BIODIVERSITY RESEARCH

Prevalence of intraspecific relationships between range size and abundance in Danish birds

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ABSTRACT

In this study, we investigate patterns in the prevalence of dynamic range–abundance relationships of the Danish avifauna, using breeding bird atlases from 1971 to 1974 and from 1993 to 1996. We focus on differences between common and rare species by dividing the assemblage into range-size quartiles. The trend in total population size was determined using an index. Range was determined as grid cell occupancy and standardized to facilitate comparisons between common and rare species. While narrow-ranging species showed strong and consistent range–abundance relationships, the relationships for widespread species were weak and exhibited considerable variation. This may be due to differences in patterns of resource use, since widespread species generally have wider niches, and so may be less affected by resource-based factors linking range and abundance. Since a tight and dynamic relationship is upheld for rare species, monitoring strategies based on range size surveys seem viable.

Keywords

Range–abundance relationships, nature management, rarity, resource use.

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INTRODUCTION

The range and abundance of organisms are usually described as two different variables, but are actually tightly related and can be seen as two aspects of the same pattern (Gregory, 1998). On a community level, the species with higher local abundances and higher global population sizes are also generally the ones with the largest ranges and the most dense within-range occupancy (Brown, 1984; Lawton, 1993). Indeed, the relationship between total abundance and spatial extent is in many cases so tight that one can be estimated fairly precisely from the other (Newton, 1997).

The existence of community-wide relationships between range and abundance has led to the inference of intraspecific relationships, in which changes in the range and abundance of any one species are predicted to dynamically track each other over time (Gaston & Curnutt, 1998). While intraspecific relationships between range and abundance have received some empirical support, correlations are often reported to be weak, and positive, negative, and non-significant relationships have been found (Pollard *et al.*, 1995; Blackburn *et al.*, 1998; Gaston *et al.*, 1999a).

Although the prevalence of intraspecific range–abundance relationships in nature is not well understood, they are potentially of great value for management-orientated species monitoring, in that they allow range size changes to be used for an indirect monitoring of trends in the abundance of species surveyed for conservation purposes (Bart & Klosiewski, 1989; Gaston, 1999; Warren *et al.*, 2003). In fact, a dynamic and tightly linked relationship

between species range and abundance is already implicitly assumed by many monitoring programmes currently in use. As an example, the Danish government is currently running an ambitious large-scale monitoring programme of several hundred species, divided into 'intensive' and 'extensive' survey categories. While intensively surveyed species are followed using abundance censuses, extensively surveyed species are monitored on a site occupancy level only (DMU, 2000). This kind of approach is also of broad relevance for the surveillance strategies to be implemented on a large scale in light of the European Union's 2010 goal of halting biodiversity loss.

In this study we investigate the prevalence of positive intraspecific relationships across the assemblage of Danish breeding birds. Emphasizing their potential role in nature management, we concentrate on differences between the range–abundance relationships of widespread and range-restricted species.

This distinction is important, since most conservation-orientated monitoring schemes are generally focused on rare, narrow-ranging species. Ecological studies, on the other hand, tend for practical reasons to focus on common species, despite the observation that most species have small ranges (Gaston, 1996a; Kean & Barlow, 2004). Recently, it has been suggested that there may be important differences in the biological processes governing the distributions of rare and common species (Jetz & Rahbek, 2002; Lennon *et al.*, 2004). While most of the variation in species richness for common species is correlated with contemporary climatic factors (Jetz & Rahbek, 2002; Lennon

et al., 2004; Ruggiero & Kitzberger, 2004) or mid-domain effects (Colwell *et al.*, 2004), distribution of rare species is not and may be more influenced by historical factors (Jetz & Rahbek, 2002; Jetz *et al.*, 2004). No sharp dichotomy between widespread and range-restricted species is inferred from these studies; rather, it should be seen as a continuum, where the two extremes differ in a qualitative manner.

