Edge Effects in the Great Tit: Analyses of Long-term Data with GIS Techniques

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Abstract: *In contemporary fragmented landscapes, edges are commonplace, and understanding the effects of edge environments is thus essential for the conservation of forest communities. The reproductive output of forest passerines is often reduced close to forest edges. Possible explanations include overcrowding by conspecifics, elevated rates of predation, and the occurrence of lower-quality habitat and/or individuals at forest edges. We attempted to separate these processes by examining edge effects in the absence of nest predation and by effectively controlling for differences in breeding density and the quality of habitats and individuals. We used an edge distance index (EDI), which accounts for the number and distribution of edges in close proximity to a breeding location, to help explain variation in breeding density, nesting success, and reproductive traits of 8308 pairs of Great Tits (*Parus major*) breeding between 1965 and 2005, in Wytham, near Oxford, United Kingdom. Results from linear mixed modeling confirmed higher breeding density and a higher proportion of immigrant individuals at forest edges. Nevertheless, independently of these effects, we also found that birds laying later, with smaller clutches but larger eggs, were typical of edge environments. The number of offspring recruited to the breeding offspring per breeding attempt was also reduced at edges, both directly and mediated through changes in clutch size and laying date. Edge effects on life histories were detectable within individual females and up to 500 m from the woodland edge. Woodland edges are increasingly common in contemporary fragmented landscapes. Therefore these results, which suggest a pervasive effect of edges on reproduction, are of considerable importance to the management and conservation of forest communities.*

Keywords: breeding density, ecotone, habitat quality, nest predation, nesting success

Efectos de Borde sobre *Parus major*: Análisis de Datos de Largo Plazo con Técnicas de SIG

Resumen: *En los paisajes fragmentados contemporáneos, los bordes son frecuentes, y por lo tanto el entendimiento de los efectos de borde es esencial para la conservación de las comunidades forestales. A menudo, la productividad de paserinos se reduce cerca de los bordes de los bosques. Las explicaciones posibles incluyen hacinamiento, tasas de depredación elevadas y la ocurrencia de hábitat y/o individuos de menor calidad en los bordes del bosque. Intentamos separar estos procesos mediante el examen de los efectos de borde en ausencia de depredación de nidos y el control efectivo de las diferencias en la densidad reproductiva y de la calidad de los hábitats y de los individuos. Utilizamos un índice de distancia al borde (IDB), que incluye el número y distribución de bordes cercanos a una localidad de reproducción, para tratar de explicar la variación en la densidad reproductiva, el éxito de anidación y las características reproductivas de 8308 parejas de* Parus major *entre 1965 y 2005, en Wytham, cerca de Oxford, Reino Unido. Los resultados de la modelación lineal mixta confirmaron una mayor densidad reproductiva y una mayor proporción de individuos inmigrantes en los bordes de bosques. Sin embargo, independientemente de estos efectos, también encontramos que aves con nidadas menores, pero huevos más grandes, eran típicas de los ambientes de borde. El número de crías reclutadas por intento reproductivo también fue más reducido en los bordes, tanto directamente como por medio de cambios en el tamaño de nidada y de fecha de puesta. Los efectos de borde sobre las historias de*

vida fueron detectables entre hembras individuales y hasta 500 m del borde del bosque. Los bordes de bosques son cada vez más comunes en los paisajes fragmentados contemporáneos. Por lo tanto, estos resultados, que sugieren un fuerte efecto de los bordes sobre la reproducción, son de importancia considerable para el manejo y conservación de comunidades forestales.

Palabras Clave: calidad de hábitat, densidad reproductiva, depredación de nidos, ecotono, éxito de anidación

Introduction

A woodland edge or ecotone is the interface between the complex and relatively stable environment of the forest interior and the simple and highly variable external environment (Saunders et al. 1991). The results of many studies show that edge environments alter the distribution, abundance, and behavior of forest communities (Murcia 1995). Such edge effects may be direct, in terms of microclimate modification (Davies-Colley et al. 2000), or indirect, due to concomitant changes in vegetation composition, food supply, and the distribution of predators and conspecifics (Gates & Gysel 1978; Murcia 1995). Many extant woodland species probably evolved in continuous forests, where abrupt edges were rare, occurring only at riparian or geologic boundaries. In contrast, edges are commonplace in contemporary fragmented landscapes. For example, just 12% of the United Kingdom is covered in woodland and 8 of 10 wooded areas are <20 ha in size (Spenser & Kirby 1992). Organisms in such habitats will thus be within 250 m of an edge. Therefore, understanding the ecological effects of forest edges is imperative for efficient management and conservation of forest communities in current environments.

Edge environments are often more diverse than interior habitats at the level of the community, probably due to the presence of both internal and external species (Leopold 1933; Odum 1971). For example, woodland birds are often found at higher densities at woodland edges (Gates & Gysel 1978; Strelke & Dickson 1980). Nevertheless, avian nesting success (e.g., Paton 1993; Bátary & Báldi 2004; Deng & Gao 2005), fledgling mass (Huhta et al. 1999), and reproductive output are often, but not always (reviewed in Lahti 2001), reduced at forest edges. Possible explanations for altered bird reproduction at forest edges include overcrowding by conspecifics (Gates & Gysel 1978; Huhta et al. 1999), a concomitant rise in the level of predation (e.g., Paton 1993; Hartley & Hunter 1998; Bátary & Báldi 2004), and suboptimal habitat quality in terms of reduced foraging area (Huhta et al. 1999) and food availability. In addition, edge effects may result from a higher incidence of young, poorer-quality, or immigrant individuals at edges (Krauss et al. 2003). Despite the wealth of studies on edge effects, however, there are few examples where statistical or experimental separation of these factors has been preformed to determine causal relationships between altered reproduction and forest edges.

