

The consistency and stability of abundance–occupancy relationships in large-scale population dynamics

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Summary

1. Abundance–occupancy relationships comprise some of the most general and well-explored patterns in macro-ecology. The theory governing these relationships predicts that species will exhibit a positive interspecific and intraspecific relationship between regional occupancy and local abundance. Abundance–occupancy relationships have important implications in using distributional surveys, such as atlases, to understand and document large-scale population dynamics and the consequences of environmental change. A basic need for interpreting such data bases is a better understanding of whether changes in regional occupancy reflect changes in local abundance across species of varying life-history characteristics.

2. Our objective was to test the predictions of the abundance–occupancy rule using two independent data sets, the New York State Breeding Bird Atlas and the North American Breeding Bird Survey. The New York State Breeding Bird Atlas consists of 5332 25-km² survey blocks and is one of the first atlases in the USA to be completed for two time periods (1980–85 and 2000–05). The North American Breeding Survey is a large-scale annual survey intended to document the relative abundance and population change of songbirds throughout the USA.

3. We found that regional occupancy was positively correlated with relative abundance across 98 ($\beta = 0.60 \pm 0.11$ SE, $P < 0.001$, $R^2 = 0.60$) and 85 species ($\beta = 0.67 \pm 0.06$ SE, $P < 0.001$, $R^2 = 0.57$) in two separate time periods. This relationship proved stable over time and was notably consistent between breeding habitat groups and migratory guilds.

4. Between 1980 and 2005, changes in regional occupancy were highly correlated with long-term abundance trend estimates for 75 species ($\beta = 5.73 \pm 0.24$ SE, $P < 0.001$, $R^2 = 0.88$). Over a 20-year period, woodland and resident birds showed an increase in occupancy while grassland species showed the greatest decline; these patterns were mirrored by changes in local abundance.

5. Although exceptions existed, we found most changes in occupancy parallel changes in local abundance. These findings support the basic predictions of the abundance–occupancy rule and demonstrate its consistency and stability in species and groups of varying life-history characteristics.

Key-words: bird guilds, breeding bird atlas, breeding bird survey, New York conservation, population dynamics, population monitoring, range change, temporal trends

Introduction

Theories focusing on the relationship between local abundance and regional occupancy are among the oldest and most well studied in ecology (Brown 1995; Gaston *et al.* 2000). Charles Darwin (1859) first noted that ‘... the dominant species – those which range widely, are the most diffused in their own country, and are the most numerous in individuals ...’. Over the past

two decades, Darwin’s observation has been restated as the abundance–occupancy rule and predicts that species of low local abundance are the most localized throughout a region and those of high abundance are the most widespread (Gaston *et al.* 2000). Although abundance–occupancy relationships are generally positive across diverse taxa (Blackburn, Cassey & Gaston 2006), recent studies have documented counterexamples and variations where individual species and entire assemblages do not always exhibit positive abundance–occupancy relationships (Fuller *et al.* 1995; Chamberlain &

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Fuller 2001; Blackburn *et al.* 2006; Reif *et al.* 2006; Symonds & Johnson 2006; Van Turnhout *et al.* 2007; Webb, Noble & Freckleton 2007). These counter-examples raise questions about the consistency of abundance–occupancy relationships for various species, communities and geographical regions.

The abundance–occupancy relationship exists in two forms: the interspecific and intraspecific comparison. Interspecific studies involve an examination of abundance and occupancy for many species during a single time period (Gaston 1996; Gaston, Blackburn & Gregory 1997b; Gaston *et al.* 1997c), while intraspecific studies focus on a single species or group of species, over time (Cade & Woods 1997; Blackburn *et al.* 1998; Gaston, Gregory & Blackburn 1999; Webb *et al.* 2007). Although intraspecific relationships are often positive, studies focusing on changes in large-scale population dynamics have found a high degree of variability among species and assemblages (Gaston *et al.* 1999). This variability is often attributed to the narrow range of variation observed in annual estimates of abundance and occupancy over limited time periods (Gaston *et al.* 2000). Less common are intraspecific examinations involving large groups of species over long periods of time (e.g., decades). In these types of studies, annual estimates can be replaced by long-term trend estimates. These trend estimates should more effectively describe intraspecific relationships because they mask the annual variation in abundance and occupancy data and counteract the effect of time-lags. A primary constraint in conducting such studies, however, has been the availability of regional data bases for many species spanning multiple years or decades.

Atlas surveys yield one type of regional occupancy data used for documenting the distribution of species and offer an opportunity for examining abundance–occupancy relationships in large-scale population dynamics (Donald & Fuller 1998; Gibbons *et al.* 2007). Atlas data are increasingly used for purposes of conservation planning and policy (Bishop & Myers 2005), assessing species-habitat associations (Trzcinski, Fahrig & Merriam 1999; Gates & Donald 2000), selecting areas for preserves (Araújo & Williams 2000; Araújo, Williams & Fuller 2002), and documenting range and population changes and their possible causes (Chamberlain & Fuller 2001; Donald, Green & Heath 2001; Donald *et al.* 2006; Van Turnhout *et al.* 2007). Given the increasing importance of atlases in ecology, there is a need to examine the consistency and temporal stability of abundance–occupancy relationships in measuring long-term, large-scale population change.