To exemplify the practical implications of the findings of this study, we discuss them in light of the 'extensive' monitoring scheme employed by the Danish government's biodiversity monitoring programme, NOVANA (det Nationale Overvågningsprogram for VAndmiljøet og NAturen).

MATERIALS AND METHODS

Range size data were taken from two atlases of all bird species breeding in Denmark ($n = 200$) covering the years 1971–74 (Dybbro, 1976) and 1993–96 (Grell, 1998). The atlases use a grain size of 5×5 km covering a total of 2121 (1971–74) and 2155 (1993–96) grid cells; the difference is caused by a slightly better coverage in the latter atlas and the retention of seven coastal cells with very little land area as separate cells. Each cell was monitored for a minimum period of 1 year by volunteers engaged in the project, which entailed more than 1000 observers in each of the 4-year periods. All breeding bird species were reported as either certain, probable, or possible breeders based on the nature of the observations (as an example, nesting females were certain, singing males in breeding habitat probable, and resting birds in breeding habitat possible signs of breeding status). For this analysis, only certain and probable breeding observations were included.

Stocked (*Anas platyrhynchos*, *Phasianus colchicus*, *Perdix perdix*), invasive (*Branta canadensis*), and pelagic (*Uria aalge*, *Cepphus grylle*, *Alca torda*) species were excluded from the analysis, leaving a total of 193 species (scientific names follow Grell, 1998, which follows Voous, 1973, Voous, 1977). Seventeen species established new breeding populations in Denmark in the period between the two atlas surveys, while no species went extinct. The immigrant species were treated as having an area of occupancy of one grid square in 1971–74 when calculating range size change.

Ranges were measured as grid cell occupancy within Denmark. As all species in the analyses are also found outside of Denmark, this is a partial range size measure (*sensu* Gaston, 1996b), which expresses the prevalence of a species *within* its extent of occurrence. This is the measure that is most usually connected with abundance (e.g. Gaston & Gregory, 1997; Kotze *et al.*, 2003; Tales *et al.*, 2004).

Abundances of species are more difficult to measure than range sizes (Gaston, 1994). Since reliable estimates of the total population size within Denmark only exist for a small number of species for the period 1971–74, we chose to represent change in population size by an index published in the most recent atlas (Grell, 1998), which is based on estimates made by the Danish Ornithological Society, BirdLife Denmark. This index represents the change in the total Danish population size in the 22 years

separating the two breeding bird atlases, on a scale ranging from −2 to +2. The scale is based on the relative change in abundance, so that 2 denotes a population change of more than 50%, 1 a change of more than 20%, and 0 a population change between −20% and +20%. The main advantage with this index is that it is available for all species regardless of commonness, thereby facilitating a comparison between common and rare birds. It is independent of the data used to measure range size, preventing spurious correlations based on sampling effects (Newton, 1997). The 17 immigrant species were assigned index values on the basis of known numbers of pairs in 1993–96 (see Appendix S1 in Supplementary Material).

For the analyses, data were divided into range size quartiles based on the 1971–74 values, so that the first quartile contains the most narrow-ranging and the fourth quartile the most wide-ranging species. This expresses the relative rarity of species as measured by their partial density of occupancy inside Denmark and does not necessarily reflect their global status.

To quantify the change in range size, we used a standardization involving the shape of the empirical rank-range size distribution of the assemblage. Comparing the range size changes for widespread and range-restricted species is not straightforward. A range size increase of one grid cell is more important for small-ranging species than for widespread species, e.g. it is more interesting to go from 10 to 20 grid cells than from 1010 to 1020. A relative increase, on the other hand, is more important for wide-ranging species, e.g. it is much more difficult to go from 1000 to 2000 grid cells than from 10 to 20. We hypothesize that this is reflected by the empirical distribution of range sizes, which is predicted to follow a logistical pattern if a species' probability of expansion is proportional both to its occupancy and to the number of unoccupied grid cells (Hanski & Gyllenberg, 1997). Based on the inference that the empirical rank-range size distribution should reflect the relative importance of decreasing or increasing a single grid cell, we standardized our measure of occupancy change by entering occupancy for each year into the inverse equation of the regression line fitted to the rank-range size distribution (Fig. 1b).