Most researchers who have examined edge effects have used the distance between the breeding location and the woodland edge (edge distance) to describe environments in terms of their edge proximity. Nevertheless, edge distance does not account for edges other than the nearest edge and it does not allow one to account for important differences in the geometric arrangement of edges. For example, consider four sites, each an equal distance from a woodland edge, that differ in their layout and number (Fig. 1). The first site is near a sharply acute edge that incises the woodland, the second is near a straight edge, the third is near two edges, and the fourth is circumvented by the edge (Figs. 1 a–d, respectively). Clearly the environment of the site in Fig. 1a is less influenced by the edge than the site in Fig. 1b, which in turn is less influenced by the edge than the sites in Figs. 1c and 1d. Nevertheless, on the basis of their edge distances, each of these four sites would be assigned the same measure of edge proximity. There is, therefore, a need to provide an edge proximity measure that accounts for edge distance and for the number and geometric arrangement of the edge relative to the breeding location.

We used a long-term data set, collected between 1965 and 2005 from a Great Tit (*Parus major*) population breeding in more than 1000 nest boxes at Wytham Woods, United Kingdom. This system offers an unusual opportunity to examine edge effects in the absence and presence of nest predation because in 1975 all the nest boxes, which remained in the same locations throughout the study, were replaced with near-predator-proof nest boxes. Thus, this system allowed us to examine edge effects on nesting success in the same territories in the presence and absence of nest predation. We devised an edge distance index (EDI) to account for both the edge distance and the number and layout of edges near breeding locations. We used a geographic information system (GIS) and linear mixed models to analyze the effect of EDI on the breeding density, nesting success, egg-laying date, clutch size, mean egg mass, mean fledgling mass, and recruitment for 8308 pairs of Great Tits.

Methods

Data

This study forms part of the Edward Grey Institute's long-term study of the Great Tit at Wytham Woods, near
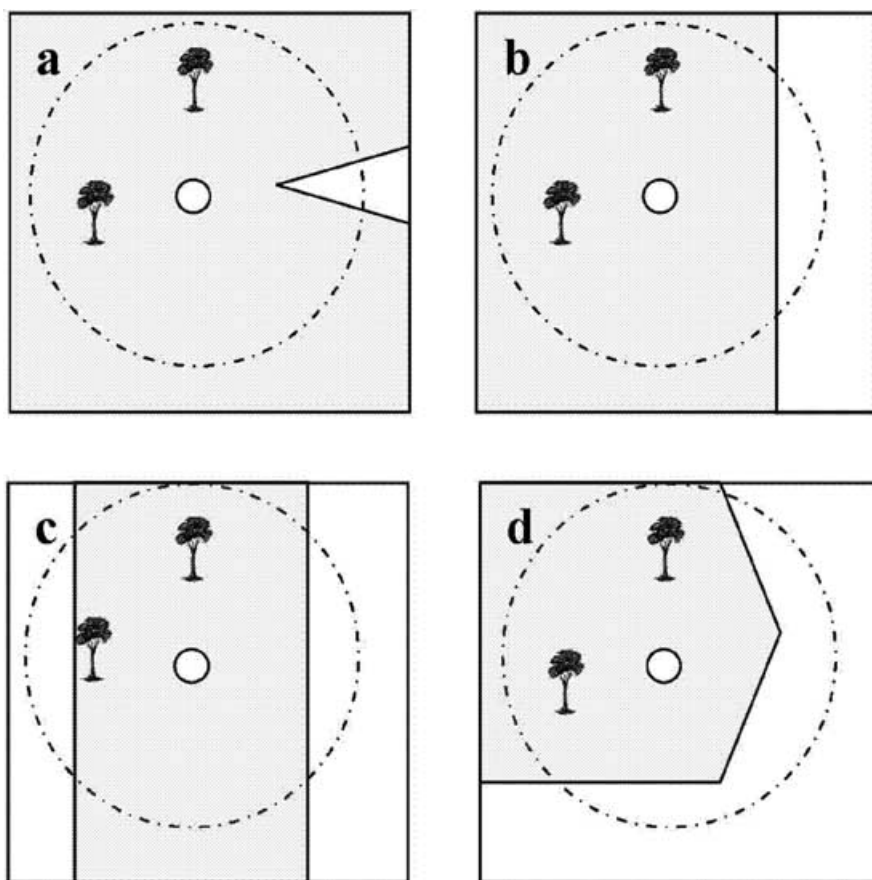
Figure 1. Representation of four sites (open circles) in a woodland (shaded area) contiguous to an area without woodland (unshaded area). Sites are adjacent to (a) a sharp incising edge, (b) a straight edge, (c) two straight edges, and (d) a circumventing edge. In each case the site is the same distance from the edge. According to the edge distance index we used, (a) is in the environment least effected by the edge, followed by, in order of increasing edge influence, (b), (c), and (d).

Oxford, United Kingdom. Data were collected between 1965 and 2005, in accordance with methods described previously (Perrins 1965, 1979; Gosler 1993). Great Tits breed almost exclusively in nest boxes in Wytham, the locations of which have remained constant throughout the study, unless a minor move was necessitated by tree fall. Nevertheless, between 1973 and 1975 the wooden nest boxes, which suffered from weasel predation rates as high as 50% in some years (McCleery et al. 1996), were replaced with woodcrete nest boxes (a mixture of sawdust, wood chips, and concrete), which were suspended away from the trunk of the tree and thus were almost predator proof. Nest boxes were visited at least once a week to ascertain clutch initiation date (lay date, where 1 April = 1), egg mass (mean of three to five unincubated eggs), and clutch size. Chicks were weighed and ringed on day 15 after hatching (hatch day was day 1), and for the purpose of this study, nestling masses at this age (fledging mass) were averaged for each brood. After the chicks reached 7 days of age, parents were trapped at the nest boxes and aged, sexed (Svensson 1994), and ringed or their identities were established from (BTO) rings that were already in place. An individual's status was either recruit or immigrant, defined as whether it hatched in a Wytham nest box or not, respectively. Immigrants to the population have come from variable, but unknown, distances outside the study area (Verhulst et al. 1997).

