCAS. 2001b. Alert distance as an alternative measure of bird tolerance to human disturbance. Implications for park design. Environmental Conservation 28: 263–269.

FERNÁNDEZ-JURICIC, E., R. SANZ, AND A. SALLENT. 2001. Frequency-dependent predation by wild birds at edges and interiors of woodland. Biological Journal of the Linnean Society 73:43–49.

FERNÁNDEZ-JURICIC, E., AND J. L. TELLERÍA. 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.

FOX, A. D., AND J. MADSEN. 1997. Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. Journal of Applied Ecology 34:1–13.

FRID, A., AND L. M. DILL [ONLINE]. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6(1):11. <http://www.consecol.org/vol6/iss1/art11> (12 June 2002).

GIESE, M. 1996. Effects of human activity on Adélie Penguin *Pygoscelis adeliae* breeding success. Biological Conservation 75:157–164.

GILL, J. A., K. NORRIS, AND W. J. SUTHERLAND. 2001a. The effects of disturbance on habitat use by Black-tailed Godwits *Limosa limosa*. Journal of Applied Ecology 38:846–856.

GILL, J. A., K. NORRIS, AND W. J. SUTHERLAND. 2001b. Why behavioural responses may not reflect the population consequences of human disturbance. Biological Conservation 97:265–268.

GUTZWILLER, K. J., AND S. H. ANDERSON. 1999. Spatial extent of human-intrusion effects on subalpine bird distributions. Condor 101:378–389.

HAILA, Y. 1988. Calculating and miscalculating density: the role of habitat geometry. Ornis Scandinavica 19:88–92.

HOLE, D. G., M. J. WHITTINGHAM, R. B. BRADBURY, G. Q. A. ANDERSON, P. L. M. LEE, J. D. WILSON, AND J. R. KREBS. 2002. Widespread local House-Sparrow extinctions. Nature 418:931.

JÄRVINEN, O., AND R. A. VÄISÄNEN. 1977. Line transect method: a standard for field-work. Polish Ecological Studies 3:11–15.

MARSDEN, S. J. 2000. Impact of disturbance on waterfowl wintering in a UK dockland redevelopment area. Environmental Management 26:207–213.

MCCULLAGH, P., AND J. A. NELDER. 1989. Generalized linear models, 2nd ed. Chapman and Hall, London.

MEENTS, J. K., J. RICE, B. W. ANDERSON, AND R. D. OHMART. 1983. Nonlinear relationships between birds and vegetation. Ecology 64:1022–1027.

MILSOM, T. P., S. D. LANGTON, W. K. PARKIN, S. PEEL, J. D. BISHOP, J. D. HART, AND N. P. MOORE. 2000. Habitat models of bird species' distribution: an aid to the management of coastal grazing marshes. Journal of Applied Ecology 37:706–727.

NEWTON, I. 1998. Population limitation in birds. Academic Press, London.

O'CONNELL, T. J., L. E. JACKSON, AND R. P. BROOKS. 2000. Bird guilds as indicators of ecological condition in the central Appalachians. Ecological Applications 10:1706–1721.

OSBORNE, P., AND L. OSBORNE. 1980. The contribution of nest site characteristics to breeding-success among Blackbirds *Turdus merula*. Ibis 122:512–517.

PEARCE, J., AND S. FERRIER. 2000. An evaluation of algorithms for fitting species distribution models using logistic regression. Ecological Modelling 128:127–147.

POGUE, D. W., AND G. D. SCHNELL. 1994. Habitat characterization of secondary cavity-nesting birds in Oklahoma. Wilson Bulletin 106:203–226.

PRODON, R., AND J.-D. LEBRETON. 1981. Breeding avifauna of a Mediterranean succession: the holm oak and cork oak series in the eastern Pyrenees, 1. Analysis and modelling of the structure gradient. Oikos 37:21–38.

RODGERS, J. A., AND H. T. SMITH. 1995. Set-back distances to protect nesting bird colonies from human disturbance in Florida. Conservation Biology 9: 89–99.

SÆTHER, B.-E., T. H. RINGSBY, O. BAKKE, AND E. J. SOLBERG. 1999. Spatial and temporal variation in demography of a House Sparrow metapopulation. Journal of Animal Ecology 68:628–637.

SAFINA, C., AND J. BURGER. 1983. Effects of human disturbance on reproductive success in the Black Skimmer. Condor 85:164–171.

SKAGEN, S. K., R. L. KNIGHT, AND G. H. ORIANS. 1991. Human disturbances of an avian scavenging guild. Ecological Applications 1:215–225.

STATSOFT, INC. 2002. Statistica, version 6. StatSoft, Inc., Tulsa, OK.

STEIDL, R. J., AND R. G. ANTHONY. 2000. Experimental effects of human activity on breeding Bald Eagles. Ecological Applications 10:258–268.

SUMMERS-SMITH, J. D. 1988. The sparrows. T. and A.D. Poyser, London.

VANHINSBERGH, D. P., AND D. E. CHAMBERLAIN. 2001. Habitat associations of breeding Meadow Pipits *Anthus pratensis* in the British uplands. Bird Study 48:159–172.

VIERLING, K. T. 2000. Source and sink habitats of Red-winged Blackbirds in a rural/suburban landscape. Ecological Applications 10:1211–1218.