The resulting measure, $P_{standard}$, was then used to calculate range size change as:

*Standardized Occupancy Change* $= P_{standard}(1993-96) - P_{standard}(1971-74)$.

Despite these efforts, the data retain some heteroscedasticity that could not be removed.

The group of bird species monitored extensively, i.e. for occupancy change only, were taken from the NOVANA report (DMU, 2000). Regression slopes were compared using an *F*-test (Zar, 1984). Significance values of regression lines were calculated by ANOVA using the SAS statistical package (SAS Institute, 2000).

RESULTS

The rank-range size distribution of the assemblage correlates tightly with a logistical pattern (Fig. 1a). Logit-transforming the occupancy values, the rank-range size distribution conformed
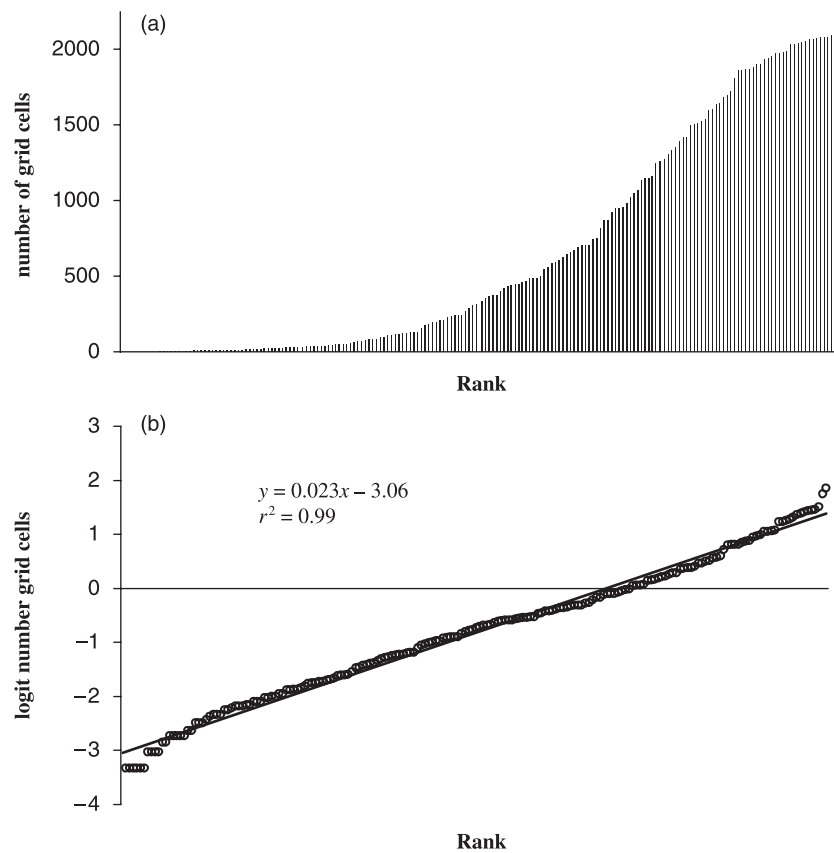
Figure 1 (a) The empirical rank-range size curve of the assemblage of Danish breeding birds. (b) After logit-transformation, the rank-range size curve follows a straight line. The regression equation was used to standardize changes in species occupancy.

