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Density-dependent habitat selection of corridors in a fragmented landscape

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This paper assesses the occurrence of density-dependent habitat selection in an urban fragmented landscape, composed of forest fragments (urban parks) connected by corridors (wooded streets), to test the hypothesis that as population density increased in the parks their suitability decreased and individuals entered alternative habitats, such as wooded streets. Density variation of six species was studied during two consecutive breeding seasons. Vegetation structure in wooded streets was significantly less complex than in urban parks, supporting the view that wooded streets were less suitable for breeding birds. Five species (Coal Tit *Parus ater*, Spotless Starling *Sturnus unicolor*, Serin *Serinus serinus*, Black-billed Magpie *Pica pica* and Woodpigeon *Columba palumbus*) showed density-dependent habitat occupation of wooded streets, while the Common Blackbird *Turdus merula* did not. As park suitability decreased with rising densities, wooded streets became a profitable alternative in terms of foraging, breeding, or for moving between parks. However, the relationships varied both between and within species in different years. Such differences could have been caused by variable rates of human disturbance, renewal of resources and predation risks in wooded streets. More detailed studies are required to determine how birds perceive and regulate their population dynamics in fragments and associated corridors, particularly for species targeted for management.

The uneven distribution of individuals may be related to spatial variation in habitat quality, such that, in some species, site suitability decreases with increasing population density (Brown 1969, Fretwell & Lucas 1970, Rosenzweig 1991). Generally, at low densities individuals are assumed to select the most suitable habitats; but as density increases, individuals should occupy alternative habitats so that their survival and reproductive success would be higher than (or at least the same as) in areas already occupied (Fretwell & Lucas 1970, Rosenzweig 1991, Kacelnik *et al.* 1992). Several mechanisms have been put forward to explain density-dependence: ideal free distribution (Brown 1969, Fretwell & Lucas 1970), ideal despotic distribution (Fretwell & Lucas 1970), site-dependent regulation (Rodenhouse *et al.* 1997), etc. Density-dependent habitat selection may stem from increased intra-specific competition for food or nest-sites, predation risk or prey depletion (Cassini & Foger 1995, Bautista *et al.* 1995, Cresswell 1997, Houston & McNamara 1997). This process is likely to occur in fragmented landscapes, due to the differential suitability of habitat patches (Morris 1995, Newton 1998), although there is little direct evidence for it.

Fragmented landscapes can be thought of as an array of islands of suitable habitat in a sea of unsuitable habitats. These island fragments may be connected by corridors (linear strips of vegetation). Provided that the suitability of fragments is higher than that of corridors, one might expect corridor occupation (either for breeding or foraging) to be a function of the density of individuals in fragments. Increased population density within fragments may trigger regulating negative feedback mechanisms (Bernstein *et al.* 1991, Pulliam & Danielson 1991, Sherry & Holmes 1996), resulting in a scatter of surplus individuals into corridors.

The purpose of this paper was to assess whether individual species occupy corridors following a density-dependent process of habitat selection across fragments. The study was conducted in an urban fragmented landscape (Madrid, Spain) during two consecutive breeding seasons. Urban landscapes are suitable to study fragmentation effects (Soulé *et al.* 1988) because urban parks can be regarded as isolated

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forest fragments that are connected by wooded streets (Fernández-Juricic in press). These wooded streets are used by several bird species according to their degree of habitat complexity and could potentially function as corridors (Fernández-Juricic 2000). This study did not aim to assess the final destination of individuals that occupy a wooded street, but to analyse patterns of wooded street occupation in relation to park density.

I first determined habitat structure differences between parks and wooded streets to examine variation in habitat quality and quantity (Knight & Morris 1996). Density-dependent habitat selection was studied following the approach of Morris (1987, 1995), by which parks and wooded streets were assumed to be adjacent habitats with different degrees of suitability (parks higher than wooded streets) (Fernández-Juricic 2000). Such relationships could be depicted by plotting density in one habitat on that in the other for each species. Significant regression slopes between park and wooded streets densities are expected if wooded street occupation follows a density-dependent process of habitat selection in parks; otherwise, species occurrence in wooded streets would be independent of park density. I also analysed how density-dependent patterns of corridor occupation varied within species, between years.

The isodar model

The isodar model (Morris 1987, 1988, 1992, 1995) was developed to test patterns of density-dependent habitat selection according to changes in population sizes in different landscape elements (generally, adjacent habitats). Consider two habitats in which fitness

