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RESEARCH PAPER

Body size and area-incidence relationships: is there a general pattern?

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ABSTRACT

Aim This paper tests firstly for the existence of a general relationship between body size of terrestrial animals and their incidence across habitat patches of increasing size, and secondly for differences in this relationship between insects and vertebrates.

Location The analysis was based on the occupancy pattern of 50 species from 15 different landscapes in a variety of ecosystems ranging from Central European grassland to Asian tropical forest.

Methods The area-occupancy relationship was described by incidence functions that were calculated using logistic regression. A correlation analysis between body size of the species and the patch area referring to the two given points of the incidence function was performed. In order to test for an effect of taxon (insects vs. vertebrates), an analysis of covariance was conducted.

Results In all species, the incidence was found to increase with increasing patch area. The macroecological analysis showed a significant relationship between the incidence in habitat patches and the body size of terrestrial animals. The area requirement was found to increase linearly with increasing body size on a log-log scale. This relationship did not differ significantly between insects and vertebrates.

Conclusions The approach highlighted in this paper is to associate incidence functions with body size. The results suggest that body size is a general but rather rough predictor for the area requirements of animals. The relationship seems valid for a wide range of body sizes of terrestrial animals. However, further studies including isolation of habitats as well as additional species traits into the macroecological analysis of incidence functions are needed.

Key words Area requirement, body size, habitat fragmentation, incidence function, insects, logistic regression, macroecology, vertebrates.

INTRODUCTION

It is generally accepted in spatially explicit population ecology that patch area is among the main factors determining the occurrence and survival of animal species (Andrén, 1994; Hanski, 1999), especially in fragmented landscapes (Settele *et al.*, 1996). Recently, an increasing number of studies (Biedermann & Appelt, 1996; Hinsley *et al.*, 1996; Zabel & Tscharntke, 1998; Rodríguez & Andrén, 1999; Kruess & Tscharntke, 2000; Biedermann, 2002) have focused on the importance of area in the occupancy pattern of animals in habitat patches of various size. In most species a positive relationship exists between the probability of occurrence and the area of habitats (but see Thomas *et al.*, 2001). However, animal species react differentially on fragmentation of their habitats. Whereas some species exhibit high occurrences even in small patches, others are more or less exclusively found in large patches. The distribution pattern of a species in habitat patches is determined by population dynamics and dispersal processes, which result in extinction and colonization of patches (Hanski, 1999). The extinction rate has been found to decrease with increasing population size or patch area (e.g. Hanski, 1994a; Biedermann, 2000), whilst a positive relationship between abundance and occupancy has been assumed (Gaston *et al.*, 2000). Further, there seems to exist a correlation between body size and abundance, with large species exhibiting lower abundances compared to small species (e.g. Blackburn *et al.*, 1993). Consequently, it would be expected that large species with low abundances have a higher extinction risk in a habitat patch of a given area. In fact, at least in vertebrates, such a relationship has been stated to pertain (Belovsky, 1987; Gaston & Blackburn, 1995, 1996; Owens & Bennett, 2000). For instance, Belovsky (1987) has shown that the extinction rate of mammals is

positively correlated with body size, which is in turn correlated with home range size. While for birds, Owens & Bennett (2000) have found a positive correlation between the extinction risk via habitat loss and body size when analysing a wide range of species from many bird families. Consequently, as the result of a higher extinction risk of animals of larger body size and thus lower population densities, the area requirement of animals species should be correlated with body size. We may thus expect to find that the distribution of species should be area-dependent and that the critical patch area derived from incidence functions should be correlated with body size. Thus the question arises whether there is a general relationship between the area requirements of animals and body size? For instance, in mammals a positive relationship between body size and home range has been found (McNab, 1963; Belovsky, 1987; Kelt & Van Vuren, 2001; Mysterud *et al.*, 2001). However, there has been no attempt to quantify this allometric relationship between body size and area dependence of species incidence in habitat patches in a comparative way, i.e. comparing the area requirements of species from several animal groups. The analysis of the area-occupancy relationship yields incidence functions (Adler & Wilson, 1985; Biedermann & Appelt, 1996), which give the probability of occurrence in relation to patch area. Including data on invertebrate and vertebrate terrestrial animals, this study tests whether there exists a general relationship between the characteristics of the incidence function and the body size of terrestrial animal species.

