

# Abundance–occupancy relationships

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## Summary

1. The abundance and distribution of species tend to be linked, such that species declining in abundance often tend also to show declines in the number of sites they occupy, while species increasing in abundance tend also to be increasing in occupancy. Therefore, intraspecific abundance–occupancy relationships are commonly positive.
2. The intraspecific pattern is mirrored by more general positive interspecific abundance–occupancy relationships: widespread species tend to be abundant, and narrowly distributed species rare.
3. Here, we review recent research on these patterns based on the flora and fauna of the British Isles. We assess their generality, describe what is currently known about their structure, and summarize the results of tests of the several hypotheses proposed to explain their existence.
4. The positive form generally exhibited by abundance–occupancy relationships, intraspecific or interspecific, has consequences for several areas of applied ecology, including conservation, harvesting, biological invasions and biodiversity inventorying. These implications are discussed briefly.

*Key-words:* abundance, density, distribution, macroecology, occupancy, range size.

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## Introduction

‘... distribution and abundance are but the obverse and reverse aspects of the same problem’ (Andre-wartha & Birch 1954, p.5).

The fauna and flora of the Earth are undergoing a spate of extinctions, with a rate of species loss estimated to be orders of magnitude greater than that of background rates in the fossil record (May, Lawton & Stork 1995). This fact has been widely lamented (Wilson 1988b, 1992). Yet, extinction is merely the end of the path of decline. The increasing numbers of species that have gone, or are in the process of going, extinct are simply the most obvious manifestation of the general malaise affecting ecosystems world-wide. The decline and loss of populations represent potentially more insidious erosions of bio-

diversity (Ehrlich & Daily 1993; Ehrlich 1994; Hughes, Daily & Ehrlich 1997). Thus, for every extant species of bird considered to be critically at risk of extinction, there are another five considered to be threatened (endangered or vulnerable), and nine considered to be near-threatened or conservation-dependent (Collar, Crosby & Stattersfield 1994). Indeed, the roll-call of assemblages known or suspected to be experiencing marked declines grows progressively longer, embracing concerns about, for example, trees (Oldfield, Lusty & MacKinven 1998), fungi (Jaenike 1991), fish (Manire & Gruber 1990; Moyle & Williams 1990; Frissell 1993; Bruton 1995), amphibians (Blaustein & Wake 1990; Wake 1991), birds (Robbins *et al.* 1989; Terborgh 1989; Hill & Hagan 1991; Noon & Young 1991; Hagan & Johnston 1992) and mammals (Cole, Reeder & Wilson 1994). Extinction is the tip of an iceberg of population declines.

In Britain, some of the severest changes have been suffered by species associated with farmland. Most obviously, between the late 1960s and the 1990s, many species of lowland farmland birds have

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become less widespread, have declined in numbers, or both (Gates *et al.* 1994; Fuller *et al.* 1995; Gillings & Fuller 1998; Siriwardena *et al.* 1998, 2000; Chamberlain *et al.* 2000; Henderson *et al.* 2000). For example, the range sizes of the ciril bunting *Emberiza cirilus* and corncrake *Crex crex* in Britain declined by more than 75% over the years 1970–90. The breeding population sizes on farmland of the corn bunting *Miliaria calandra* and tree sparrow *Passer montanus* declined by similar proportions in the same period (Fuller *et al.* 1995; Brickle *et al.* 2000).

The declines in range size or population abundance suffered by individual species would be cause enough for concern if they occurred separately. However, more often than not, the two are associated. Many species have experienced not only a contraction of range size, but also a decline in density at those sites at which they have continued to persist (see below for references). This is more than simply to state that the abundance and occupancy of a species covary. That would scarcely be surprising, given that the loss of territory will almost invariably entail the loss of individuals. Rather, it is to say something more profound. If, as the range of a species contracts, it also declines in average density across the sites at which it remains, this means that there is a proportionately greater loss of individuals than would be predicted as a result simply of range reduction. The reciprocal also seems to be true: increases in range size are often accompanied by a greater increase in population size than would be predicted as a result simply of range expansion (i.e. the average density at occupied sites increases). This association between density and occupancy means that species commonly exhibit positive intraspecific abundance–occupancy relationships.