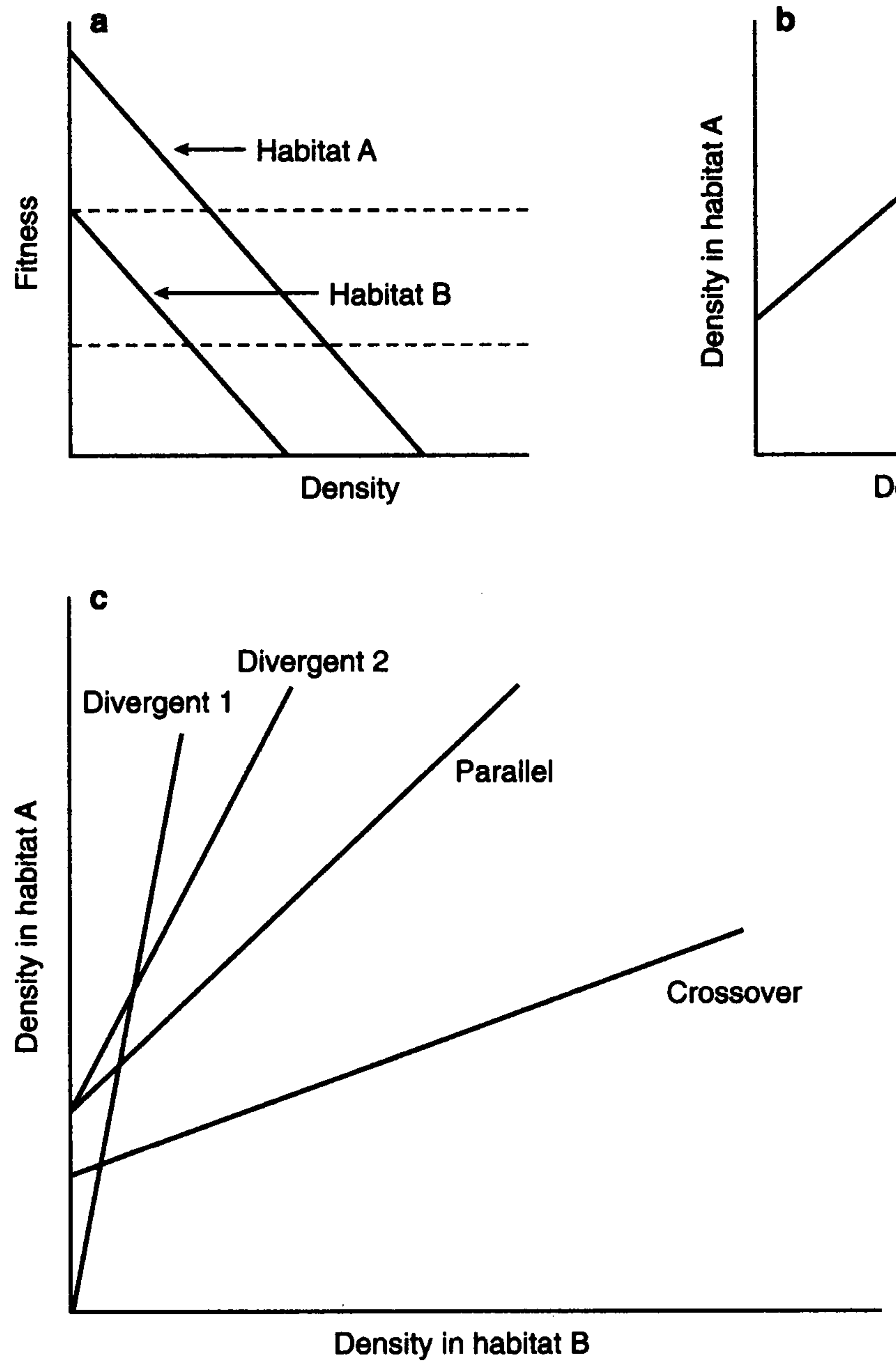

Figure 1. Schematic representation of the isodar model. (a) Habitats A and B have different fitness–density relationships. At low density, individuals should occupy habitat A due to greater fitness; but as density increases, fitness will be reduced in habitat A, and individuals begin occupying habitat B. Horizontal lines indicate similar fitness values in both habitats. (b) The isodar generated from the intersection of the functions represented in (a). (c) Four isodar models of density-dependent population regulation: parallel, divergent 1 (quantitatively similar habitats), divergent 2 (quantitatively different habitats), and crossover.

decreases with density, but fitness in habitat A is double that in habitat B (Fig. 1a). At low densities, individuals would occupy habitat A. After increased density reduces fitness in habitat A to that found in habitat B, individuals should occupy either habitat. Densities in both habitats will be equivalent to the intersection of the fitness-density function of each habitat with a set of horizontal lines corresponding to equal fitness in both habitats (Fig. 1a). Densities in each habitat can be plotted to give a line (isodar) in which the expected reproductive success is the same in both habitats (Fig. 1b, Morris 1988, 1995). The slope of the isodar indicates qualitative variations in both habitats (e.g. habitats offer different kinds of resources); whereas the intercept indicates quantitative differences (e.g. habitats offer similar resources but in different amounts).

The isodar analysis allows one to examine quantitative and qualitative differences between habitats, which may serve to infer the form of population regulation (Fig. 1c, Morris 1987, 1988). For example, when habitats differ quantitatively, individuals will have equal foraging rates in each; however, individuals foraging in the rich habitat will have more resources to convert into reproduction and survival, giving rise to a parallel regulation (intercept > 0, Fig. 1c), in which individuals would move from high- to low-density habitats (Morris 1988). Habitats that differ qualitatively show two forms of divergent regulation, taking into account that they do or do not differ quantitatively (Fig. 1c). In the latter case, the effects of density on fitness are more pronounced in the habitat with lower foraging efficiency. When habitats differ both qualitatively and quantitatively, with lower foraging rates in the more productive habitat, the resulting regulation is crossover (Fig. 1c). These patterns of population regulation have broad implications (Morris 1995), including the assessment of habitat selection criteria for scale-dependent processes (e.g. foraging, dispersal), the spatial and temporal effects of disturbance, and the value of different landscape elements based on species' perceptual ranges. Differences in isodar slopes and intercepts are then useful for establishing hypotheses to be tested regarding habitat selection between landscape elements (Morris 1995).