Although the strength and form of the abundance–occupancy has been found to vary across different ecological systems (Blackburn *et al.* 2006), relatively few studies have addressed this relationship using atlas data due to the rarity of repeat atlases (Gibbons *et al.* 2007). Those that have reported inconsistent results and offer a diversity of recommendations for using occupancy data in assessing large-scale population dynamics (Fuller *et al.* 1995; Böhning-Gaese & Bauer 1996; Donald & Fuller 1998; Chamberlain & Fuller 2001; Symonds & Johnson 2006; Van Turnhout *et al.* 2007). Böhning-Gaese & Bauer (1996) found that although changes in the occupancy and abundance of 151 species were highly correlated over a

10-year period, atlas data alone would not have identified large declines in abundance for entire assemblages of species (i.e., migratory groups). Similarly, in their analysis of Britain's two Breeding Bird Atlases, Chamberlain & Fuller (2001) found that 20 species of farmland birds showed no evidence of range contraction despite significant declines in abundance and further warned that a reliance on occupancy data alone could provide a misleading impression of large-scale population dynamics. In contrast, a study of two national atlases in the Netherlands found that 80% of 157 bird species showed similar changes in their abundance and occupancy over a 25-year period and concluded that, given adequate coverage, it is possible to assess population change using atlas data (Van Turnhout *et al.* 2007). The prominence of abundance–occupancy relationships provides a theoretical underpinning for using atlases to describe population dynamics, but as the preceding studies suggest, examples where no positive abundance–occupancy relationships were found do exist.

Our objective was to test the predictions of the abundance–occupancy rule using two independent data sets, the New York State Breeding Bird Atlas and the North American Breeding Bird Survey. The use of these two independent surveys offers a test of concurrence for detecting large-scale and long-term avian population change in New York State. We predicted that: (i) a positive interspecific relationship existed between abundance and occupancy in two separate time periods (1980–85 and 2000–05), (ii) a positive intraspecific relationship existed between changes in occupancy and abundance over the 20-year sampling period, and (iii) these relationships were stable over time and consistent between breeding habitat and migratory groups. The predictions of the abundance–occupancy rule provide a theoretical foundation for examining these patterns and evaluating the usefulness of occupancy data in describing regional population dynamics.

Methods

OCCUPANCY DATA

The New York State Breeding Bird Atlas (hereafter BBA) is a comprehensive, statewide survey with the objective of documenting the distribution of breeding birds in New York (Fig. 1). The BBA was conducted in two time periods: the first atlas project (hereafter atlas1980) was conducted from 1980 to 1985 (Andrle & Carroll 1988) while New York's second atlas (hereafter atlas 2000) was conducted from 2000 to 2005 following the same protocol of the first BBA. Both surveys used a grid of 5332 blocks each measuring 5 × 5 km and cover the entirety of New York State (125 384 km²). This represents one of the largest and finest resolution atlas data sets in the world (Gibbons *et al.* 2007).

The BBA implemented a set of protocols to achieve consistent coverage within each atlas block. The state was stratified into 10 regions and regional coordinators in each area were responsible for recruiting volunteers and overseeing coverage of the blocks in their region. Atlas observers were assigned to survey one or more blocks and were expected to spend at least 8 hours in the block, visiting each habitat represented, and recording at least 76 species. Although the

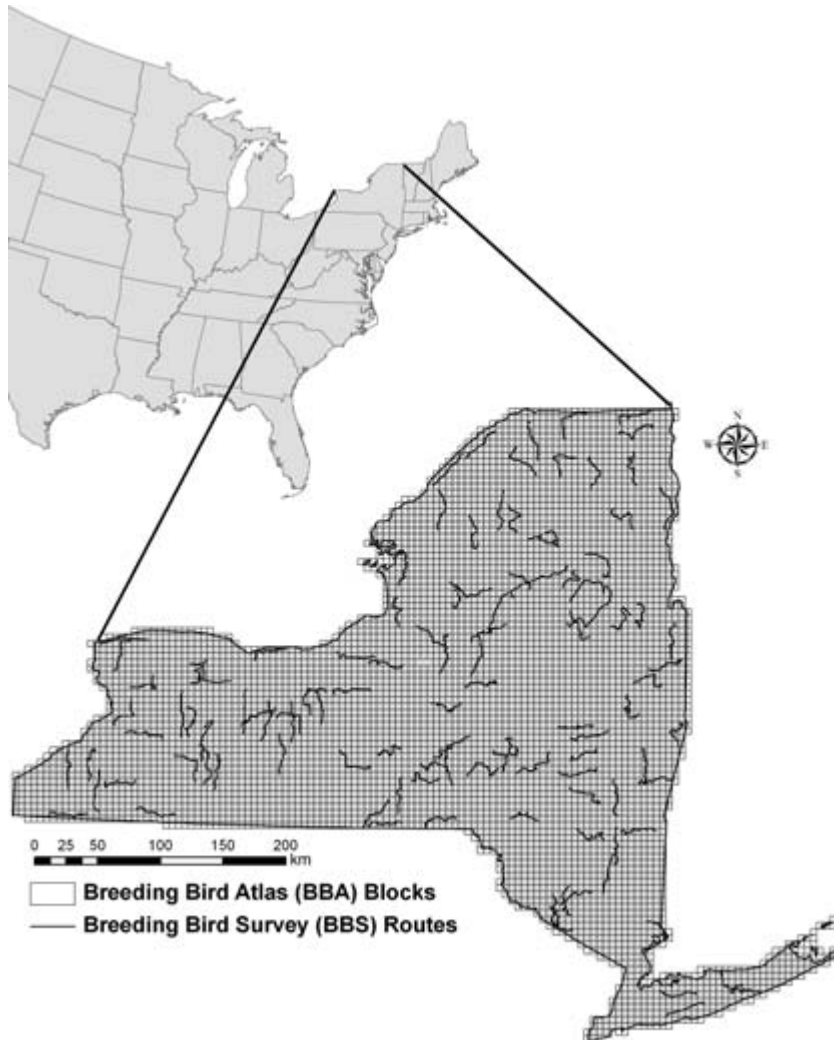


Fig. 1. The New York State Breeding Bird Atlas was conducted in 1980–85 and 2000–05 and used a survey grid of 5332 blocks that each measure 25 km². The BBA provides a measure of statewide occupancy. The US Geological Survey's North America Breeding Bird Survey consists of roadside routes that are randomly distributed throughout the road network of New York State and measure 39.4 km long. There are 198 routes that have been sampled on an annual basis. BBS data provide measures of long-term trend estimates and relative abundance.