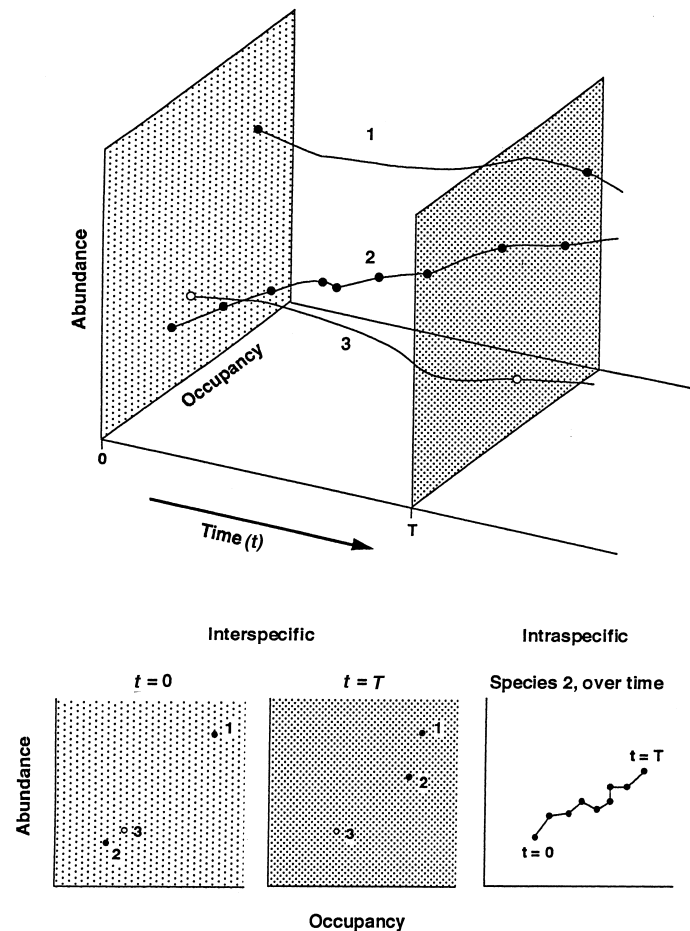
Even species with relatively stable populations will tend to show variation in abundance and occupancy over time. If this variation causes individual species to shift their positions along positive intraspecific abundance–occupancy relationships, and if these relationships are sufficiently bounded, then one might expect that positive *interspecific* abundance–occupancy relationships will also exist. There is ample evidence that these occur widely (Gaston 1996a). Indeed, this may be one of the most general patterns in ecology.

In this paper, we review the current state of knowledge about regional scale abundance–occupancy relationships, both intraspecific and interspecific, and their determinants, and call attention to some of their practical implications (see also Caldow & Racey 2000; Ormerod & Watkinson 2000). We draw particularly on our own recent published studies of these patterns for the flora and fauna of Britain. These constitute the most comprehensive set of such analyses conducted to date. In so doing, we have two goals. First, we aim to extract the essential messages from this extensive work, particularly where these

have some applied consequences. The existence of abundance–occupancy relationships, and their wide relevance, have remained remarkably poorly acknowledged in some quarters. Secondly, we aim to highlight the insights that may usefully result from consideration of the broad perspective that macroecological patterns offer, ignoring the, often difficult to obtain, details of the dynamics and biologies of individual species (Lawton 1993, 1995, 1996a, 1999; Gaston 1994a; Brown 1995; Brown, Mehlman & Stevens 1995; Gaston & Blackburn 1995, 1996a, 1999; Maurer 1999). This approach is complementary to the more common species-by-species one.

Throughout, unless otherwise specified, we use the following standardizations. (i) The relationships discussed concern densities averaged across occupied sites only. The areas of occupancy of species (*sensu* Gaston 1991, 1994b) are expressed in terms of the number of sites at, or areas in, which they are found to occur. (ii) Intraspecific abundance–occupancy relationships concern time-series data of the covariation of local abundance and regional occurrence: each point on an intraspecific relationship refers to density and occupancy at a different time. (iii) Interspecific abundance–occupancy relationships concern local abundances and regional occurrences of species, either at a given time or averaged across time. Imagine species moving through a three-dimensional space with axes of local abundance, occupancy and time (Fig. 1). Intraspecific abundance–occupancy relationships chart the movement of individual species in this space as it would appear if the time axis ran directly away from (or towards) the observer. Interspecific relationships chart the position of all species in this space in a slice taken perpendicular to the time axis (their position averaged over some relatively short time period). (iv) Interspecific relationships concern assemblages of reasonably closely related species. Although we can provide no unambiguous definition of the degree of relatedness appropriate to such assemblages, examples include those composed of vascular plants, moths, birds or mammals. Comparisons between such assemblages may be illuminating, but plots combining them are more than likely not.