When analyzing life-history traits we used only first clutches (second clutches are rare at Wytham) and only those in which four or more eggs were laid to exclude clutches laid under atypical conditions such as disturbance or poor health (as in Wilkin et al. 2006). Reproductive success was measured as the number of young from each brood that were recruited to the breeding population in subsequent years (as in McCleery & Perrins 1985). This figure does not reflect the total number that survives to breed because many leave Wytham and breed elsewhere. Hence, we assumed that the number of recruits is an accurate measure of the relative success of nesting attempts (Verhulst et al. 1997 for some relevant data). For each wooden and woodcrete nest box, the percentage of successful breeding attempts (i.e., those that fledged at least one young) was used as a measure of total nesting success, whereas the fledgling success was measured as the proportion hatched clutches that fledged at least one nestling. The spring temperature each year was recorded as the sum of the maximum temperatures for each day between 1 March and 25 April (the warmth sum), as in McCleery and Perrins (1998). We used the habitat classification scheme proposed by Gibson (1988) in which there are five habitat categories: ancient, semi-natural woodland; 18th- and 19th-century broadleaf plantations; 20th-century plantations; secondary, regenerated wood pasture; and grasslands. There are three main soil

types at Wytham: Corallian limestone, sand, and Jurassic clay (Arkell 1947).

Digital Mapping

At Wytham we digitally mapped the locations of 1020 nest boxes and clearings exceeding 0.5 hectares (ha) with a Differential GPS system with submeter accuracy (Omnistar, Houston, Texas), a Laser range finder (LTI, Centennial, Colorado) and a Husky handheld rugged personal computer (Itronix, Coventry, United Kingdom) with PocketGIS software. We used Map Info Professional (version 7.8) and Vertical Mapper (version 3) to produce detailed maps of the location of the nest boxes within the woodland perimeter (20 km in length). An elevation reading for each nest box location was extracted from a land-form profile digital-terrain-model (DTM) data set provided by Ordnance Survey.

The shortest distance was measured between each nest box and (1) the perimeter of the woodland, (2) the perimeter or the woodland clearings, and (3) the perimeter, clearings, and an access road leading from the main entrance to the center of the woodland. To assess the distances we converted the perimeter into a series of points 10 m apart that were combined with the nest-box locations in a shortest-distance query in MapInfo (version 7.8). Circular buffers with 75-m radii were formed around each nest box and the area (square meters) of woodland that lay within each buffer was extracted. A radius of 75 m was chosen because the resulting buffer is 1.75 ha in size (πr^2). This area represents the maximum territory of a Great Tit most commonly found in the literature (Perrins 1965; Krebs 1971; Both et al. 2000) and exceeds in size two-thirds (67%) of the territories identified by tessellating space for the current population (Wilkin et al. 2006). In addition, results of studies of a closely related species, the Blue Tit (*Cyanistes caeruleus*), show that most provisioning trips are within 50 m of the nest box even in low-quality habitats (Stauss et al. 2005). Consequently, we expected that buffers stretching 75 m from each nest box in every direction would in all cases overlap the core of the territory, in most cases include all the foraging area, and in some cases contain the entire territory and represent a sensible measure of space for this species. We used the following equation to calculate the proportion of habitat to nonhabitat within the buffers:

$$P(r) = \frac{A(r)}{\pi r^2},$$

where *P* is the proportion of habitat within radius *r* and *A* is the area of habitat within radius *r*. We calculated an EDI value for each nest box by multiplying its edge distance (>0) by the proportion of habitat within its 1.75-ha buffer. Thus, nest boxes farther than 75 m from the woodland edge were assigned an EDI value equal to their edge distance, whereas nest boxes within 75 m of the woodland edge were assigned an EDI value in proportion to the incidence of woodland within their 1.75-ha buffers. For example, a nest box located close to an acute incising edge (Fig. 1a) would have a buffer dominated by woodland and would accordingly be assigned an EDI barely less than its edge distance. A nest box circumvented by an edge (Fig. 1d) would have a buffer with a smaller proportion of woodland and would therefore be assigned an EDI value considerably lower than its edge distance. The distribution of EDI was skewed in the current data set and so was square-root-transformed to achieve a normal distribution. Hereafter EDI refers to the transformed data.

In our models we controlled for differences in nest-box spacing by including the areas of Thiessen polygons (see Wilkin et al 2006) that were formed around all nest boxes and restricting the areas to within the perimeter of the woodland (nest-box spacing polygons). Differences in local breeding density were controlled for at the level of the individual pair by including the areas of Thiessen polygons, hereafter referred to as tessellated territories, formed around nest boxes that were occupied in each breeding season. A drawback of the tessellated territories is that extremely large territories are formed around nest boxes in low-density areas. Using a previously tested procedure to address this limitation, we capped territory sizes through a range of maxima, with the greatest effect in the lay-date model when territories were capped at 1 ha and in models when territories were capped at a mean of 2 ha (Wilkin et al. 2006).

Statistical Methods

We first assessed the degree of correlations at the level of the nest box to define the relationships between EDI and other environmental variables such as elevation, nest-box density (nest-box spacing polygons), and habitat type. The mean age and status scores (recruit = 1, immigrant = 0) were calculated for each nest box and were assessed, with respect to their EDI, in general linear models (GLM) with normal error structures.