METHODS

Study area

This study was conducted in the city of Madrid (Spain) during the springs (May to July) of 1997 and 1998. The city has an extensive network of urban parks; many of them connected by wooded streets. Bird communities in this urban landscape have similar patterns of spatial and temporal distribution to other fragmented habitats (Fernández-Juricic in press). A previous study (Fernández-Juricic 2000) showed that wooded streets were intermediate landscape elements between parks and the urban matrix, used by several bird species that inhabited urban parks, and could potentially function as corridors, increasing the overall connectivity of the landscape.

Urban parks used in this study ranged from 4 to 110 ha and were representative of the parks of this city, with deciduous and coniferous trees, and large areas of watered grass. Wooded streets were lined with a mix of deciduous and coniferous trees at least 4 m high. These trees were arranged linearly on pavements 2–3 m apart, giving the appearance of a continuous linear green cover. Most old trees had holes that offered potential nesting sites. The sampling design was such that each sampled street was located near a sampled park, so that replicated pairs of parks and wooded streets were obtained. Thus, the basic unit upon which analyses were conducted consisted of a park and a wooded street. Some parks were connected to small parks by wooded streets. To avoid misinterpretation of the results due to the influence of these small parks, I only sampled the first 150–250 m (about 25–30% of the total street length) of the wooded streets from the focal parks.

Wooded streets were selected according to their similarity in habitat structure, since species occupation is related to corridor structural complexity (Fernández-Juricic 2000). The same criterion was used for urban parks, although they differed in size. However, park area affected neither the density nor the probability of corridor occupation of any species (Fernández-Juricic unpubl. data). The variability in the amount of suitable habitat in urban parks due to size differences could be used to examine how habitat selection took place over a gradient of differently suited parks in relation to structurally similar wooded streets (see below, Fig. 2). The number of parks and wooded streets that were suitable for sampling was much less than the total available, and I sampled all the units in this landscape that met the above criteria, totalling 12 parks and 12 wooded streets.

Bird surveys

Parks were surveyed four or five times per year in the morning (07:00–11:00 h) to determine species richness and the density of individual bird species (birds/10 ha). I recorded the number of individuals seen and vocalizing in 100 × 50 m fixed line transects in large parks; in small ones, I surveyed by thorough searching (see Tellería & Santos 1997).

I surveyed each street weekly (six or seven visits per year) to determine the number and density of bird species. Each survey lasted at least 20 minutes. As I walked along pavements at a steady pace, I recorded only those birds seen or heard up to 20 m from the ground, just below the uppermost canopy layer to ensure that individuals were using trees within streets. When birds were detected on the ground, I counted them as using wooded streets only if they landed (after fleeing) in nearby trees within the street. The analysis included only breeding individuals belonging to species observed within wooded streets when they were (1) present on at least 25% of visits, (2) observed on at least two consecutive visits, and (3) recorded when singing, building a nest, or carrying food. This procedure effectively assessed bird use of wooded streets (Fernández-Juricic 2000).

Species of Anatidae and Apodidae were excluded from the analyses as their distributions are determined by features that are not uniformly distributed through the urban landscape. House Sparrows *Passer domesticus* and Rock Doves *Columba livia* were also excluded, since they are widespread in urban habitats (Adams & Dove 1989), and their distributions violate the assumption that parks and wooded streets were the only suitable elements in this landscape.

Wooded street abundance estimates were expressed as density estimates (dividing by [wooded street width × transect length]). Estimations of density were based on measures averaged over only those parks and wooded streets at which the species was present.

Vegetation structure

The underlying assumption of this work is that wooded streets are less suitable than urban parks. I compared vegetation structure between these landscape elements to confirm the habitat subdivision, at least in terms of habitat complexity, to assess density-dependent habitat selection (Knight & Morris 1996). Several vegetation traits were measured in 25-m radius circular plots distributed at 30-m intervals along transects in parks and wooded streets, and randomly in small parks (see Tellería & Santos 1997). Cover variables were estimated visually following Prodon and Lebreton (1981). Vegetation traits included grass cover, shrub cover, number of shrub species, shrub height, coniferous cover, deciduous cover, number of tree species, tree height and the number of stems < 10, 10–30, 30–50, and > 50 cm dbh.

Statistical analyses

A discriminant function analysis (DFA) was performed to assess quantitative differences in habitat structure between parks and wooded streets. Significant variables were selected by forward stepwise procedures (F-to-enter = 3.5), and the *a priori* probabilities for classification were selected proportional to group sizes because of unequal sample sizes. The results of the DFA were interpreted considering the significance of the discriminant function, the significance of the variables finally entered into the model, and the accuracy of the classification of cases into groups.