BBA did not provide a definitive statement concerning the absence of a breeding record for a species not listed in a block, absence indicates that species could not be found given adequate effort and observer ability, or that the species occurs in low enough densities to escape detection (Trzcinski *et al.* 1999). Both atlas projects enlisted over 1000 volunteers and resulted in 361 594 records for 246 species in the 1980 BBA and 383 051 records for 251 species in the 2000 BBA.

ABUNDANCE DATA

The North American Breeding Bird Survey (hereafter BBS) provides information on the relative abundance of bird species at state and regional scales (Sauer, Hines & Fallon 2005). The survey consists of 39.4-km long roadside routes that are randomly located along secondary roads. Routes are surveyed once each year and an observer conducts 50 3-min point counts at 0.8-km intervals on the roadside, recording all birds heard or seen within 0.4 km of the stop. Within New York State, the survey consists of approximately 198 roadside surveys located along secondary roads (although not every route is conducted every year) (Fig. 1). The BBS provides a measure a relative abundance expressed as the average number of individuals per route. Abundance estimates for a species are calculated as the number of

individuals per survey route, averaged only across those routes at which the species was recorded. In addition, because the BBS is conducted on an annual basis, trend estimates can be expressed as percentage change per year (Link & Sauer 1994, 1996).

Not all bird species are adequately sampled by roadside surveys. Small sample sizes, low relative abundances on survey routes, and missing data all can compromise BBS results (Link & Sauer 1996; Sauer, Peterjohn & Link 1994). The BBS provides guidelines by which to omit species with deficient data from comparative analyses. For all analyses, we excluded those species that were found on fewer than 14 routes (small sample size) or had a regional abundance of less than 0.1 birds route⁻¹ (very low abundance).

GUILD CLASSIFICATIONS

Species were classified by their migratory status and breeding habitat guild. Migratory status and breeding habitat were assigned based on BBS guild classifications groups (Sauer *et al.* 1999; DeGraaf & Yamasaki 2001). Breeding habitat guild classification included woodland species, scrub-successional, generalists, grassland, wetland, and urban species. Migratory status classifications included resident, short-distance migrant, and Neotropical migrant species.

ANALYSIS

We predicted that species would demonstrate a positive interspecific relationship between abundance and occupancy in the two separate time periods, 1980 to 1985 and 2000 to 2005. We calculated statewide occupancy (number of atlas blocks occupied) and relative abundance (number of individuals per BBS route) for species that met the BBS criteria for estimating accurate estimates of abundance. Occupancy was logit transformed and abundance was logarithmically transformed (Williamson & Gaston 1999; He & Gaston 2000; Williamson & Gaston 2005). For interspecific comparisons, abundance estimates were calculated separately over the atlas periods, 1980–85 and 2000–05. To examine the predicted linear nature of the abundance–occupancy relationship (Gaston *et al.* 2000), we used ordinary least-squares regression to examine the occupancy (BBA) and relative abundance (BBS) of species in the two separate time periods of 1980–85 and 2000–05 (Faraway 2004).

For interspecific comparisons, we used analysis of covariance (ANCOVA) to test whether the positive relationship between abundance and occupancy was exhibited in all breeding habitat and migratory guilds. We developed ANCOVA models for the two separate time periods and for breeding habitat groups and migratory groups (Crawley 2005). We examined whether the slope of the abundance–occupancy relationship is different between guilds by adding an interaction term between the species group and the abundance estimate as a covariate. A significant interaction term suggests that the slope of the relationship (e.g., between abundance and occupancy) is different between the categorical groupings (e.g., breeding habitat group) (Crawley 2005).

Range change data are often highly left skewed because contractions can never be less than –100% but range expansions can be greater than 100% (Böhning-Gaese & Bauer 1996; Symonds & Johnson 2006). In our study, the range change data were skewed and we examined several transformations but chose to use a data transformation defining occupancy change as (the number of occupied blocks in 2000–2005 – the number of occupied blocks in 1980–85)/[(number of occupied blocks in 1980–85 + number of occupied blocks in 2000–05)/2] (Böhning-Gaese & Bauer 1996). This formula produces a new metric of occupancy change (hereafter status), with values ranging from –2 (maximum retraction) and +2 (maximum expansion), and has been used successfully in analyses of atlas changes (Böhning-Gaese & Bauer 1996; Van Turnhout *et al.* 2007). We checked the appropriateness of this model for use in ordinary least squares (OLS) regression by examining the residuals against the fitted values, the Q-Q plot of the normal error distribution, and the square-root of the standardized residuals against the fitted values (Crawley 2005).

We calculated abundance trend estimates for each species using the BBS data collected between 1980 and 2005 (Sauer *et al.* 2005). We estimated these regional trend estimates using the route-regression method (see Geissler & Sauer 1990 for details), and determined the estimated population trend (in percentage year⁻¹), its statistical significance, and the number of routes found on which trends were estimated. We included only those species on at least 14 routes during the sampling period of 1980 to 2005. We examined changes in occupancy and abundance using two separate ANCOVA models. In both ANCOVA models, we included the change in occupancy (status) as the response variable and the trend estimate as a covariate. We used breeding habitat group as the factor variable in the first model and migratory status as the factor variable in the second model. In addition, we plotted the relative number of block losses and gains for each species against their initial relative abundance in the first

time period of 1980 to 1985. We calculated relative losses and gains by dividing the number of block gains and losses for a species in the second atlas by its original occupancy in the first atlas.