MATERIALS AND METHODS

The appropriate statistical method to demonstrate the area-dependence of the occurrence of species is to calculate incidence functions (Adler & Wilson, 1985; Biedermann & Appelt, 1996). A survey of the occurrence of a species in a set of habitat patches of various area yields the presence-absence pattern. This pattern was analysed using logistic regression (Hosmer & Lemeshow, 2000). The incidence functions were taken from the literature or logistic regression was used to obtain incidence functions in the case of published or unpublished raw data. The logistic model is a sigmoid term:

$$I = \frac{1}{1 + e^{-b \cdot A - c}} \qquad (1)$$

where I is the incidence, A is the patch area, b and c are coefficients provided by the logistic regression procedure. The resulting incidence function yields the probability of occurrence — the incidence — with respect to patch area (Fig. 1).

The computation of the incidence functions was based on studies where habitat area was found to affect the distribution of terrestrial animals in fragmented landscapes. In total, the analysis was based on the occupancy pattern of 50 species from 15 different landscapes (Table 1). The data included 19 insect, 27 bird, 1 reptile, and 3 mammal species and were derived from a variety of ecosystems ranging from Central European grassland to Asian tropical forest. The area of the patches was within the range of 1 m^2 to about 25 000 000 m^2, i.e. eight orders of magnitude. The body lengths of the species ranged from 1.9 mm in the beetle *Brachypterus urticae* up to 559 mm in the lion-tailed macaque *Macaca silenus*.

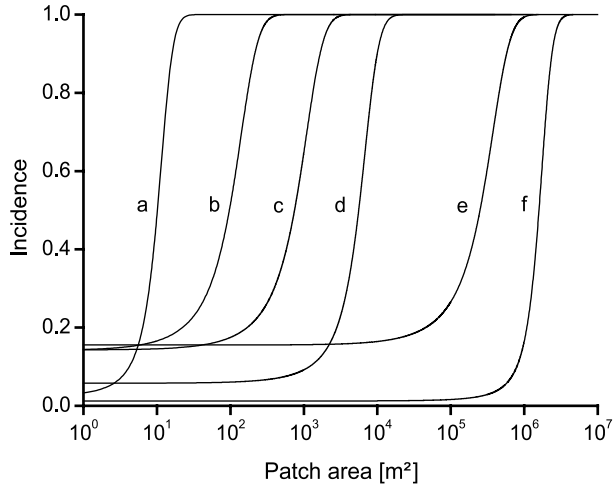

Fig. 1 Examples of incidence functions (a) planthopper (*Kelisia haupti*) (b) psyllid (*Arytaina genistae*) (c) spittlebug (*Neophilaenus albipennis*) (d) butterfly (*Chazara briseis*) (e) lesser spotted woodpecker (*Dendrocopos minor*) and (f) goshawk (*Accipiter gentilis*). See Table 1 for further details.

Each data set comprises the patch occupancy pattern in a set of habitat patches of given area in a single landscape. The number of patches in the data sets was within the range of 18–506 patches per landscape, with a median of 171 patches. Three kinds of data were used for the analysis:

- published incidence functions (Celada *et al.*, 1994; Biedermann & Appelt, 1996; Hinsley *et al.*, 1996; Seufert & Grosser, 1996; Zabel & Tscharntke, 1998; Kruess & Tscharntke, 2000) (n = 18 species);
- published data (Schönbrodt & Spretke, 1989; Bright *et al.*, 1994; Hanski *et al.*, 1994; Hanski, 1994b; Sarre *et al.*, 1995; Umapathy & Kumar, 2000) (n = 23);
- unpublished data (n = 9) on patch occupancy and patch area.

The results of the logistic regression analyses are given in Table 1; except for the study of Hinsley *et al.* (1996), where the minimum areas were read off graphically. The body length was taken as a measure of body size; birds, reptiles and mammals were considered without tails. The body lengths of the species are mean values taken from the literature.