The isodar approach has proved reliable to account for density-dependent patterns of habitat selection within adjacent habitats (Morris 1987, 1988, 1992, 1995, Ovadia & Abramsky 1995, Rodriguez 1995). Densities in parks and their associated wooded streets were regarded as replicated samples in habitats assumed to have different overall suitability. Urban parks were assumed to be better for most species because of their greater area, more complex habitat structure and less disturbance (pedestrian and traffic load, Fernández-Juricic & Tellería 2000, Fernández-Juricic in press). Furthermore, with a higher edge/core ratio, wooded streets could be regarded as marginal habitats within the urban landscape (Fernández-Juricic 2000). As a result, it would be expected that the relationships between these habitats would reflect the preference of individuals to maximize their fitness in urban parks.

Not all wooded streets were occupied by every species. For analysis only those species occupying at least six wooded streets in each year were considered (Morris 1987). I plotted park density versus wooded street density, assuming that individuals in both habitats distributed according to an ideal free distribution (for the assumptions and caveats of this procedure see Morris 1987, 1988, 1995, Knight & Morris 1996).

The isodar equation applied to this scenario for each species is:

$$N_{\text{parks}} = C + b\, N_{\text{wooded streets}}$$

where N_{parks} and $N_{\text{wooded streets}}$ are the densities of a given species, C is the intercept, and b the slope of the regression (Morris 1989). Non-significant slopes denote that habitat selection is independent of density;

while significant slopes indicate a density-dependent habitat selection process. Significant slopes > 1 suggest a density-dependent process which is more pronounced in wooded streets, and intercepts > 0 demonstrate that initial differences in the overall survival and reproductive success are higher in parks than in wooded streets. Isodars were analysed by geometric linear regression (Morris 1988). Departures from unity of slopes were tested by *t*-tests, and of intercepts from 0 by calculating confidence intervals. I checked for non-linearity in the residuals of the isodar models, but no such pattern was found. I also analysed the different types of density-dependence (Fig. 1), which may cast some light on the way in which species are affected by qualitative and quantitative differences between urban parks and wooded streets. See Table 1 for scientific names of species mentioned in the text.

RESULTS

Vegetation structure differed quantitatively between the two landscape elements. Wooded streets had significantly less grass, deciduous and coniferous tree cover, and fewer stems in each of the three lowest dbh classes (DFA, Wilks' Lambda = 0.012, $F_{6,17} = 227$, $P < 0.001$, Fig. 2). From the discriminant function 100% of cases were correctly assigned to their proper habitats. Moreover, the squared Mahalanobis distance between the two centroids was significant (SMD = 320.46; $P < 0.001$), supporting the view of wooded streets and parks as structurally distinct habitats.