very well to a straight line ($r^2 = 0.99$ for the 1993–96 assemblage; Fig. 1b). The resulting equation for calculating $P_{standard}$ (year) was:

$$P_{standard}(year) = (\log(p/(1-p)) + 0.036)/0.023.$$

We found a clear and significant relationship between *Standardized Occupancy Change* and overall population trend (Fig. 2). This relationship held up for all four range size quartiles. While the species with smallest ranges (the two first range-size quartiles) exhibited strong and highly significant relations between trends in occupancy and population size (ANOVA, first quartile $F = 51.55$, $P < 0.001$, $r^2 = 0.53$; second quartile $F = 139.27$, $P < 0.001$, $r^2 = 0.75$), the pattern was much less clear for the two quartiles comprising the more widespread species (Fig. 3). Instead, we see a rather flat relationship in which most species tend to increase in occupancy regardless of the trend in population size. The regressions are still significant, although for the third quartile only barely so, but r-squares are much lower than for the first two quartiles (ANOVA, third quartile $F = 9.46$, $P < 0.05$, $r^2 = 0.17$; fourth quartile $F = 20.06$, $P < 0.001$, $r^2 = 0.30$). The slopes of the four regression lines are significantly different (F-test, $F_{46} = 23.59$, $P < 0.001$), which in part is due to the larger variance of the two first quartiles.

The species chosen for extensive surveying in the NOVANA monitoring programme mainly belong to the two first range-size quartiles, and consequently, the range–abundance relationship is stronger for these species than for the assemblage as a whole ($r^2 = 0.69$, F-test for difference of slope between species selected

for extensive monitoring in NOVANA and those species not chosen: $F_{22,169} = 4.76$, $P < 0.05$; Fig. 2).

DISCUSSION

The analysis confirms the expectation of an overall dynamic relationship between occupancy and population size for the Danish breeding bird assemblage. There are, however, some differences in the relationships exhibited by rare and common species. While rare species showed a highly consistent relationship between trends in population and abundance, the pattern seems to break down for the more widespread species. These species generally tended to increase their occupancy regardless of the trend in population size. The decoupling of the temporal dynamics of range and abundance, for the two quartiles containing the most widespread species, points to possible differences in the ecology of narrow-ranging and widespread species.