Table 1 List of species included in the analysis of area-incidence relationships, with body size, landscape size, minimum and maximum patch area, and statistics obtained by logistic regression (coefficients *b* and *c*, goodness-of-fit R^2)

Species	Body size (mm)	Landscape size	Number of patches	Minimum–maximum patch area	Coefficients *b*	Coefficients *c*	R^2
Insects							
Brachypterus urticae [12]	1.9	—	32	5–1000 m^2	0.135†	−0.71†	—
Cidnorhinus quadrimaculatus [12]	2.9	—	32	5–1000 m^2	0.042†	−0.66†	—
Kelisia haupti [13]	3	18 km^2	21	1–3137 m^2	0.3699†	−3.7506†	0.85***
Ribautodelphax pungens [13]	3	17 km^2	73	1–6450 m^2	0.00050†	−2.0811†	0.12*
Tychius quinquepunctatus [7]	3.3	400 km^2	18	300 m^2–70 ha	1.0322§	−8.9890§	0.52***
Arytaina genistae [13]	3.5	21 km^2	237	1–252 m^2	0.0185†	−1.7742†	0.17***
Adarrus multinotatus [13]	4	17 km^2	506	1–7233 m^2	0.2953†	0.7128	0.22***
Gonioctena olivacea [13]	4	21 km^2	237	1–252 m^2	0.0132†	−0.5478†	0.08***
Gonioctena olivacea [13]	4	110 km^2	29	1–129 m^2	0.0735†	−2.2792†	0.52***
Macropsis scutellata [12]	4.9	—	32	5–1000 m^2	0.004†	−1.97†	—
Gargara genistae [13]	5	17 km^2	24	1–2125 m^2	0.0527†	−1.2164†	0.73***
Gargara genistae [13]	5	21 km^2	237	1–252 m^2	0.0215†	−1.6078†	0.20***
Neophilaenus albipennis [13]	5	17 km^2	506	1–7233 m^2	0.0024†	−1.7911†	0.14***
Phyllobius pomaceus [12]	8.5	—	32	5–1000 m^2	0.011†	−0.24†	—
Hesperia comma [5]	14	—	64	80 m^2–7.3 ha	1.3294‡	0.6444‡	0.15*
Cydia nigricana [7]	14	400 km^2	18	300 m^2–70 ha	2.4691§	−14.7119§	0.73*
Melitaea cinxia [4]	15	30 km^2	50	12 m^2–4.6 ha	0.00095†	0.00059†	0.33***
Chazara briseis [10]	19	132 km^2	190	30 m^2–3.3 ha	0.0005†	−2.7883†	—
Oedipoda caerulescens [1]	22	30 km^2	304	3–7490 m^2	0.0022†	−0.7401†	0.17***
Reptiles							
Oedura reticulata [8]	64	1680 km^2	32	0.1–8 ha	0.5592‡	−0.1009‡	0.21*
Birds							
Aegithalos caudatus [9]	52	770 km^2	271	0.7–808 ha	0.0567‡	−2.0313‡	0.17***
Aegithalos caudatus [6]	52	2450 km^2	151	200 m^2–30 ha	—	—	—
Parus palustris [6]	55	2450 km^2	151	200 m^2–30 ha	—	—	—
Phylloscopus collybita [9]	57	770 km^2	271	0.7–808 ha	0.1158‡	−0.0702‡	0.15***
Phylloscopus collybita [6]	57	2450 km^2	151	200 m^2–30 ha	—	—	—
Troglodytes troglodytes [9]	61	770 km^2	271	0.7–808 ha	0.0567‡	−0.7368‡	0.11***
Troglodytes troglodytes [6]	61	2450 km^2	151	200 m^2–30 ha	—	—	—
Certhia brachydactyla [9]	66	770 km^2	271	0.7–808 ha	0.0442‡	−0.6035‡	0.08***
Certhia familiaris [9]	74	770 km^2	271	0.7–808 ha	0.0624‡	−3.0145‡	0.24***
Certhia familiaris [6]	74	2450 km^2	151	200 m^2–30 ha	—	—	—
Prunella modularis [9]	82	770 km^2	271	0.7–808 ha	0.0831‡	0.1935‡	0.10***
Erithacus rubecula [9]	82	770 km^2	271	0.7–808 ha	0.0261‡	−0.5714‡	0.05**
Erithacus rubecula [6]	82	2450 km^2	151	200 m^2–30 ha	—	—	—
Phylloscopus sibilatrix [9]	82	770 km^2	271	0.7–808 ha	0.0248‡	−2.3236‡	0.10***
Fringilla coelebs [6]	83	2450 km^2	151	200 m^2–30 ha	—	—	—
Muscicapa striata [9]	84	770 km^2	271	0.7–808 ha	0.0892‡	−0.8815‡	0.17***
Dendrocopos minor [9]	89	770 km^2	271	0.7–808 ha	0.0677‡	−1.6927‡	0.18***
Sitta europaea [9]	95	770 km^2	271	0.7–808 ha	0.0348‡	−0.9267‡	0.07***
Dendrocopos major [9]	142	770 km^2	271	0.7–808 ha	0.0871‡	−0.6831‡	0.16***
Dendrocopos major [6]	142	2450 km^2	151	200 m^2–30 ha	—	—	—
Turdus philomelos [9]	146	770 km^2	271	0.7–808 ha	0.0684‡	0.0895‡	0.09***
Turdus philomelos [6]	146	2450 km^2	151	200 m^2–30 ha	—	—	—
Garrulus glandarius [9]	196	770 km^2	271	0.7–808 ha	0.0239‡	−1.9807‡	0.08***
Asio otus [9]	208	770 km^2	271	0.7–808 ha	0.0211‡	−1.7033‡	0.07***
Strix aluco [9]	211	770 km^2	271	0.7–808 ha	0.0355‡	−1.1798‡	0.08***
Dryocopus martius [9]	294	770 km^2	271	0.7–808 ha	0.0439‡	−2.3858‡	0.15***
Accipiter gentilis [9]	311	770 km^2	271	0.7–808 ha	0.0276‡	−4.3787‡	0.30***
Mammals							
Muscardinus avellanarius [2]	75	4200 km^2	114	2 – > 100 ha	0.0408‡	−1.0662‡	0.27***
Sciurus vulgaris [3]	240	135 km^2	34	5000 m^2–32 ha	2.26¶	−2.19¶	0.20***
Macaca silenus [11]	559	987 km^2	25	1–2500 ha	0.0167‡	−1.7795‡	0.51***