Phylogenetic approaches are rarely warranted for abundance and occupancy data because closely related species can have very different distributions and population dynamics. As a precautionary step, however, we checked all regression analyses for phylogenetic relatedness at the family-level using generalized estimating equations as described by Paradis & Claude (2002). We classified birds using the phylogenies of Sibley & Ahlquist (1990) obtained from DNA–DNA hybridization data. We did not find any evidence of phylogenetic autocorrelation and all results are reported without controlling for phylogenetic relatedness. All analyses were performed using R (R Development Core Team 2006).

Results

INTERSPECIFIC RELATIONSHIPS

In the first time period of 1980–85, 98 species met the criteria for adequate BBS sampling and were included in the analysis. As predicted, occupancy was positively correlated with relative abundance for all 98 species (Fig. 2a; $\beta = 0.60 \pm 0.11$ SE, $t = 6.21$, $P < 0.001$, $R^2 = 0.60$). In the second time period of 2000–05, occupancy was positively correlated with relative abundance for 85 species (Fig. 2b; $\beta = 0.67 \pm 0.06$ SE, $t = 5.52$, $P < 0.001$, $R^2 = 0.57$).

In the 1980–85 time period, the common slope between occupancy and relative abundance was positive and significantly different than zero across the six different breeding habitat groups (Fig. 3; ANCOVA: $F_{1,98} = 154.12$, $P < 0.001$). We did not find strong evidence that the slopes were significantly different among the breeding habitat groups ($F_{5,98} = 1.63$, $P = 0.16$), suggesting that the slope of the abundance–occupancy relationship was consistent among all habitat groups. Pairwise comparisons between individual groups showed significant differences in slopes between grassland and scrub-successional species ($F_{1,27} = 5.31$, $P = 0.03$) and scrub-successional and wetland species ($F_{1,25} = 9.21$, $P = 0.006$) (Fig. 3). Within the same time period, abundance remained highly correlated with occupancy among Neotropical migrants, short-distance migrants, and resident species (Fig. 4; $F_{1,98} = 145.11$, $P < 0.001$). Like the breeding habitat groups, the interaction term was not significant ($F_{2,98} = 2.18$, $P = 0.12$), suggesting that the slope of the relationship was not significantly different between the migratory groups.

We found similar results for the second time period. Abundance was highly correlated with occupancy for all six breeding habitat groups (ANCOVA: $F_{1,85} = 111.94$, $P < 0.001$). The interaction term was not significant ($F_{2,85} = 0.78$, $P = 0.38$), and the pairwise comparisons with significant covariate terms included scrub-successional and wetland breeding birds ($F_{1,22} = 8.70$, $P = 0.009$). For migratory groups, the relationship between occupancy and abundance was consistent across the three groups ($F_{1,85} = 107.86$, $P < 0.001$), and the interaction term was not significant ($F_{2,85} = 1.15$, $P = 0.32$).

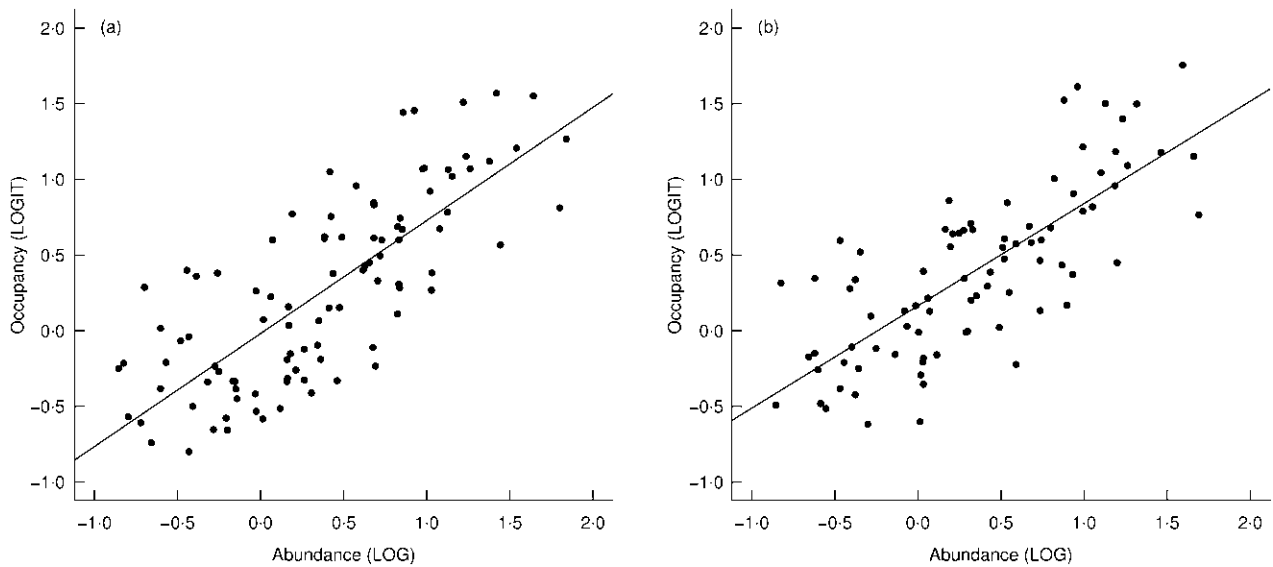


Fig. 2. The relationship between statewide occupancy and relative abundance in two time periods: (a) 1980 to 1985 and (b) 2000 to 2005 in New York State. In the first time period, the occupancy of 98 species was positively correlated with their relative abundance throughout the state. The same pattern was observed across 85 species in the second time period.