A possible explanation for this pattern is that widespread species are more generalist, i.e. have larger niches than narrow-ranging species. Differences in resource use have been strongly implicated in the causality of range–abundance relationships (Gaston & Lawton, 1997; Kotze *et al.*, 2003; Harcourt *et al.*, 2005). Current attention focuses on the 'resource availability' hypothesis, which states that species are widespread and abundant because they use resources that are themselves more widespread (Hanski *et al.*, 1993; Gregory & Gaston, 2000; Heino, 2005). According to this theory, the availability of specialized resources influences the range size and abundance of a species independently.
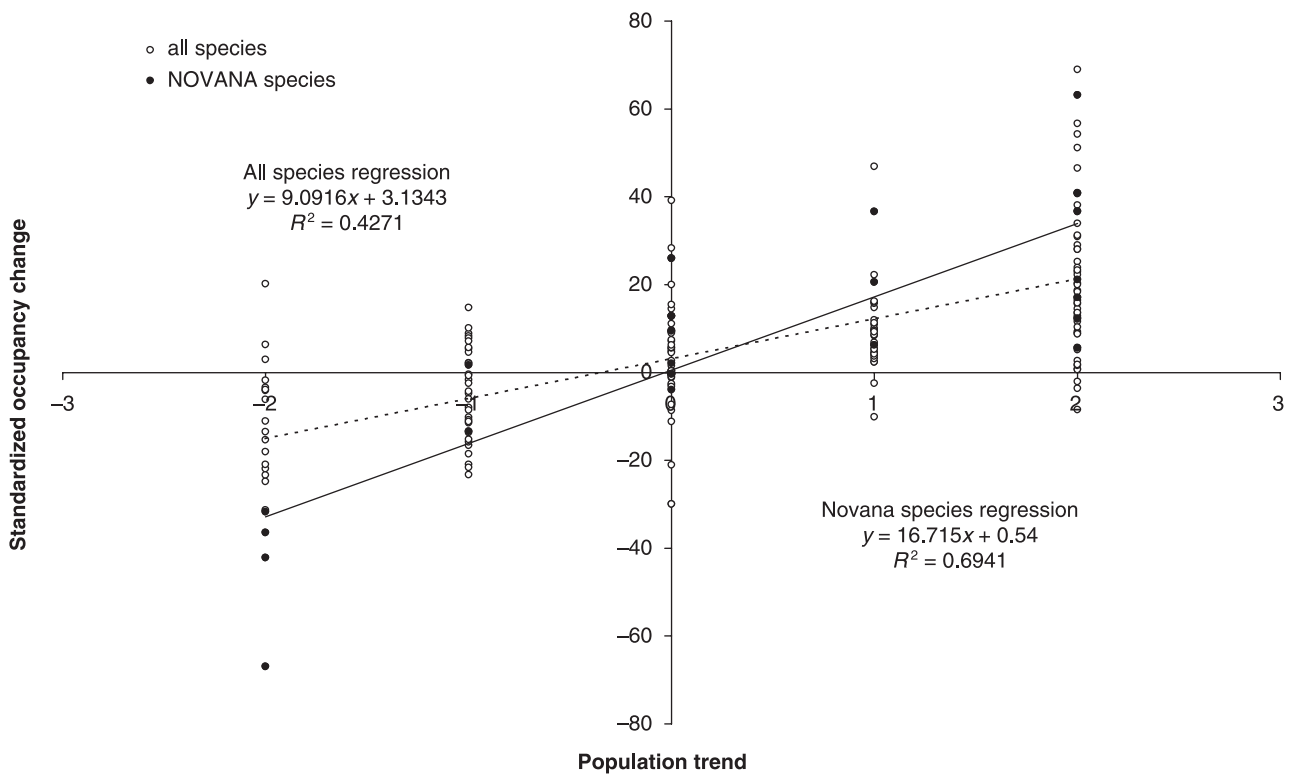
Figure 2 The relationship between standardized change in occupancy and the population trend index (see Appendix S1). A separate regression line is shown for the species monitored extensively in the Danish government's conservation monitoring programme.

There is no direct causal link between range size and abundance, and a dynamic relationship is created as both range and abundance track trends in the availability of these resources over time (Gaston & Lawton, 1997).

This mechanism may work less strongly for widespread species, which are generally found to have wider niches and less specialized resource preferences (Harcourt *et al.*, 2002; Kotze *et al.*, 2003; Gregory & Gaston, 2000; found this pattern within the group of widespread species only). The greater range of resources available to these species would enable them to maintain high levels of occupancy, even as population sizes decline as a result of decreasing availability of favoured resources. This finding is in accordance with the general tendency of human-induced habitat deterioration to cause range expansion of already widespread species (McKinney & Lockwood, 1999; Nijboer & Schmidt-Kloiber, 2004), and threaten extinction of species with highly specialized resource requirements (Miller *et al.*, 2005).

An alternative interpretation involves the higher resilience of subpopulations of the more widespread species to local extinction. Local populations of a species experiencing population decline will be less likely to disappear if there is a steady input of dispersing individuals from nearby sites (the 'rescue effect', Hanski & Gyllenberg, 1993).

The tight dynamic link between range and abundance among the most narrow-ranging half of the assemblage is very consistent and exhibits few negative relationships. The most probable explanation for the difference between this and earlier studies of the intraspecific relationship is the reduction of noise associated with time lags in the response of one variable to changes in the other. Such time lags are predicted to result from metapopulation dynamics, and have been shown to stretch over several years, e.g. 4 years in an arctiid moth species (Conrad *et al.*, 2001). Since most studies of the intraspecific abundance relationship have examined correlations of range and abundance using every single year as a separate data point (Blackburn *et al.*, 1998; Gaston *et al.*, 1999a,b), time lags could profoundly distort the detection of patterns. By using data points separated by a span of more than 20 years this effect is reduced to a minimum in the present study.