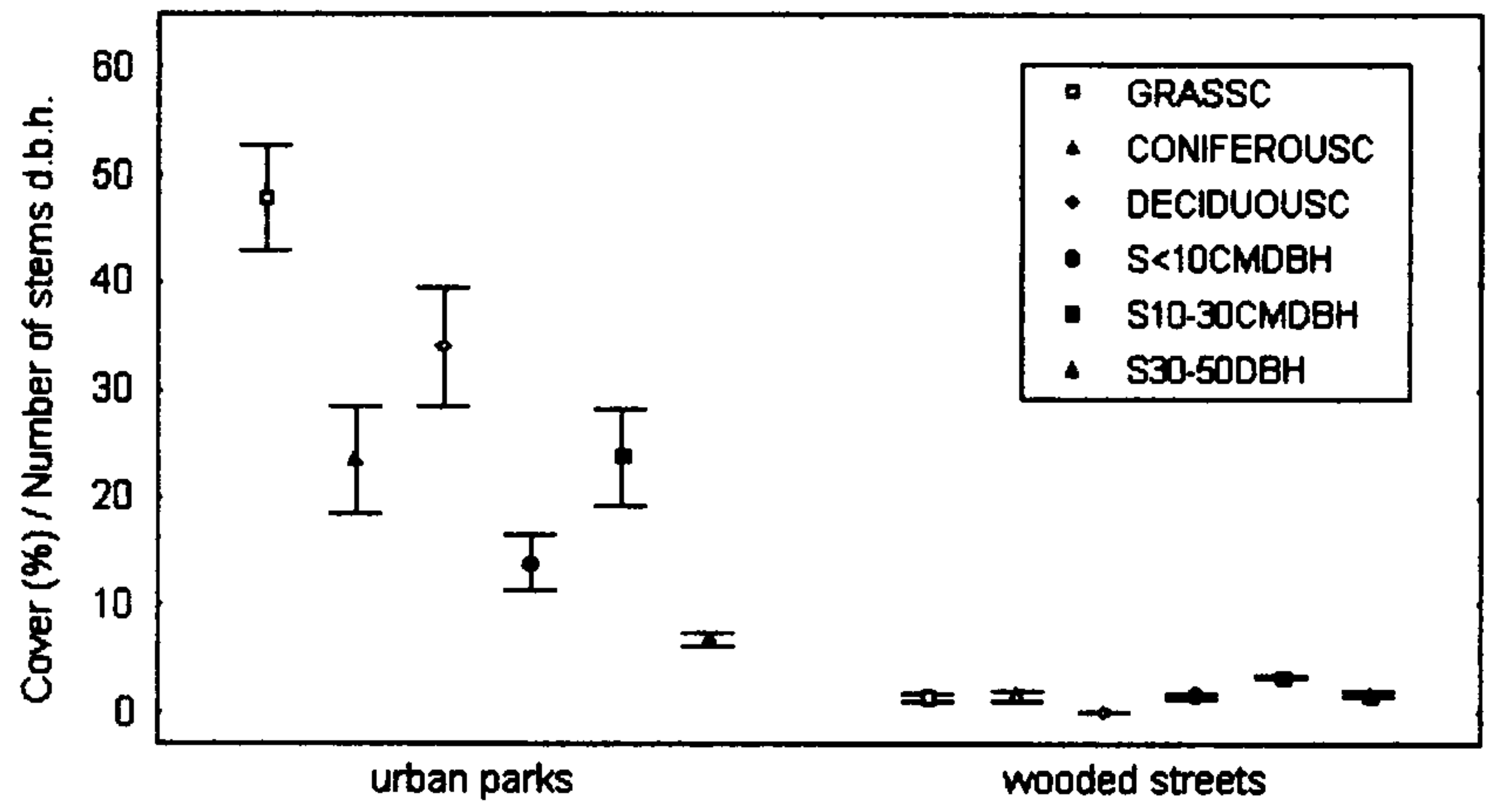

Figure 2. Structural differences between parks and wooded streets in the city of Madrid (Spain). Cover variables (percentages) include: grass cover (GRASSC), coniferous cover (CONIFEROUSC) and deciduous cover (DECIDUOUSC). Categories showing the number of stems are: stems less than 10 cm dbh (S < 10CMDBH), stems between 10 and 30 cm dbh (S10–30CMDBH), stems between 30 and 50 cm dbh (S30–50DBH).

Fourteen species were detected in wooded streets in both years (Table 1). However, only six species could be modelled by isodar analyses (≥ 6 wooded streets occupied). Eight out of ten models yielded significant regressions, highlighting a density-dependent process of wooded street occupation (Figs 3 & 4). The scatter of densities appeared not to follow a curvilinear response (at least over the range of sampled densities) and regression models accounted for 50–90% of the variability in density between habitats. Only two models were not significant, implying that corridor occupation was density-independent. Isodars varied between species, within species, and also between years.

Table 1. Species found in urban parks and wooded streets during 1997–98 breeding seasons in the city of Madrid (Spain). Densities are expressed as number of individuals/10 ha. Park densities, the species found in wooded streets, and the number of wooded streets occupied are shown for each year.

Species	Park density		Wooded streets occupied	
	1997	1998	1997	1998
Common Blackbird *Turdus merula*	62.07	33.12	6	8
Spotless Starling *Sturnus unicolor*	43.62	26.5	5	6
Serin *Serinus serinus*	35.24	35.4	6	9
Woodpigeon *Columba palumbus*	43.95	18.94	8	8
Black-billed Magpie *Pica pica*	37.16	18.94	8	9
European Greenfinch *Carduelis chloris*	11.92	12.14	5	5
White Wagtail *Motacilla alba*	2.4	5.51	1	2
Coal Tit *Parus ater*	7.66	6.29	4	6
Great Tit *Parus major*	5.48	3.09	5	2
Tree Sparrow *Passer montanus*	4.50	4.68	1	1
Blue Tit *Parus caeruleus*	4.88	4.45	2	3
Hoopoe *Upupa epops*	2.43	2.26	1	1
Green Woodpecker *Picus viridis*	2.5	2.59	1	1
Jackdaw *Corvus monedula*	1.18	3.08	1	2