Significance: (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Data sources: [1] Biedermann & Appelt (1996); [2] Bright *et al.* (1994); [3] Celada *et al.* (1994); [4] Hanski *et al.* (1994); [5] Hanski (1994b); [6] Hinsley *et al.* (1996); [7] Kruess & Tscharntke (2000); [8] Sarre *et al.* (1995); [9] Schönbrodt & Spretke (1989); [10] Seufert & Grosser (1996); [11] Umapathy & Kumar (2000); [12] Zabel & Tscharntke (1998); [13] unpublished data. †area in m^2, ‡area in ha, §area in ln (m^2), ¶area in ln (ha); — not available.

A rigorous approach was followed concerning the delimitation of patches of suitable habitat (Kotliar & Wiens, 1990). Only those studies with an exact assessment of patch edges and thus exact measurements of patch area were considered in the analysis, for instance host plant patches in phytophagous insects or small woods in woodland birds. All studies were focused on spatial population structure or metapopulation dynamics, that is on the analysis of extinction and colonization of local populations. Consequently, in all studies the patches were delimited in a way that patches comprise considerable local populations, meaning that patches are much larger than the home range of individual animals. The dispersal between patches is assumed to be limited. Studies where the stated area comprises, for instance, whole islands or vegetation complexes, were omitted from the analysis. Also excluded from the analysis were data sets derived from short-time fragmentation experiments, because it can be assumed that no colonization-extinction equilibrium has been achieved.

In all species a significant relationship between the incidence and habitat area was found in the logistic regression analysis. In order to obtain a measure for the characteristic of the incidence function, the patch area at two points of the function was calculated: the patch area referring to the inflection point of the function (incidence of 0.5) and the patch area referring to an incidence of 0.95. The inflection point is interpreted as the threshold where the occurrence in the patches shifts from low to high incidence (see Fig. 1). The incidence of 0.95 indicates the area where a patch is classified as occupied with a statistically acceptable amount of uncertainty. From the incidence functions the patch area at the inflection point and at an incidence of 0.95 was calculated or read off graphically in the case of some published incidence functions. In almost all data sets (48 of 50) the maximum patch sizes were large enough to reach an incidence of 0.95.

The correlation analysis between body size of the species and the patch area referring to the two given points of the incidence function (inflection point 0.5 and incidence of 0.95) was performed using the Pearson coefficient. In some cases ($n = 5$) negative values for the patch area were obtained at the inflection point, due to low sample size of very small patches. These cases were omitted from the correlation analysis. In order to test for an effect of taxon (insects vs. vertebrates), an analysis of covariance was conducted. The variable taxon was entered as a factor into a GLM with patch area as the dependent and body size as the independent variable.