Our study gives support to the feasibility of using distribution-based surveys in monitoring programmes similar to the Danish NOVANA programme. Since most of the observed inconsistencies in temporal relationships stem from interannual noise and the influence of common species, it seems sound to use this method in monitoring the group of narrow-ranging species for which it is usually employed. It is not advisable to use it for short-term investigations or very rare or threatened species, since it is not sufficiently sensitive to rapid changes in population size, and the effects of time lags may delay detection of negative trends.

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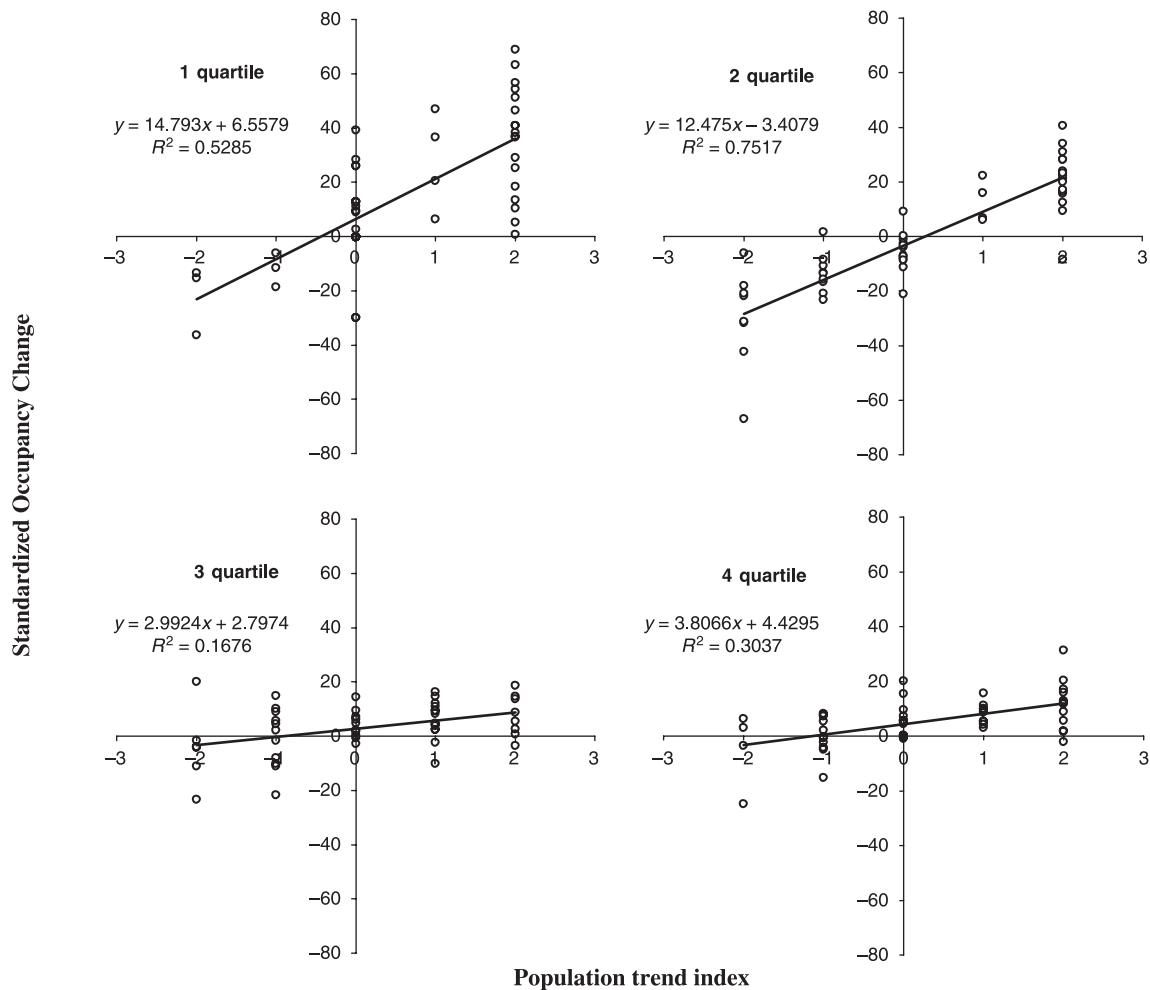
Figure 3 The distribution–abundance relationship from Fig. 2 separated into range size quartiles, 1st and 4th being the 25% of the species with the smallest and largest ranges, respectively.