We used a linear mixed model (LMM) in Genstat (version 8; VSN Intl 2005) to investigate the relationship between breeding density and EDI. Uncapped tessellated territory size was the dependent variable in the model (*n* = 8168), whereas EDI, nest-box elevation, habitat type, and nest-box spacing polygons were included as fixed effects. Nest box, female identities, and year were included as random effects to account for nonindependence within these subsamples.

For each nest box the proportion of successful nests was related to EDI in a GLM of binomial proportions by logits. We performed this analysis separately on data collected from wooden and woodcrete nest boxes. Similarly we analyzed fledging success with respect to EDI by using the proportion of broods in that nest box that fledged at least one young. We used a paired *t* test to test whether

nesting or fledging success differed between the two nest-box types.

We used linear mixed models (LMM) with normal errors to assess the effect of EDI on lay date, clutch size, egg mass, and fledgling mass. A generalized linear mixed model (GLMM) with a Poisson error structure was used to assess the effect of EDI on the number of recruits to the breeding population. We included female identity and year of reproduction in each model as random effects and EDI and environmental variables as fixed effects. By including year as a random effect we controlled for between-year differences in the environment. By including female identity as a random effect we controlled for systematic differences between females (due, e.g., to differences in biometrics and condition). Thus, our analyses tested whether during the lifetime of an individual, a change in EDI between years was mirrored by a change in the dependent variable. This analysis assumes that "quality" is relatively fixed within the lifetime of individuals; thus, it would not detect an effect due to individuals being excluded to edge environments in years in which their quality is reduced. Nevertheless, because breeding-site fidelity is high in this population (a median of 71 m between successive breeding attempts in the current data; see also Harvey et al. 1979 for additional studies), we judged this process to be unlikely. Our analyses therefore specifically and effectively considered variation within annual environments and within individuals.

The significance of factors in explaining variation was assessed from the Wald statistic, which is distributed asymptotically as chi square (VSN Intl 2005). We constructed models by backwards-stepwise removal of non-significant factors, depending on their Wald statistic. To test for quadratic effects we centered the EDI data by subtracting mean EDI from each EDI value and then ran the models with both the centered EDI data and centered EDI data squared. This approach renders the linear and quadratic terms uncorrelated, which results in the accurate separation of the two trends. For models in which the quadratic term was significant, we performed linear tests on data restricted to both above and below the centered EDI mean to illustrate directional trends within the nonlinear effect.

The lay-date model controlled for the age of the female, spring temperature (warmth sum), elevation, female status, habitat type, and restricted, tessellated territory size. The resulting clutch size LMM included lay date, the age of the female, and restricted territory size as fixed effects. The egg-mass model controlled for the age of the female, soil type, and lay date. The fledgling mass model controlled for clutch size, mean egg mass, elevation, lay date, and restricted territory size as fixed effects. The number-of-recruits model controlled for lay date, fledgling mass, restricted territory size, elevation, female status, and clutch size as fixed effects.

The models explained variation in a sequence of reproductive stages by including the previous stages as covariates (including, e.g., lay date in the clutch-size model). Thus our analyses investigated the independent effect of EDI on each stage. For ease of presentation, effects are displayed graphically as residuals formed by removing EDI from the model and rerunning the analysis. Models were run with, in turn, the EDI that acknowledged (1) the woodland perimeter; (2) the perimeter and the clearings; and (3) the perimeter, clearings, and the access road. The significance of the three types of EDI was determined in each model from the Wald statistic.

Results

Edge distances (m) were calculated for 1020 nest boxes at Wytham and ranged from 0.7 to 535.5 m (mean = 120.9, SD 104.0). The proportion of woodland to nonwoodland within 75 m of each nest box ($n = 1020$) ranged from 0.32 to 1.0 (mean = 0.9, SD 0.16) and 0.56 to 1.75 ha, respectively. The product of these two values, the EDI, ranged from 0.3 to 535.5 (mean = 118.9, SD 105.7). The EDI was positively associated with elevation (Pearson correlation, $r = 0.237$, $p < 0.001$) and with nest-box spacing polygon size (Pearson correlation, $r = 0.334$, $p < 0.001$); thus, edge nest boxes were at lower elevations and were closer together than interior nest boxes. The former is likely to be partly an effect of the geographical arrangement of the site, a forest cloaking a low hill. The distribution of EDI was right skewed, so we performed a square-root transformation for the following analyses; hereafter, EDI refers to the transformed data.

For a given nest box, EDI was a significant predictor of the average immigration status of both females ($t_{1001} = 3.19$, $p = 0.001$) and males ($t_{989} = 3.96$, $p < 0.001$), such that that there was a higher incidence of immigrants at the woodland edge when controlling for differences in elevation ($t_{1001} = 1.71$, $p = 0.087$; $t_{989} = 2.44$, $p = 0.015$). Therefore we controlled for status, and retained it when the values were significant, in life-history models. In contrast, EDI was not related to a higher incidence of first-year females ($t_{993} = -1.2$, $p = 0.232$) or first-year males ($t_{988} = 0.87$, $p = 0.386$) when controlling for differences in elevation ($t_{993} = 3.05$, $p = 0.002$; $t_{988} = 3.05$, $p = 0.002$) and size of the nest-box spacing polygon ($t_{993} = 3.43$, $p < 0.001$; $t_{988} = 2.22$, $p = 0.027$). Hence, although the breeding age of individuals was unrelated to edge proximity, a higher proportion of first-year birds were found at higher elevations and at lower densities.

We found a significant relationship between tessellated territory size and EDI ($t_{8618} = 41.98$, $p < 0.001$) when controlling for nest-box spacing ($t_{8618} = 576.12$, $p < 0.001$), elevation ($t_{(8618} = 86.59$, $p < 0.001$), and habitat

type ($t_{8618} = 48.99$, $p < 0.001$). Thus, breeding density was higher near the woodland edge, independent of the higher density at low elevation, in older habitats and in areas where nest boxes were closer together.