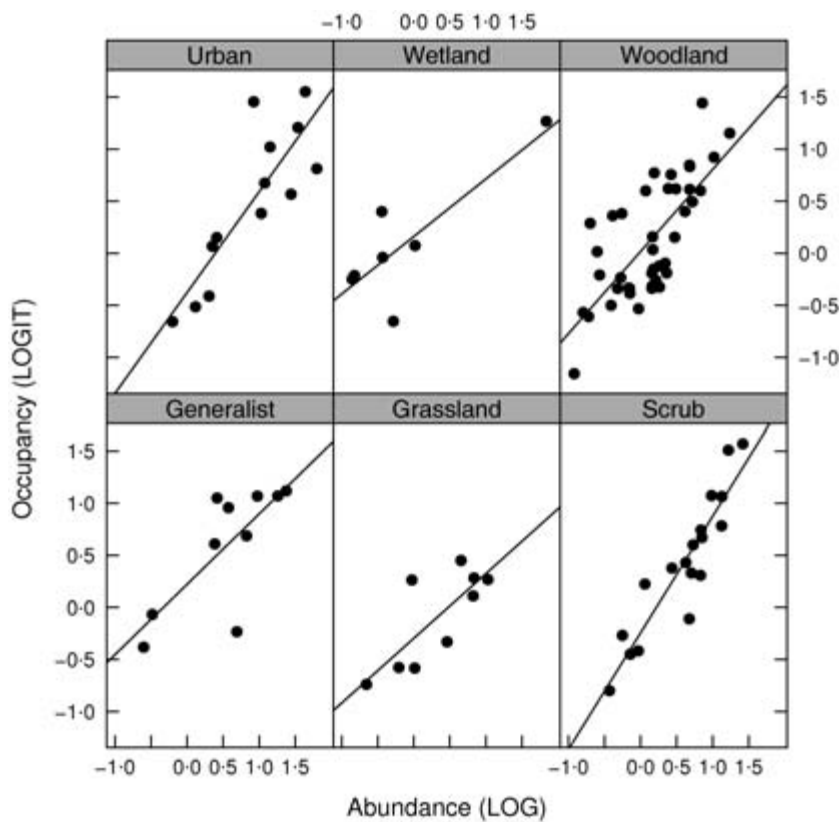


Fig. 3. The positive interspecific relationship between abundance and occupancy was consistent among breeding habitat groups in the first time period of 1980–85 in New York State. The slope of this relationship was significantly different for comparisons between grassland and scrub-successional species and scrub-successional and wetland species.

INTRASPECIFIC RELATIONSHIPS

Species showed a wide variation in occupancy changes ranging from widespread declines (–65%, Upland sandpiper, *Bartramia longicauda* [Bechstein 1812]) to large increases

(310%, Carolina wren, *Thryothorus ludovicianus* [Latham 1790]). Despite these changes, species that were relatively widespread in the state remained widespread while rare species remained relatively rare (0.92 ± 0.02 SE, $P < 0.001$, $R^2 = 0.96$). Although the status transformation created a symmetrical distribution

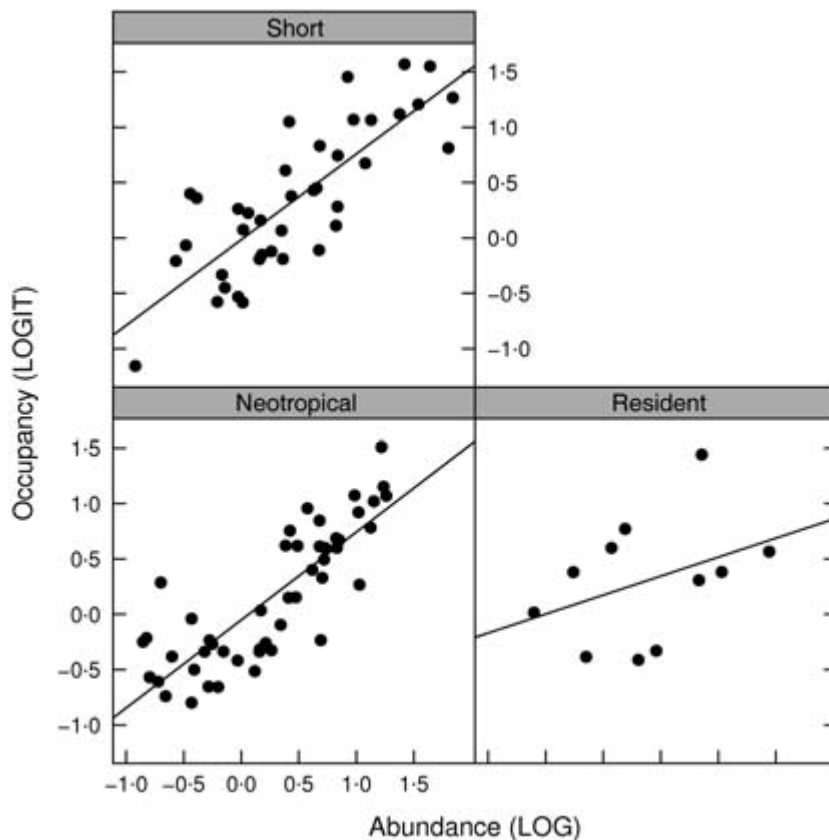


Fig. 4. The positive interspecific relationship between abundance and occupancy was consistent among migratory groups in the first time period of 1980–85 in New York State. The slope of this relationship was not significantly different for any of the migratory guilds.