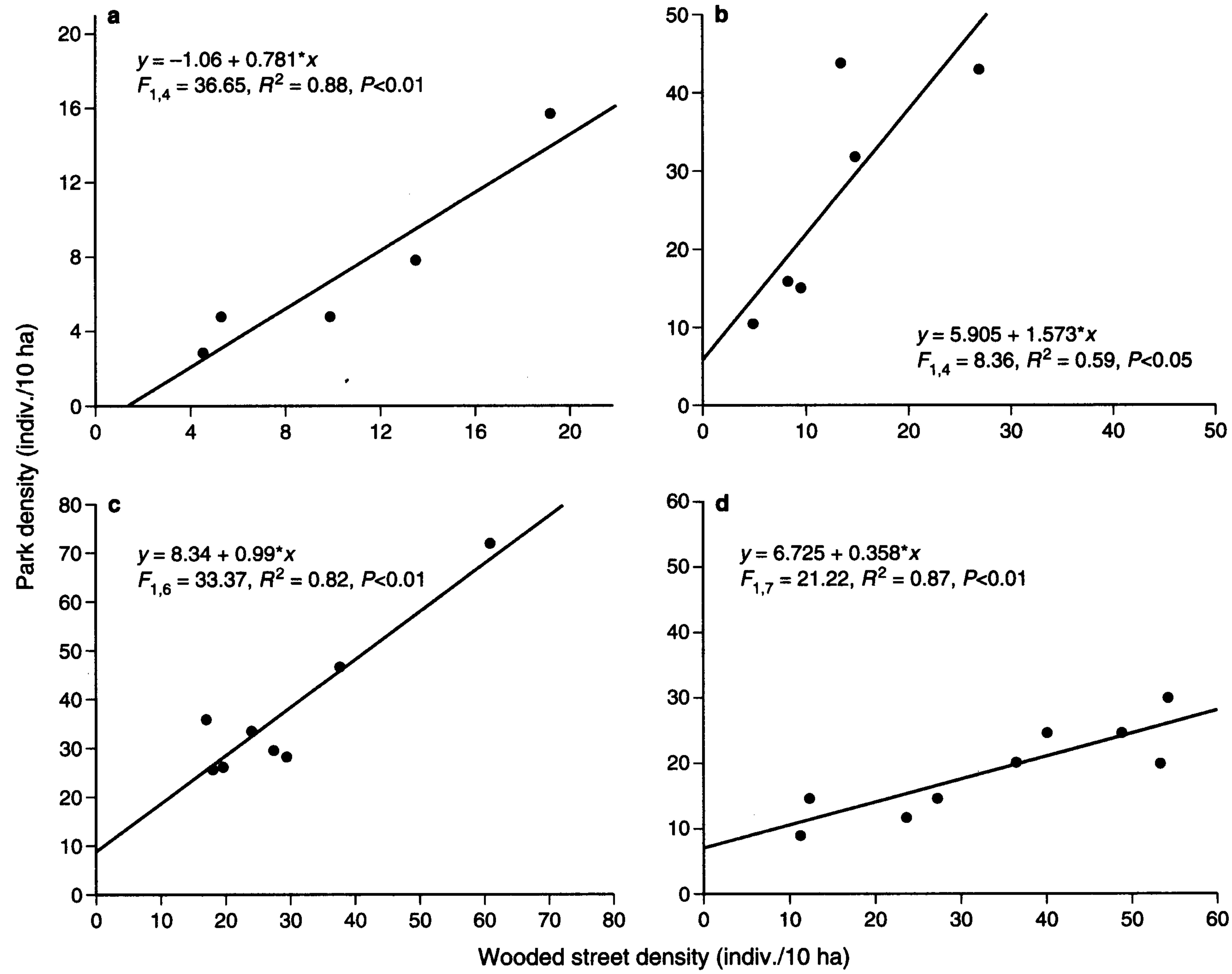

Figure 3. Isodar plots of (a) Coal Tit (1998), (b) Spotless Starling (1998) and (c) Magpie (1997) and (d) Magpie (1998) in urban parks and wooded streets in Madrid. Shown are the linear equations fitted by geometric regressions and F, R^2, and P values for each species.

Common Blackbirds selected habitats independent of density in both years (1997, $y = 95.49 - 0.57x$, $F_{1,4} = 0.75$, $R^2 = 0.01$, $P = 0.435$; 1998, $y = 67.68 - 0.557x$, $F_{1,6} = 2.07$, $R^2 = 0.13$, $P = 0.20$). Coal Tit and Spotless Starling isodar slopes did not differ from unity and the intercepts did not differ from 0, suggesting a congruent regulation (Morris 1988), by which parks and wooded streets appear to be qualitatively and quantitatively similar (Fig. 3a & 3b, Table 2). In 1997 and 1998, the intercepts for isodar plots of Black-billed Magpies were significantly different from 0, indicating quantitative differences between habitats, but isodar slopes differed between years (Fig. 3c & 3d, Table 2). In 1997, the slope was not different from one (parallel regulation, parks and wooded streets only differed quantitatively), while in 1998, the slope was significantly less than 1.0 (Table 2), supporting a crossover regulation (parks were quantitatively superior but qualitatively less suitable than wooded streets). Exactly the same relationships between years applied for Woodpigeons, with a parallel regulation in 1997, and a crossover regulation in 1998 (Fig. 4a & 4b, Table 2). Finally, Serins also presented inter-annual differences in the density-dependent process of wooded street occupation. In 1997, the intercept did not differ from 0, nor the slope from 1, indicating a congruent regulation (parks and wooded streets were quantitatively and qualitatively similar) (Fig. 4c, Table 2). In 1998, the intercept was greater than 0 and the slope was significantly less than 1 (Fig. 4d, Table 2), suggesting a crossover regulation.

DISCUSSION

The results of this study suggest that for many species

Table 2. Relationships between park and wooded street densities in Madrid. Data show the results of t-tests to determine whether (a) isodar intercepts differed from 0 and (b) isodar slopes differed from 1. Abbreviations: df, degrees of freedom; Intcp, intercept; CI, confidence intervals.

	Intercept different from 0			Slope different from 1			
Species	Intcp	T (df)	*P*	CI	Slope	t (df)	*P*
Coal Tit 1998	–1.05	–0.751 (4)	0.494	± 3.91	0.78	–1.69 (4)	0.1650
Spotless Starling 1998	5.91	0.728 (4)	0.501	± 22.55	1.573	1.05 (4)	0.353
Black-billed Magpie 1997	8.34	2.46 (6)	< 0.05	± 7.36	0.98	–0.0642 (6)	0.9509
Black-billed Magpie 1998	6.72	2.56 (7)	< 0.05	± 6.53	0.358	–8.337 (8)	< 0.01
Woodpigeon 1997	21	2.54 (6)	< 0.05	± 20.2	1.96	1.596 (6)	0.1617
Woodpigeon 1998	18.64	3.33 (6)	< 0.05	± 13.47	0.376	–4.065 (6)	< 0.01
Serin 1997	13.85	1.24 (4)	0.283	± 31.05	0.577	–2.14 (4)	0.091
Serin 1998	19.99	2.79 (7)	< 0.05	± 16.85	0.399	3.76 (7)	< 0.01

density in urban parks can affect patterns of wooded street occupation, denoting a density-dependent process of habitat selection (Pulliam & Danielson 1991, Morris 1995). Differences in habitat quantity