Mean nesting success was significantly lower in wooden compared with woodcrete nest boxes (means $= 0.49$ and 0.76, respectively; paired t test: $t_{737} = 17.25$, $p < 0.001$). Nevertheless, nesting success was unrelated to EDI in wooden ($t_{702} = 0.22$, $p = 0.826$) and woodcrete ($t_{994} = 0.59$, $p = 0.553$) nest boxes. Mean fledging success for those nests in which at least some eggs hatched was also significantly lower in wooden than in woodcrete nest boxes (means $= 0.73$ and 0.85, respectively; paired t test: $t_{695} = 8.77$, $p < 0.001$). Fledging success was positively associated with EDI in wooden ($t_{702} = 2.21$, $p = 0.027$) but not woodcrete ($t_{994} = 1.40$, $p = 0.162$) nest boxes (Fig. 2) when controlling for nest-box spacing. This means that broods from wooden nest boxes near the edge were less likely to fledge than broods in the interior. The differences between the total number of nest boxes ($n = 1020$) and the sample sizes in the preceding analyses represented the number of nest boxes that were not occupied by Great Tits during the separate phases of the study period (11 and 31 years, respectively).

Life-History Traits

Associations between EDI and lay date ($\chi_1^2 = 19.71$, $p < 0.001$), clutch size ($\chi_1^2 = 16.18$, $p < 0.001$), and egg mass size ($\chi_1^2 = 43.44$, $p < 0.001$; Table 1) were strong and independent when the whole data set (1965–2005) was included in the analyses. Birds breeding in environments closer to the edge laid smaller clutches of larger eggs later in the season. These analyses controlled for confounding factors such as immigrant status, elevation, and density. In contrast, EDI was only weakly related to fledgling mass ($\chi_1^2 = 3.07$, $p = 0.080$) and recruitment ($\chi_1^2 = 3.85$, $p = 0.050$) independent of the effects of EDI on previous life-history stages (Table 1). Removing clutch size and lay date increased the significance of EDI in explaining variation in recruitment ($\chi_1^2 = 6.87$, $p = 0.009$), which suggests an additional indirect effect of EDI on recruitment.

We tested for quadratic effects by including centered EDI and centered EDI squared in the above models. The linear and quadratic terms were strong predictors of lay date ($\chi_1^2 = 10.26$, $p = 0.001$; $\chi_1^2 = 26.52$, $p < 0.001$) and clutch size ($\chi_1^2 = 10.46$, $p = 0.001$; $\chi_1^2 = 13.45$, $p < 0.001$). In the lay-date model, a nonsignificant trend was detected below the EDI mean ($\chi_1^2 = 1.31$, $p = 0.252$), and a strong negative trend was returned for data falling above the EDI mean ($\chi_1^2 = 12.45$, $p < 0.001$). In the clutch size model, below the EDI mean ($\chi_1^2 = 3.71$, $p = 0.054$) the trend was nonsignificant and above the EDI mean ($\chi_1^2 = 10.67$, $p < 0.001$) the trend was strong and positive. The quadratic term was not associated with egg mass ($\chi_1^2 = 0.32$, $p = 0.573$) or fledging mass ($\chi_1^2 = 1.98$, $p = 0.182$). Recruitment was related to both the linear and quadratic terms ($\chi_1^2 = 6.41$, $p = 0.011$ and $\chi_1^2 = 5.8$, $p = 0.016$); a strong positive trend was detected below the EDI mean ($\chi_1^2 = 9.55$, $p = 0.002$), but no trend was detected above the EDI mean ($\chi_1^2 = 0.23$, $p = 0.633$).

Edge Type

Including woodland clearings of more than 1 ha in size in the EDI explained more variation in lay date ($\chi_1^2 = 27.05$, $p < 0.001$) than the standard EDI, based on comparison of the Wald statistic for the edge term in the two models. Nevertheless, including clearings made little difference to the effect size of EDI with respect to clutch size ($\chi_1^2 = 17.61$, $p < 0.001$), egg mass ($\chi_1^2 = 39.58$, $p < 0.001$), fledgling mass ($\chi_1^2 = 3.57$, $p = 0.059$), and recruitment ($\chi_1^2 = 3.62$, $p = 0.057$) models. Including the main access road and the clearings reduced the explanatory power of the EDI in the lay-date ($\chi_1^2 = 13.00$, $p < 0.001$) model but induced little or no change in other models.
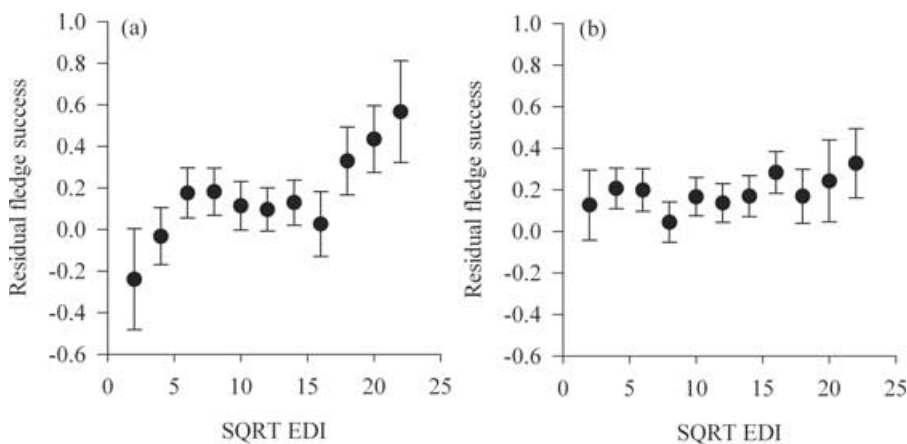

Figure 2. The residual fledging success of Great Tit broods in (a) wooden ($t_{702} = 2.23$, p = 0.023) and (b) woodcrete ($t_{994} = 1.40$, p = 0.162) nest boxes at Wytham woods, United Kingdom, with respect to the square-root-transformed edge distance index (SQRT EDI). Values of SQRT EDI increase with distance from the woodland edge.