REFERENCES

Bart, J. & Klosiewski, S.P. (1989) Use of presence–absence to measure changes in avian density. *Journal of Wildlife Management*, **53**, 847–852.

Blackburn, T.M., Gaston, K.J., Greenwood, J.J.D. & Gregory, R.D. (1998) The anatomy of the interspecific abundance–range size relationship for the British avifauna: II. Temporal dynamics. *Ecology Letters*, **1**, 47–55.

Brown, J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255–279.

Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2004) The mid-domain effect and species richness patterns: What have we learned so far? *American Naturalist*, **163**, 1–23.

Conrad, K.F., Perry, J.N. & Woiwod, I.P. (2001) An abundance-occupancy time-lag during the decline of an arctiid tiger moth. *Ecology Letters*, **4**, 300–303.

DMU (2000) *NOVANA Programbeskrivelse Del 3, Bilag 1: Natur-typer og arter*. Danmarks Miljøundersøgelser, Kalø'.

Dybbro, T. (1976) *De danske ynglefugles udbredelse*. Dansk Ornitologisk Forening, Copenhagen.

Gaston, K.J. (1994) *Rarity*. Chapman & Hall, London.

Gaston, K.J. (1996a) Species-range-size distributions: patterns, mechanisms and implications. *Trends in Ecology & Evolution*, **11**, 197–201.

Gaston, K.J. (1996b) The multiple forms of the interspecific abundance–distribution relationship. *Oikos*, **76**, 211–220.

Gaston, K.J. (1999) Implications of interspecific and intraspecific abundance–occupancy relationships. *Oikos*, **86**, 195–207.

Gaston, K.J. & Curnutt, J.L. (1998) The dynamics of abundance–range size relationships. *Oikos*, **81**, 38–44.

Gaston, K.J. & Gregory, R.D. (1997) Interspecific abundance–range size relationships: Range position and phylogeny. *Ecography*, **20**, 390–399.

Gaston, K.J., Blackburn, T.M. & Gregory, R.D. (1999a) Intra-specific abundance–occupancy relationships: case studies of six bird species in Britain. *Diversity and Distributions*, **5**, 197–212.

Gaston, K.J., Gregory, R.D. & Blackburn, T.M. (1999b) Intraspecific relationships between abundance and occupancy among species of Paridae and Sylviidae in Britain. *Ecoscience*, **6**, 131–142.

Gaston, K.J. & Lawton, J.H. (1997) Interspecific abundance–range size relationships: an appraisal of mechanisms. *Journal of Animal Ecology*, **66**, 579–601.

Gregory, R.D. (1998) An intraspecific model of species' expansion, linking abundance and distribution. *Ecography*, **21**, 92–96.

Gregory, R.D. & Gaston, K.J. (2000) Explanations of commonness and rarity in British breeding birds: separating resource use and resource availability. *Oikos*, **88**, 515–526.

Grell, M.B. (1998) *Fuglenes Danmark*. Gads Forlag, Copenhagen, Denmark.

Hanski, I. & Gyllenberg, M. (1993) Two general metapopulation models and the core-satellite species hypothesis. *American Naturalist*, **142**, 17–41.

Hanski, I. & Gyllenberg, M. (1997) Uniting two general patterns in the distribution of species. *Science*, **275**, 397–400.

Hanski, I., Kouki, J. & Halkka, A. (1993) Three explanations of the positive relationship between distribution and abundance of species. *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R.E. Rickleffs and D. Schluter), pp. 108–116. University of Chicago Press, Chicago & London.