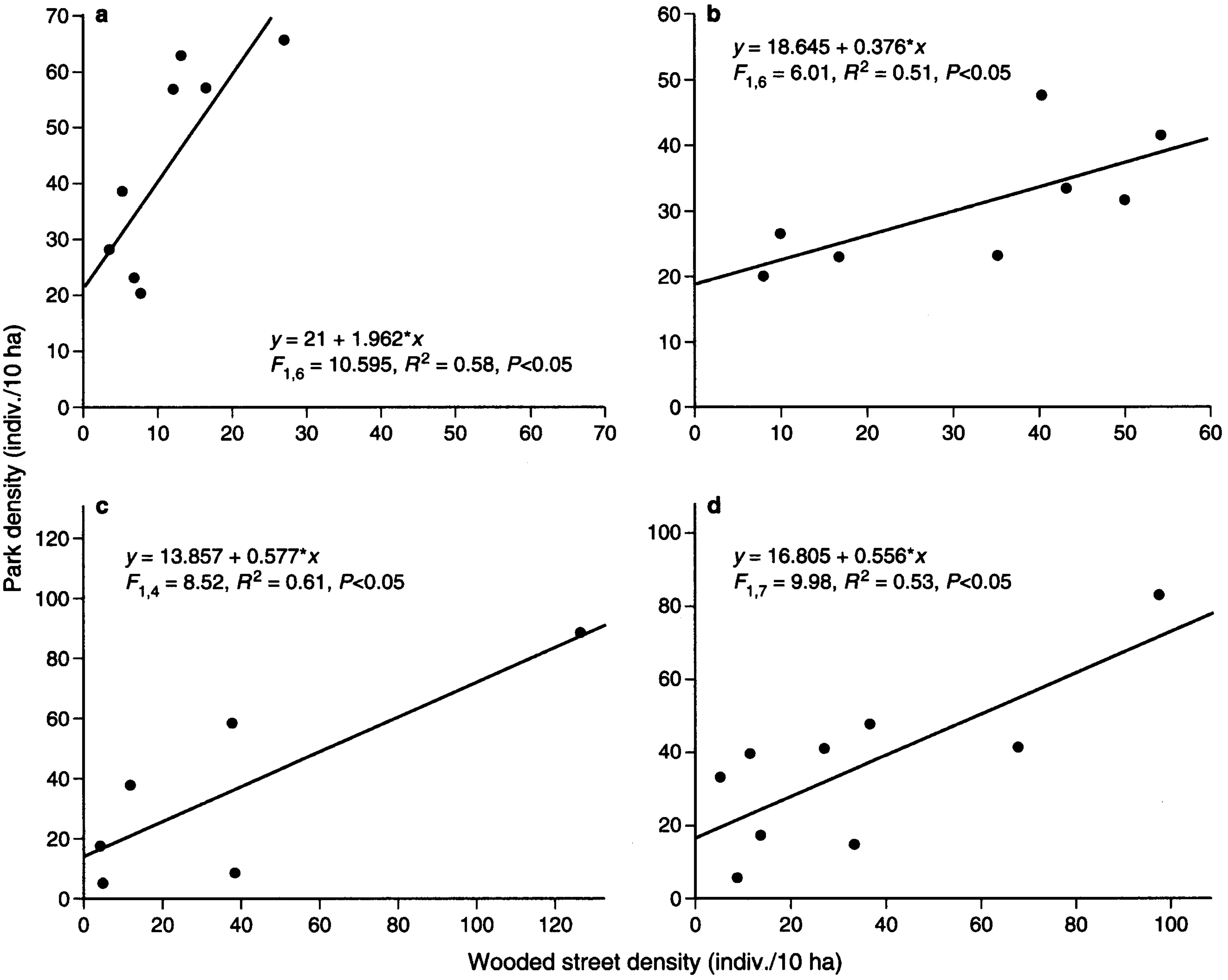

Figure 4. Isodar plots of (a) Woodpigeon (1997) and (b) Woodpigeon (1998) and (c) Serin (1997) and (c) Serin (1998) in urban parks and wooded streets in Madrid. Shown are the linear equations fitted by geometric regressions and F, R^2, and P values for each species.

between parks and wooded streets are bound to increase the likelihood of density-dependent processes in parks. As park suitability is diminished by the overcrowding of individuals, wooded streets provide profitable alternatives in terms of foraging, breeding or moving into other suitable parks (Fernández-Juricic 2000). The increase observed in the occupation of these alternative habitats is predicted by both the ideal free and despotic distributions (O'Connor 1986, Bernstein *et al.* 1991), even though with the available data it could not be concluded which mechanism might be operating.