Table 1. Results from linear mixed models explaining variation in the life-history traits of 8308 pairs of Great Tits breeding in Wytham nest boxes between 1965 and 2005.*

Dependent/independent factor	Wald χ^2	df	Effect (SE)		p
Lay date ($n = 8308$)					
elevation	100.3	1	0.03276	(0.003271)	<0.001
spring temperature	95.93	1	−0.08661	(0.008843)	<0.001
female age	83.9	1	−0.6509	(0.07106)	<0.001
habitat type	63.73	3			<0.001
female status	20.95	1	Rec < Imm		<0.001
edge distance index	19.71	1	−0.08228	(0.018532)	<0.001
territory size (max 1 ha)	11.04	1	−1.3	(0.3825)	<0.001
Clutch size ($n = 8308$)					
lay date	954.38	1	−0.06768	(0.002191)	<0.001
female age	40.61	1	0.09427	(0.014793)	<0.001
territory size (max 2 ha)	31.45	1	0.1809	(0.03225)	<0.001
edge distance index	16.18	1	0.01525	(0.003792)	<0.001
Egg mass ($n = 6994$)					
lay date	124.78	1	0.002319	(0.0002076)	<0.001
edge distance index	43.33	1	−0.002199	(0.0003341)	<0.001
female age	41.19	1	−0.008241	(0.0012841)	<0.001
soil type	12.29	2	1 >2 >3		0.002
Fledgling mass ($n = 5913$)					
lay date	157.13	1	−0.3498	(0.02791)	<0.001
clutch size	139.04	1	−1.309	(0.1110)	<0.001
elevation	50.69	1	−0.05012	(0.007040)	<0.001
egg mass	48.47	1	8.920	(1.2813)	<0.001
territory size (max 2 ha)	26.65	1	1.710	(0.3312)	<0.001
edge distance index	3.07	1	0.06224	(0.035521)	0.08
Recruitment ($n = 6671$)					
fledgling mass	167.44	1	0.01794	(0.001386)	<0.001
lay date	137.82	1	−0.03311	(0.002820)	<0.001
clutch size	33.37	1	0.06366	(0.011019)	<0.001
elevation	7.11	1	0.001858	(0.0006971)	0.008
territory size (max 2 ha)	5.32	1	0.07356	(0.031893)	0.021
edge distance index	3.85	1	0.006779	(0.0034535)	0.05
female status	3.84	1	Rec > Imm		0.05

Sample sizes (n) reflect the availability of data. Edge distance index refers to the distance between a nest box and the woodland edge or edges (see text). Models include female identity (n = 5436) and year of reproduction (n = 41) as random effects and whether a female was a recruit or immigrant, defined as whether she hatched in a Wytham nest box or not, respectively.

Discussion

Our results demonstrate that the EDI can be used effectively to describe a breeding environment in terms of its edge proximity. Edge environments were independently and significantly associated with higher breeding density and later, smaller clutches that consisted of larger eggs. All these terms are typically associated with poorer-quality breeding locations (e.g., the associations with breeding density are similar). The index also predicted the number of offspring recruited to the breeding population per breeding attempt, both directly and indirectly through changes in clutch size and lay date. Analyses restricted to a 9-year period of high nest predation showed no relationship between EDI and nesting success, although the effect was present in terms of fledging success. Our results suggest that edge effects may be surprisingly persistent because the relationship between EDI and the life-history variables was still detectable several hundred meters (per-

haps up to 500 m) from the woodland edge. Hence, such effects may be present in all woodland fragments of <80 ha because this is the area necessary for the most interior of individuals to be more than 500 m from the edge. We believe that these results are therefore of importance for the conservation and management of fragmented forests.