RESULTS

Incidence functions were computed from the data sets of terrestrial animals. In all species, the logistic regression analysis showed a significant relationship between the presence of the species in the habitat patches and the area of the patches, i.e. incidence increases with increasing patch area (for examples

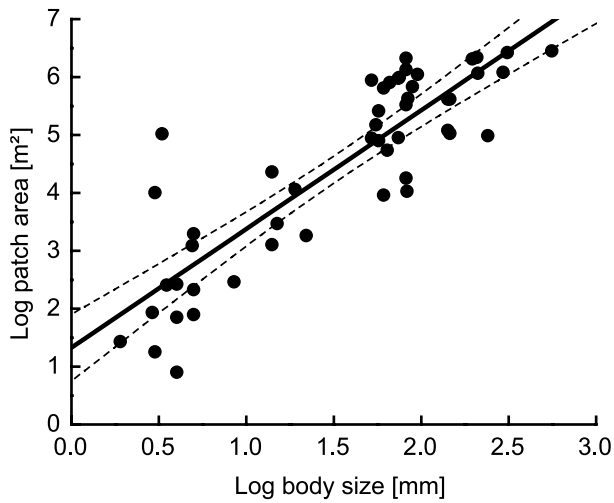

Fig. 2 Relationship between body size and patch area at an incidence of 0.95 ($r = 0.87$, $P < 0.001$, $n = 50$, log (patch area) = 2.050*log (body size) + 1.327). Regression line with 95% confidence intervals.

see Fig. 1). Analysis of the relationship between body size and the area at the two given points of the incidence function revealed a positive correlation (Fig. 2). On a log-log scale a linear relationship was found between the body size and the patch area at the inflection point of the incidence function (Pearson correlation coefficient $r = 0.86$, $P < 0.001$, $n = 45$). The patch area increases with increasing body size. The resulting equation is log (patch area) = 2.040*log (body size) + 0.806. A similar relationship was found when referring to an incidence of 0.95 (Fig. 2). Again body size was positively correlated with patch area ($r = 0.87$, $P < 0.001$, $n = 50$, log (patch area) = 2.050*log (body size) + 1.327). In order to test a possible relationship between the scatter about the regression line (Fig. 2) and the quality of the logistic regression, the absolute residuals of the linear regression (incidence of 0.95) were plotted (Fig. 3) against the goodness-of-fit R^2 (see Table 1). There was no significant relationship between residuals and R^2 ($r = 0.27$, $P = 0.107$, $n = 36$).

The correlation between body size and patch area is not simply the result of differences in the effect of patch area between vertebrates and insects. When analysed separately, in vertebrates (inflection point: $r = 0.47$, $P < 0.05$, $n = 29$, log (patch area) = 1.443*log (body size) + 2.071; incidence of 0.95: $r = 0.44$, $P < 0.05$, $n = 31$, log(patch area) = 1.134*log (body size) + 3.244), as well as in insects (inflection point: $r = 0.39$, $P = 0.133$, $n = 16$, log (patch area) = 1.277*log (body size) + 1.239; incidence of 0.95: $r = 0.47$, $P < 0.05$, $n = 19$, log (patch area) = 1.662*log (body size) + 1.509) a positive correlation between body size and patch area exists. In order to test for an effect of taxon (insects vs. vertebrates), an analysis of covariance was conducted. There was no effect of taxon (inflection point: $F = 1.86$, $P = 0.103$,

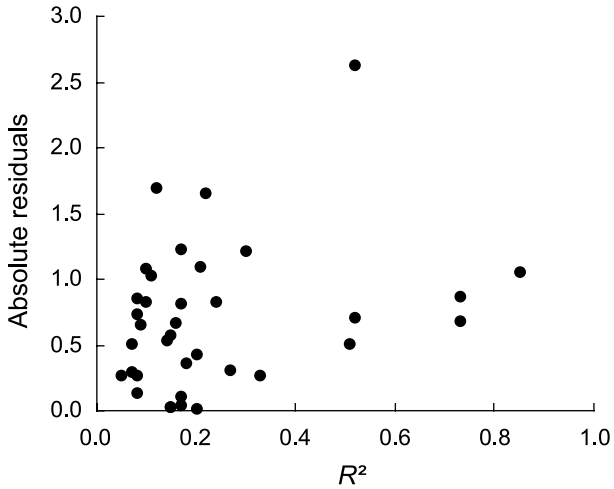

Fig. 3 Relationship between the absolute residuals of the linear regression of body size vs. patch area at an incidence of 0.95 (Fig. 2) and the goodness-of-fit R^2 of the logistic regressions.