needed for regression, the interpretation is no different than for traditional percentage change data. We included 120 species that met the BBS criteria for quantifying trend estimates (i.e., found on more than 14 routes in the state) in the analysis. Estimates of abundance trends were positively correlated with changes in occupancy ($n = 127$, $\beta = 5.10 \pm 0.24$ SE, $t = 12.25$, $P < 0.001$, $R^2 = 0.57$). When we restricted the analysis to only those species demonstrating a significant change in abundance (as determined by the BBS) ($P < 0.10$), the relationship was even stronger (Fig. 5; $n = 75$, $\beta = 5.73 \pm 0.24$ SE, $t = 23.47$, $P < 0.001$, $R^2 = 0.88$). Of these 75 species, 46.7% were increasing in their abundance and occupancy, 42.6% were declining, and only 10.7% demonstrated opposite changes in abundance and occupancy (e.g., an increase in occupancy and a decrease in abundance). The ratio of change between abundance and occupancy, as estimated by the regression coefficient, was approximately 1:6, that is, a 1% change in abundance was associated with a 6% change in occupancy throughout the state (on the transformed scales).

Only woodland birds demonstrated a significant increase in occupancy between the two atlas periods ($n = 53$, mean = 0.18, $t = 3.51$, $P < 0.001$) while grassland birds showed the only significant decrease in occupancy ($n = 11$, mean = -0.33, $t = -3.58$, $P < 0.001$) (Fig. 6). Within migratory guilds, only resident species showed a significant increase in occupancy ($n = 16$, mean = 0.30, $t = 2.54$, $P = 0.013$) (Fig. 7). Neotropical migrants ($n = 45$, mean = 0.006, $t = 1.5$, $P = 0.14$) and

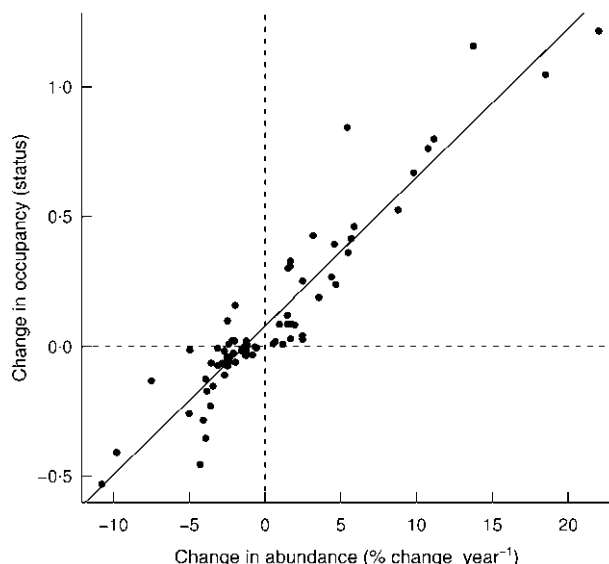


Fig. 5. Between 1980 and 2005, changes in occupancy (status) were highly correlated with trend estimates in abundance for 75 species demonstrating a significant ($P < 0.10$) change in their abundance in New York State. For most species, changes in occupancy were paralleled by changes in abundance, both in the direction and magnitude of change. Species of increasing relative abundance showed a comparable increase in occupancy and species of declining abundance showed a decline in occupancy.

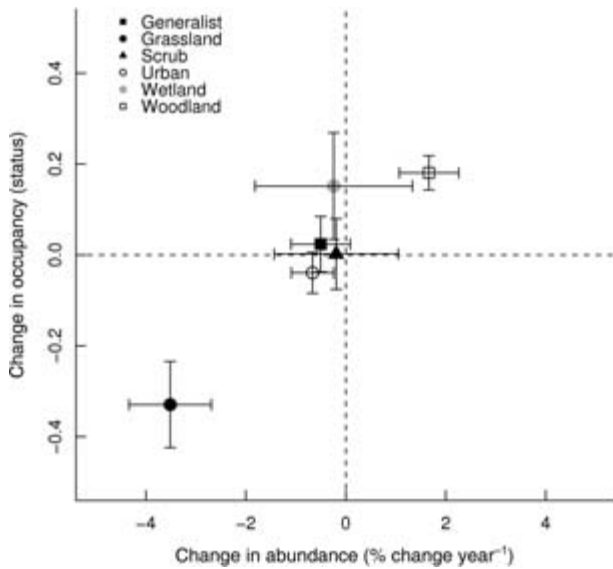


Fig. 6. Mean changes in occupancy (status) and abundance (percentage year⁻¹) for breeding habitat groups between 1980 and 2005. Woodland birds were the only group to increase in their occupancy while grassland birds demonstrated a significant decline. Trends in occupancy for entire habitat assemblages were mirrored by changes in abundance. Standard error bars are shown.

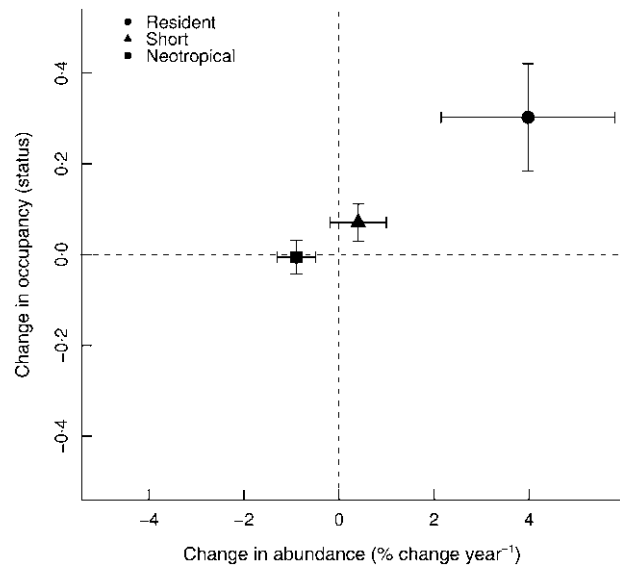


Fig. 7. Mean changes in occupancy (status) and abundance (percentage year⁻¹) for migratory groups between 1980 and 2005 in New York State. Resident birds showed the greatest increase in occupancy and abundance. Overall, trends in occupancy for entire habitat assemblages were mirrored by changes in abundance. Standard error bars are shown.

short-distance migrants ($n = 59$, mean = 0.07, $t = -1.23$, $P = 0.22$) showed no significant changes in occupancy. For both ANCOVA models, changes in the occupancy were highly correlated with changes in abundance for breeding habitat groups ($F_{5,120} = 280.4$, $P < 0.001$) and migratory status ($F_{2,120} = 244.0$, $P < 0.001$).