Harcourt, A.H., Coppeto, S.A. & Parks, S.A. (2002) Rarity, specialization and extinction in primates. *Journal of Biogeography*, **29**, 445–456.

Harcourt, A.H., Coppeto, S.A. & Parks, S.A. (2005) The distribution–abundance (i.e. density) relationship: its form and causes in a tropical mammal order, primates. *Journal of Biogeography*, **29**, 445–456.

Heino, J. (2005) Positive relationship between regional distribution and local abundance in stream insects: a consequence of niche breadth or niche position? *Ecography*, **28**, 345–354.

Holt, A.R., Gaston, K.J. & He, F.L. (2002a) Occupancy–abundance relationships and spatial distribution: a review. *Basic and Applied Ecology*, **3**, 1–13.

Holt, A.R., Warren, P.H. & Gaston, K.J. (2002b) The importance of biotic interactions in abundance–occupancy relationships. *Journal of Animal Ecology*, **71**, 846–854.

Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species richness. *Science*, **297**, 1548–1551.

Jetz, W., Rahbek, C. & Colwell, R.K. (2004) The coincidence of rarity and richness and the potential signature of history in centres of endemism. *Ecology Letters*, **7**, 1180–1191.

Kean, J. & Barlow, N. (2004) Exploring rarity using a general model for distribution and abundance. *American Naturalist*, **163**, 407–416.

Kotze, D.J., Niemela, J., O'Hara, R.B. & Turin, H. (2003) Testing abundance–range size relationships in European carabid beetles (Coleoptera, Carabidae). *Ecography*, **26**, 553–566.

Lawton, J.H. (1993) Range, population abundance and conservation. *Trends in Ecology & Evolution*, **8**, 409–412.

Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2004) Contribution of rarity and commonness to patterns of species richness. *Ecology Letters*, **7**, 81–87.

McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, **14**, 450–453.

Miller, G.H., Fogel, M.L., Magee, J.W., Gagan, M.K., Clarke, S.J. & Johnson, B.J. (2005) Ecosystem collapse in Pleistocene Australia and a human role in megafaunal extinction. *Science*, **309**, 287–290.

Newton, I. (1997) Links between the abundance and distribution of birds. *Ecography*, **20**, 137–145.

Nijboer, R.C. & Schmidt-Kloiber, A. (2004) The effect of excluding taxa with low abundances or taxa with small distribution ranges on ecological assessment. *Hydrobiologia*, **516**, 347–363.

Pollard, E., Moss, D. & Yates, T.J. (1995) Population trends of common British butterflies at monitored sites. *The Journal of Applied Ecology*, **32**, 9–16.

Ruggiero, A. & Kitzberger, T. (2004) Environmental correlates of mammal species richness in South America: effects of spatial structure, taxonomy and geographic range. *Ecography*, **27**, 401–416.

SAS Institute I. *SAS*. [8.02]. (2000) SAS Institute, Cary, NC, USA.

Tales, E., Keith, P. & Oberdorff, T. (2004) Density–range size relationships in French riverine fishes. *Oecologia*, **138**, 360–370.

Voous, K.H. (1973) List of recent Holarctic bird species, non-passerines. *Ibis*, **115**, 612–638.

Voous, K.H. (1977) List of recent Holarctic bird species, passerines. *Ibis*, **119**, 367–406.

Warren, M., McGeoch, M.A. & Chown, S.L. (2003) Predicting abundance from occupancy: a test for an aggregated insect assemblage. *Journal of Animal Ecology*, **72**, 468–477.

Zar, J.H. (1984) Biostatistical analysis. Prentice Hall, New Jersey.

SUPPLEMENTARY MATERIAL

The following material is available online at www.blackwell-synergy.com/loi/ddi

Appendix S1 Abundance, occupancy, and trends of Danish breeding birds