Breeding Density at the Edge

Breeding density was higher at the woodland edge (Fig. 3a), a phenomenon that is supported extensively in the literature (e.g., Gates & Gysel 1978; Flaspohler et al. 2001). Woodland edges may be attractive habitats for some birds because of an increase in vegetation cover (Ratti & Reese 1988), which improves conditions for nesting (Yahner & Cypher 1987), foraging (Harris & Reed 2002), or singing (Strelke & Dickson 1980; Morgan & Gates 1982). Nevertheless, it is unclear why Great Tits breeding in nest boxes should do so at higher densities
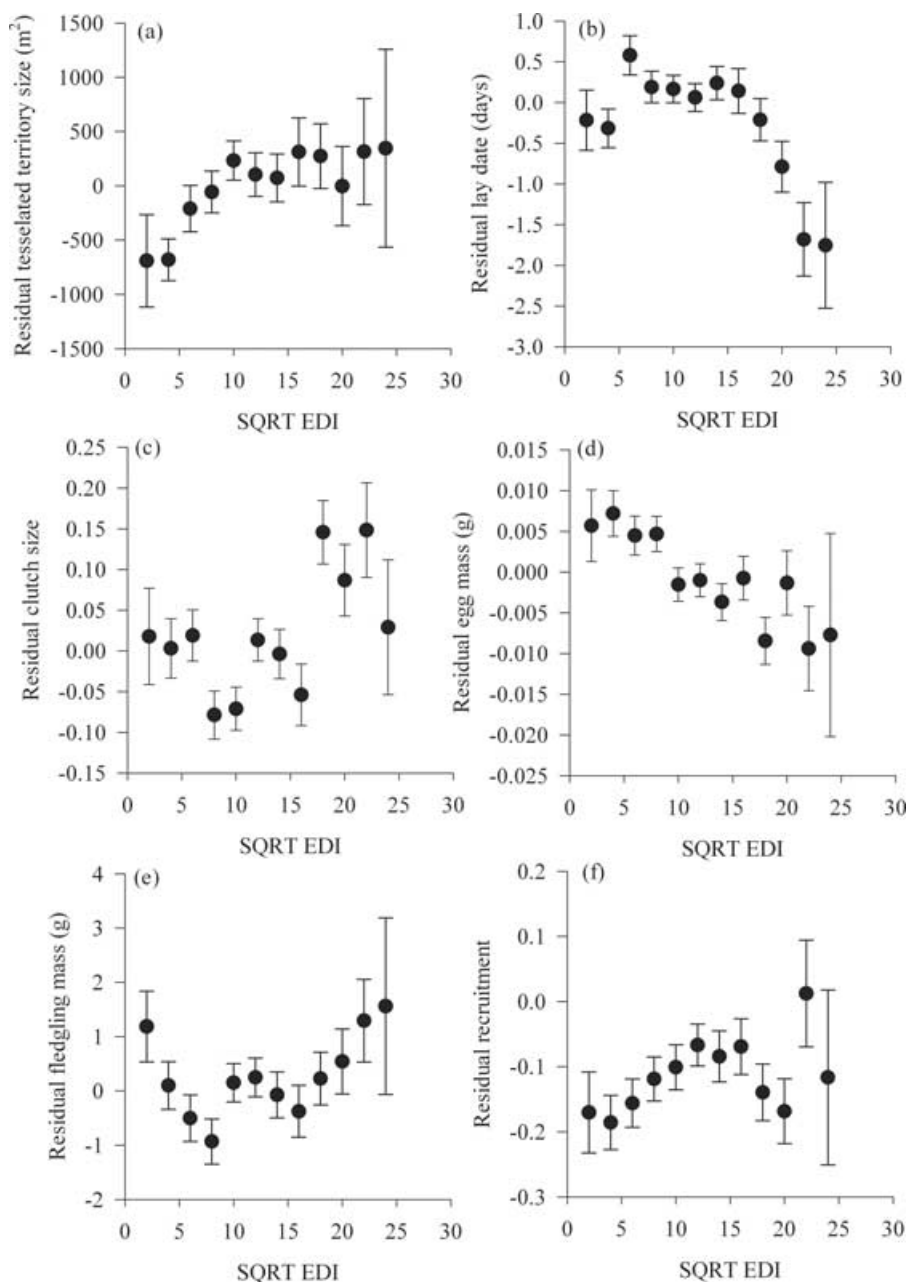
Figure 3. Relationships between the square-root-transformed edge distance index (SQRT EDI) and residual (a) tessellated territory size, (b) lay date, (c) clutch size, (d) mean egg mass, (e) mean fledgling mass, and (f) recruitment. Residuals were obtained from models including potentially confounding environmental variables and previous life-history traits (see Table 1 and text for details). Values of SQRT EDI increase with distance from the woodland edge.

at the woodland edge. A possible explanation is that for immigrating birds, high densities at the woodland edge represent a better option than breeding at lower densities in marginal habitats, such as hedgerows or small forests. Our results suggest an edge effect on breeding density that extends at least 100 m into the woodland (Fig. 3a).

Results of another study on forest passerines show an edge effect on the nest density of some species that extends over 300 m from the edge (Flaspohler et al. 2001). Several factors may influence the depth at which edge effects penetrate woodland. For example, edge effects will presumably vary in strength and/or depth between woodlands that adjoin agricultural areas and woodlands that

are next to seminatural environments or urban developments (Morrison & Bolger 2002; Piper & Catterall 2004). In addition, the abruptness of an edge (e.g., whether it is sharply delineated or gradual) may also influence how far the edge effect penetrates the woodland (Suarez et al. 1997). For the most part, Wytham is surrounded by agricultural areas, although the River Thames and a highway pass within 20 m of the woodland to the northwest and southeast, respectively. The edges are abrupt in nature because the woodland perimeter is entirely fenced off from the surrounding areas. These features may have some influence in determining the strength and depth of the edge effects at Wytham.

Nesting Success

Nesting and fledging success was much poorer in wooden than in woodcrete nest boxes, probably due to higher predation by weasels and woodpeckers in the wooden boxes. In wooden nest boxes, fledging success was lower in edge environments, suggesting that broods near the edge were more likely to have suffered predation. Increased nest predation is a common, but not constantly (Keyser et al. 1998), reported edge effect for ground-nesting (Manolis et al. 2002) and cavity-nesting (Deng & Gao 2005) birds. Possible explanations include an increase in predator density and/or richness owing to the higher density of their prey and the incidence of both internal and external predators, respectively.

Life-History Traits

We found a higher incidence of immigrant birds at the woodland edge. This result is not particularly surprising because we expected immigrants to settle closer to their natal habitats, which are by definition outside of the main woodland. Nevertheless, our results also suggest that immigrants lay later and recruit fewer individuals to the breeding population than resident birds. Intuitively, one might assume that this effect is due to unfamiliarity with the environment. Nevertheless, these effects were persistent throughout the lifetime of an immigrant individual such that immigrants that survive to breed several times do so consistently later than resident birds, as shown by the absence of an interaction between female status and age on breeding date (status × age: $\chi^2_1 = 2.42, p = 0.120$). Therefore there must be some other processes at work. There are three possible processes. First, there may be a long-lasting effect of being born in poor environments (e.g., Reid et al. 2003), although there is little evidence for such effects in studies of short-lived passerine birds. Second, immigrants may differ genetically in their lay date. Nevertheless, given the relatively low heritability of this trait in the current population (McCleery et al. 2004), high rates of immigration, and that there was no effect of being born to an immigrant mother on lay date ($\chi^2_1 = 0.97$, $p = 0.326$; dam status added to lay-date model in Table 1), this mechanism is unlikely. Lastly, there may be some form of environmental or maternal priming of offspring that is related to their date of hatching, which would represent a process by which maternal effects induce a closer match in offspring phenotypes to the current environment, but we have no way to assess this at present.