Species of low initial abundance during the first atlas period were the most likely to demonstrate significant

changes in their occupancy (Fig. 8). The relative number of blocks where a species was recorded in the first but not the second atlas (loss) was negatively correlated with its initial abundance ($n = 98$, $\beta = -0.20 \pm 0.028\text{SE}$, $t = -7.08$, $P < 0.001$, $R^2 = 0.34$). In addition, the relative number of blocks where a species was recorded in the second but not the first atlas (gain) was also negatively correlated with its initial abundance ($n = 98$, $\beta = -0.26 \pm 0.02\text{SE}$, $t = -12.72$, $P < 0.001$, $R^2 = 0.62$).

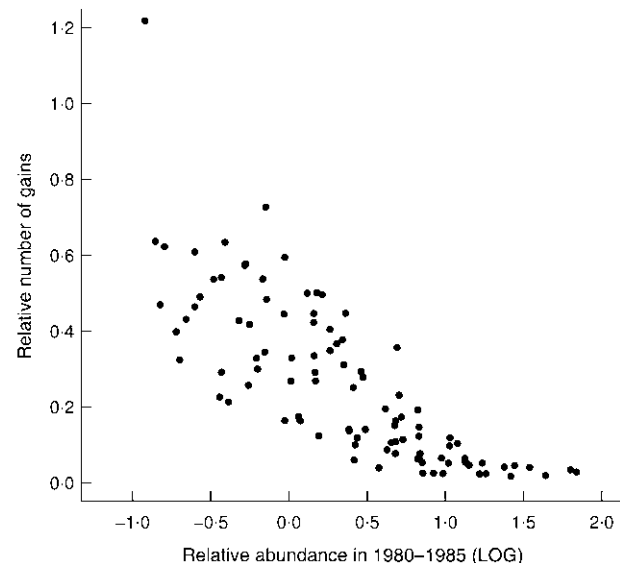
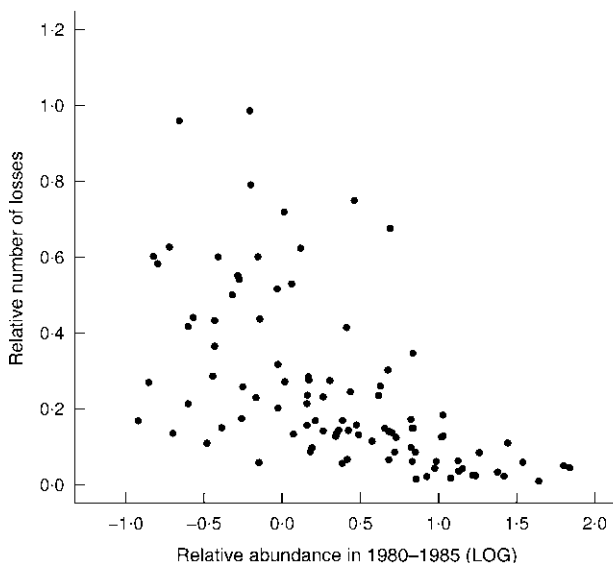


Fig. 8. The relative number of block losses and gains were higher in species of low initial abundance in New York State. Species of initial low abundance demonstrated the largest changes in relative block losses and gains between the two atlases.

Discussion

INTERSPECIFIC AND INTRASPECIFIC PATTERNS

Most species in this analysis conformed to the predictions of the abundance–occupancy rule as species with relatively high abundance throughout the region were also those of high occupancy. This pattern was the same in both time periods, emphasizing the temporal stability of this relationship over two decades of change (Gaston, Blackburn & Gregory 1997a; Blackburn *et al.* 1998; Hurlbert & White 2007). In a review of abundance–occupancy relationships in multiple species and ecological systems, Blackburn *et al.* (2006) found that the form and strength of interspecific abundance–occupancy relationships to vary considerably, and that this variability was likely affected by dispersal capabilities and to be weakest in more fragmented systems. We found these relationships to be notably consistent among breeding habitat groups and migratory guilds. This positive relationship was a general characteristic of species despite their varying habitat requirements. Interestingly, the only groups demonstrating a statistically different relationship between abundance and occupancy, in terms of their slopes, were species associated with spatially discontinuous habitats such as grassland, scrub-successional, and wetlands. However, although the slopes of the relationship between abundance and occupancy between these groups were significantly different, the positive relationship remained consistent.

The applicability of occupancy data for assessing population dynamics relates to its concurrence and accuracy in describing temporal changes in local abundance. Although species showed a wide degree of change in occupancy between the two atlases, common species remained common while rare species remained rare. This type of temporal concordance in multispecies examinations of abundance and occupancy has been found in other studies (Blackburn *et al.* 1998; Webb *et al.* 2007). As predicted by the intraspecific abundance–occupancy relationship, most species demonstrating a significant change in their local abundance also demonstrated a comparable change in their regional occupancy. Although past studies have used occupancy to estimate abundance (e.g., He & Gaston 2000), we agree with Holt & Gaston (2003) that causality lies in the effects of abundance on patterns of occupancy (Holt *et al.* 1997; Freckleton, Noble & Webb 2006). Like the filling of an ice cube tray, the mechanism driving the filling of atlas blocks appears to be changes in local abundance, and as such, an increase in local abundance over time will likely drive an overall increase in regional occupancy. The likelihood of this mechanism is supported by the relatively large amount of variance in the occupancy data that are attributable to changes in local abundance (58–88%), a pattern that is unusually robust compared to other ecological studies (Møller & Jennions 2002; Blackburn *et al.* 2006).