n = 45; incidence of 0.95: F = 2.18, P = 0.069, n = 50) on the relationship between area requirement and body size (inflection point: F = 6.69, P < 0.01, n = 45; incidence of 0.95: F = 11,78, P < 0.01, n = 50). Consequently, the regression lines do not differ between insects and vertebrates.

DISCUSSION

The results of this study suggest a general relationship between the body size of animals and the area-dependency of their incidence in habitat patches. The relationship seems valid for a wide range of body sizes of terrestrial animals. The separate analysis showed that this relationship was not simply the result of differences in area requirements of insects and vertebrates. Owing to the well-known correlation between body size and home range (e.g. McNab, 1963; Belovsky, 1987; Mysterud *et al.*, 2001), the results may not be surprising in some animal groups like mammals, however, this study showed that the relationship is similar within and across various groups.

As the habitat of animals is regularly fragmented to some extent, one central question in the conservation of animals is what minimum areas are required in order to maintain viable populations? (Doak & Mills, 1994; Caughley, 1994; Margules & Pressey, 2000). One possible way to deduce minimum areas would be to conduct population viability analyses (Boyce, 1992) for every single species. Given the large number of species, or even only the increasing number of endangered species, such a task seems impossible to realize. However, the comparative analysis of a considerable number of species and the extraction of general relationships between species traits (e.g. life-history traits, morphological traits) and the area-incidence relationship of species seems an encouraging approach (Davies *et al.*, 2000; Fagan *et al.*, 2001). Concerning minimum areas, it would be desirable to have quantitative predictors for the area requirements. The approach highlighted in this paper is to associate incidence functions with body size, which seems to be a general but rather rough predictor for the area requirements of animals.

There may, however, be several limitations to the generality of this relationship. First, as a consequence of the rigorous approach delimiting the habitat patches, the analysis was restricted to specialist species. In generalist species the delimitation of the habitats would be more complex as these species are not restricted to a distinct habitat type. The incidence functions used in this study derived from population ecological studies that have been focused on species with well known and distinct habitat requirements. Thus, the correlation reported between minimum patch area and body size possibly holds true only for specialist species. Second, there was residual variance in the relationship between body size and critical patch area (Fig. 2). As the incidence and the resulting incidence functions have been found to be fairly stable over time (Hinsley *et al.*, 1996; Gaston *et al.*, 1999), the remaining variance may be explained by other factors. Looking at a single species, the area-incidence relationships from different landscapes are not always concordant (Table 1), indicating that body size alone will not be enough to predict area requirements precisely. Although, additional species traits may be important in the area-incidence relationships, the main source of variance is likely to be the different scale of the studies and especially differences in the isolation of the habitat fragments. Isolation is an important factor for species occurrence in fragmented landscapes (Settele *et al.*, 1996) and has been shown to affect the probability of occurrence (e.g. Hanski, 1999; Biedermann, 2000). At present, however, sufficient suitable data sets are not available in order to test this issue in general, i.e. comparing species over a broad range of body sizes. In conclusion, it is clear that further studies including isolation and other species traits into the macroecological analysis of incidence functions are needed. Especially studies of incidence functions of the same species in, for instance, different parts of the species' range or different types of landscapes would be useful. The availability of more studies on area requirements — with an exact delimitation of habitat — could also help to clarify the frequency and underlying processes of occasionally reported negative area-incidence relationships. In illustration and in contrast to most studies (e.g. Biedermann & Appelt, 1996; Hinsley *et al.*, 1996; Hanski, 2001; Vos *et al.*, 2001), where positive relationships between area and occurrence in the patches have been recorded, Robbins *et al.* (1989) report a decreasing incidence of woodland birds with increasing patch area. However, in this study the species with a negative area-incidence relationship are not typical woodland inhabitants and thus the

incidence may be higher at the edges than in the interior of the woodland fragments.

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