The significant isodars indicate the importance of local rather than regional factors on the functioning of urban community structure (Clergeau *et al.* 1998), since park densities determine the occupation of landscape elements that might hold surplus individuals. Similar directional relationships between suitable and marginal habitats have been found for other bird species (O'Connor 1986, Bensch & Hasselquist 1991, Holmes *et al.* 1996, Newton 1998, Chamberlain & Fuller 1999). Such a scenario supports the view that dynamics in marginal habitats (wooded streets) are strongly tied to the ecological factors that regulate habitat selection in more suitable patches (urban parks), at least for the majority of species studied in this landscape (Pulliam & Danielson 1991). The lack of density-dependent patterns for Blackbirds may reflect regional influences, since urban landscapes may be considered sinks occupied by surplus individuals from suburban areas. Another possibility is that the increasing adaptation of Blackbirds to urban areas may have modified their perception of landscape elements, by which parks, wooded streets, and the urban matrix differ qualitatively in ways not recognized in this study.

Five out of six species modelled show density-dependent habitat selection in at least one year (Figs 3 & 4). Comparisons of isodar slopes and intercepts deepen our understanding of density-dependent relationships and their implications for different species (Morris 1987). It is interesting that some species appear to differ in the strength of density-dependence between years. Such differences within species may stem from variable annual patterns of population regulation or from low sample size. The isodar model has been successfully employed to test density-dependence in rodents with similar sample sizes to those used in this study (Morris 1987, 1988, 1995, Rodriguez 1995). Therefore, it is conceivable that the observed differences were related to the inherent variability of urban habitats due to disturbance, predation, etc. (Blair 1996, Jokimäki *et al.* 1996, Fernández-Juricic & Tellería 2000, Fernández-Juricic in press).

For Coal Tit (1998) and Starling (1998), parks and wooded streets apparently did not differ quantitatively, denoting a congruent regulation. Such population regulation could be interpreted as being due to the scale of habitat use (Morris 1992); these species might be using wooded streets and parks equally as foraging patches within their home ranges (Morris 1992, 1995). Mixed exploitation of both habitats may diminish the putative high quality of parks and increase the low quality of wooded streets (Morris 1995). A similar congruent regulation was found for Serin (1997) but this pattern appears to be driven by a single point of high density (Fig. 4c). In 1997, the Magpie and Woodpigeon exhibited parallel regulation (Morris 1987), which suggests that wooded streets were quantitatively inferior to parks, but foraging use was similar in the two habitats. From parallel regulation both species turned to a crossover regulation in 1998 (Morris 1988), which implies that even though wooded streets were quantitatively inferior habitats, birds foraged with greater efficiency. A similar crossover pattern held for the Serin in 1998.

Differences in intercepts indicate that parks are of higher quality than wooded streets at lower density. Differences in slope demonstrate that, at least for some species, wooded streets were more suitable in 1998 than in 1997, being preferred at moderate density. Such increases in wooded street suitability may result from lower rates of pedestrian disturbance in 1998 (mean 1997 = 12.37, mean 1998 = 4.26, $t = 4.5$, df = 11, $P < 0.001$), which could have allowed expanded foraging and breeding opportunities (Fernández-Juricic & Tellería 2000). Other causes (not mutually exclusive) include a greater renewal of resources in wooded streets (Morris 1988), lower predation risks, and differences in the proportion of sexes or age classes occupying corridors. It is noteworthy that species with different habitat requirements (e.g. Coal Tits and Starlings) have similar dynamics of corridor occupation. Further testing in this regard is required.

Conservation implications

Although urban parks show similar patterns of species distribution to other forested landscapes (Fernández-Juricic in press), these results should be applied with care, since the general connectivity of this landscape, along with the habitat selection patterns of species with specific habitat requirements, may differ greatly (Rolando *et al.* 1997). Moreover, the study was conducted in a subset of the wooded streets potentially available to birds. The results, however, have important implications for current corridor theory (Saunders & Hobbs 1991, Rosenberg *et al.* 1997).

First, corridor suitability must be examined for each species targeted for management. In a narrow sense, corridors appear to be less suitable than their associated fragments. However, the variations in density-dependence encountered between these habitats suggest that for some species, and in some years, corridors may also be suitable elements in terms of foraging or reproduction. Indeed, corridors may be classified according to their suitability (Saunders & Hobbs 1991), depending on the availability of resources, density of individuals, disturbance loads and interactions with competitors. More detailed studies are required to assess how bird species perceive and regulate their population dynamics in different habitats (Lima & Zollner 1996, Knight & Morris 1996).

Secondly, corridors may increase the likelihood of dispersal to other patches (Taylor *et al.* 1993, Tischendorf & Wissel 1997). Provided a species follows a density-dependent pattern of corridor occupation, it could be argued that density in fragments needs to reach a certain threshold before individuals begin spilling into corridors. Therefore, species density in fragments should be evaluated before corridor implementation, as an alternative indicator of the probabilities of corridor occupation. If the density of a species in fragments is small, corridors may end up being useless, and alternatives (such as re-introduction) would be far more effective.

Finally, the potential negative effects of corridor implementation should also be taken into account (Simberloff *et al.* 1992), particularly in light of the density-dependent process of corridor occupation. For example, if a non-native predator is introduced into the system, its density might increase rapidly, altering the pattern of density-dependent habitat selection. The presence of corridors may raise the probability of movement to other fragments, increasing the negative effects of the predator over the whole landscape. Consequently, including the concept of density-dependent corridor occupation could enhance our understanding of species dynamics in fragmented landscapes and improve our ability to manage populations.

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