Over the 20-year interval, several species demonstrated a lack of concurrence between changes in occupancy and abundance that may be a consequence of population dynamics occurring at two different resolutions. Among species show-

ing a lack of agreement in occupancy and abundance, 22 of 24 showed a negative trend in abundance and an increase in occupancy. For example, the black-throated blue warbler, *Dendroica caerulescens* (Gmelin 1789), showed a large increase in occupancy of 10.4% but a declining abundance trend of -2.48% year⁻¹. In general, these negative abundance trends were slight and ranged from -0.2% year⁻¹ to -2.5% year⁻¹. Regression analysis produced a slope of 6.04, suggesting that an abundance trend estimate of 1% year⁻¹ manifested itself as an average distributional change of 6%. This slope value is important because it may be an indication of the distribution of habitat suitability throughout the region. Freckleton *et al.* (2006) developed a simple modelling framework relating local abundance, regional occupancy and habitat connectivity. They found that when the slope of the abundance–occupancy relationship was greater than 1, changes in large-scale distributions are highly dependent on local-scale processes due to the non-uniform distribution of habitat. This may be the case in our study system as environmental stressors and resource availability may be occurring at different spatial scales. For example, range-wide stresses, such as climate change or acid precipitation may be driving occupancy changes, and site-specific changes such as habitat loss may be influencing local abundance.

Initial abundance was an important predictor of changes in occupancy of New York State birds during this time period. Rarity has long been considered to portend extinction (Darwin 1859), and an implication of the abundance–occupancy rule is that species of declining abundance and occupancy face ‘double jeopardy’ (Lawton 1993, 1996a,b). In these cases, low abundance increases the likelihood of stochastic extinction, while limited regional occupancy increases the likelihood that the few remaining populations may be influenced by similar environmental stressors (Gaston *et al.* 2000; Hanksi 2000). We found that species of low initial abundance were more likely to demonstrate a higher number of block losses than species of high initial abundance. Although relative losses and gains will generally be greater for low than for high occupancy species, this trend supports the importance of low abundance in identifying species in danger of range contractions. Species showing the highest number of relative block losses between the two atlases (e.g., grasshopper sparrow, *Ammodramus savannarum* [Gmelin 1789], 822 to 477 atlas blocks) tended to be species of relatively low abundance in New York State. Conversely, species showing the highest number of relative block gains in the second atlas (e.g., pine warbler, *Dendroica pinus* [A. Wilson 1911], 348 to 1113 atlas blocks) also tended to be of relatively low abundance during the first atlas. In this case, the term ‘double trouble’ (Gaston 1999) accurately captures the potential of increasing species, such as the Canada goose, *Branta canadensis* (Linn 1758), to simultaneously dominate local and regional communities. This increased variance in regional occupancy in low density species has been found in other studies, suggesting that species occurring at higher densities may have lower extinction rates and increased occupancy of less favourable habitat (Freckleton *et al.* 2006; Hurlbert & White 2007).

It appears that changes in the occupancy of these groups are a reflection of increasing resource availability. Resources are comprised of a shifting mosaic of habitat types being driven by a 50-year decline in agricultural land and farmland abandonment (Whitney 1994). Consistent with this trend, woodland birds showed the greatest overall increase in abundance and regional occupancy while grassland birds continue a decline that is being observed throughout the north-eastern USA (Askins 1993, Dettmers 2003). Other geographical regions throughout the world have documented this pattern of increasing woodland species and declining grassland or heathland species, although the causes of these changes are undoubtedly different (e.g., shifting agricultural practices in Britain) (Chamberlain & Fuller 2001; Van Turnhout *et al.* 2007). Climate change may also be a cause for the increasing distributions of resident birds. One might expect warmer winters to lead to declining distributions of long-distance migrants if those conditions favour resident birds which, in turn, impose increasing competitive pressure on migrants (O'Connor 1990; Böhning-Gaese & Lemoine 2004).

Conclusions

The study of large-scale population dynamics requires that we understand the consistency and stability of abundance–occupancy relationships for multiple species and in various geographical regions (Gaston 1999; Gaston *et al.* 2000; Blackburn *et al.* 2006; Freckleton *et al.* 2006; Gaston 2006). Despite a growing interest in the interplay of local abundance and regional occupancy, most studies on the subject have been confined to Britain because this is one of the few regions in the world that have distributional data collected for various species in different time periods (Gaston *et al.* 2000). Our findings broaden support for the strength of abundance–occupancy relationships that have been tested elsewhere and provide further evidence on the temporal stability of these relationships over two decades of regional population change. The consistency of these relationships in species of different life-history characteristics emphasize the common mechanisms linking changes in abundance and occupancy dynamics (Freckleton *et al.* 2006). It is this common mechanism that provides further support for the role of resource availability (e.g., regional reforestation) and environmental change (e.g., climate change) in effecting local and regional population dynamics. Environmental phenomena such as climate change, shifting land-use practices, and human overpopulation will demand unprecedented and large-scale investigations of population dynamics in the future (Gaston 2006). Given these threats, there will be an increasing reliance on occupancy data, and its relationship with local abundance, for describing population dynamics.

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