Independent of a higher incidence of immigrant individuals at the edge, birds that bred close to the woodland edge bred significantly later than birds that bred away from the edge (Fig. 3b). This effect has not been seen before in the current population, possibly because it was concealed by the opposing and stronger effect of earlier breeding at low elevations, which happen to be nearer the edge. Birds at the edge also laid significantly fewer eggs than birds in the interior (Fig. 3c). Both effects were apparent when controlling for higher densities in edge environments and for the age of individuals. The latter affects lay date and clutch size, but was independent of distance from the edge.

Lay date and clutch size are determined by characteristics of the individual years (spring temperature), individual (genotype and phenotype), and territory (size, food availability) (Perrins 1965). Our analyses effectively controlled for differences between individuals and years, so we assumed that edge territories were of lower quality than interior territories. This assumption was, to some extent, confirmed by the somewhat unexpected finding that birds at the woodland edge laid heavier eggs than birds in the interior (Fig. 3d). This effect was independent of lay date (egg mass increased with seasonal advancement) and the age of individuals (older birds laid lighter eggs). Heavier eggs are sometimes associated with poor-quality habitats (see Christians 2002 and references therein). In addition, larger eggs may confer a fitness advantage in low-quality environments (Smith et al. 1995; Smith & Bruun 1998; Christians 2002) and some growth advantages to newly hatched nestlings (Williams 1994). Evidence of a poor habitat quality in edge environments was also provided for the current population by a video-camera study that showed fewer caterpillars (the preferred food for nestlings) being provided to nestlings in edge environments (GLM $t_{18} = 2.86, p = 0.011$) than in interior environments when controlling for elevation and brood size (L. King & T. Wilkin, unpublished data). Fewer caterpillars at the woodland edge, and therefore reduced territory quality, may be due to the more exposed environment that subjects invertebrates and the trees themselves to desiccation pressure (Laurance 2004).

In the current population smaller clutches have been linked recently with longer incubation periods, probably because they lose heat more readily than a large clutch (T.A.W., unpublished data). Recent analyses also show that, when controlling for clutch size, clutches with larger eggs are incubated for shorter periods than those with smaller eggs. This is probably because larger eggs are more thermally retentive than smaller eggs. Therefore, it is conceivable that birds breeding at the edge may be compensating for their smaller clutches and for a more exposed and presumably colder environment by producing larger eggs that retain more heat (Massaro et al. 2004).

The effect of edge environments on the number of offspring recruited to the breeding population was weak when controlling for edge effects on other life-history traits, which determine recruitment. This result is a little surprising, given that random dispersal would lead to those born on edges being more likely to disperse outside a patch and breed elsewhere than individuals born near the center, a process that would result in lower recruitment to the breeding population from edge nests. Nevertheless, in agreement with our findings, Matthysen (2002)

found that the likelihood of a bird recruiting outside of a woodland patch is unrelated to the distance between the natal nest and the woodland edge.

By including quadratic terms in our models, we found that the relationship between EDI and these life-history characters was often nonlinear and that this nonlinearity was not simply due to a difference between nests close to the edge versus all others. For example, in the case of lay date and clutch size, edge effects were not apparent between birds breeding within 200 m of the edge; rather, a linear trend was observed between birds breeding farther than 200 m from the edge. These results are important because they imply that edge effects may not be detectable as linear trends in smaller woodlands.

Edge Type and Scale

The EDI explained lay date better when small woodland clearings were designated as edges. Including woodland clearings, nevertheless, did not increase the explanatory power, based on the test statistic, of the EDI in models explaining variation in other, later life-history traits. If the effect is genuine, it is possible that the invertebrates are more prone to desiccation pressure or rely more heavily on sheltered habitats early in the season, which would explain edge effect on breeding time near woodland clearings. For example, the main food item of Great Tits in March is the Curculionid beetle *Strophosomus melanogrammus* (Betts 1955), which falls from vegetation and burrows into the ground on exposed or frosty days (Parry 1981). This could result in birds close to woodland edges, including small woodland clearings, suffering from poorer food availability and thus their being unable to reach breeding condition as early as interior birds. The main access road through the woodland did not affect Great Tit life histories, suggesting that long, narrow edges are insufficiently exposed to change habitat quality in adjacent areas. This result agrees with those of previous studies that show no effect of forest roads on nest predation levels (Ortega & Capen 2002), nesting success, clutch initiation date, clutch size, or fledgling success (King & DeGraaf 2002).

Edge effects were persistent over a distance of 500 m from the woodland edge. Edge effects on nest predation have been documented at distances of 600 and 200–500 m from the woodland edge (Wilcove 1985; Andrén & Angelstam 1988, respectively), whereas edge effects on nesting success (Manolis et al. 2002; Huhta et al. 2004; Deng & Gao 2005) and density (Flaspohler et al. 2001) have been documented at distances of 500 and 300 m, respectively. These findings are of considerable importance to the conservation of forest communities because if edge effects penetrate woodlands up to 500 m from the edge, effects would be omnipresent in woodlands of <80 ha. An unanswered question is the extent to which such effects are direct or indirect. For example, high densities at

an edge, caused by high rates of immigration, may have cascading effects on the distribution of individuals over large distances. Our results suggest that further investigation into the causes of edge effects in other long-term studies for which large quantities of data are available may provide useful insight into the effect of habitat structure on productivity.

Acknowledgments

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