Many of the analyses summarized here concern data from the British Trust for Ornithology (BTO) Common Birds Census (CBC). The CBC constitutes the main scheme by which the breeding populations of common British birds have been monitored, where ‘common’ refers to species with breeding populations of more than about 100 000 pairs. The census technique involves repeated visits by an observer to a defined site (or ‘plot’) during the breeding season (March–July). The observer maps the positions of all species encountered during visits, and these maps are analysed by BTO staff to give estimates of the number of pairs of each species breeding on the plot. Further details are provided



**Fig. 1.** A diagrammatic representation of the association between interspecific and intraspecific abundance–occupancy relationships. The trajectories of three species (1, 2 and 3) through abundance–occupancy space are plotted over time. Species 1 and 3 change little in either abundance or occupancy, but species 2 shows concurrent increases in both. The change in abundance and occupancy shown by species 2 is revealed by comparison of the temporal snapshots provided by the two interspecific relationships, and by its intraspecific abundance–occupancy relationship.

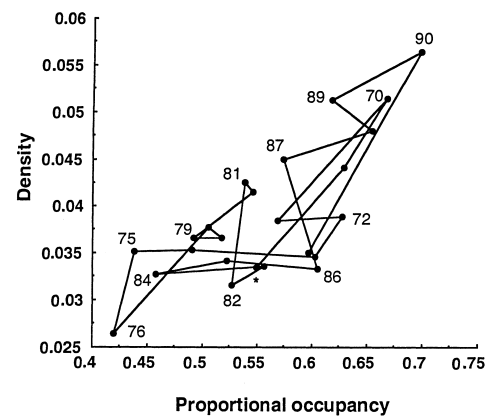
by Marchant *et al.* (1990) while other large-scale work by the BTO is described in this issue (Baillie *et al.* 2000; Paradis *et al.* 2000). Census sites are defined on the basis of the habitat they encompass. We have analysed separately those based on farmland or in woodland; species abundances are not directly comparable between the two. References to woodland or farmland birds or sites concern analyses based on these data.

### Intraspecific abundance–occupancy relationships

#### WHAT IS THE RELATIONSHIP?

Positive intraspecific relationships between abundance and occupancy (Fig. 2), or evidence suggestive of such relationships, have been documented by a number of studies. These include investigations of plants (Boecken & Shachak 1998), butterflies (Polar, Moss & Yates 1995; van Swaay 1995), fish (Winters & Wheeler 1985; Crecco & Overholtz 1990; MacCall 1990; Rose & Leggett 1991; Swain & Wade

1993; Swain & Sinclair 1994) and birds (Gibbons, Reid & Chapman 1993; Smith *et al.* 1993; Ambrose 1994; Tucker & Heath 1994; Fuller *et al.* 1995;



**Fig. 2.** The relationship between abundance and occupancy for the chiffchaff *Phylloscopus collybita* on farmland CBC sites between 1968 and 1991. 1968 is indicated by an asterisk.

Hinsley *et al.* 1996; Cade & Woods 1997; Gaston, Blackburn & Lawton 1997; Newton 1997; Blackburn *et al.* 1998; Donald & Fuller 1998; Gaston & Curnutt 1998; Gaston, Blackburn & Gregory 1998; Venier & Fahrig 1998; Telleria & Santos 1999).

There are also some clear counter-examples, where positive intraspecific abundance–occupancy relationships do not pertain (plants: Boecken & Shachak 1998; fish: Marshall & Frank 1994; Swain & Morin 1996; birds: Ambrose 1994; Blackburn *et al.* 1998; Donald & Fuller 1998; Gaston & Curnutt 1998; Gaston, Blackburn & Gregory 1998). In the literature at least, these are reasonably scarce, although the extent to which this reflects a publication bias is unclear (they are typically noted in the context of reports of positive relationships).

The only attempt to determine the frequency of positive relationships amongst a reasonably large assemblage of species has been for breeding birds in Britain, using data derived from the CBC over a 24-year period. Of 75 bird species occurring on farmland sites, 69% exhibited positive relationships, and 40% exhibited relationships that were both positive and statistically significant (Blackburn *et al.* 1998). Of 56 bird species occurring on woodland sites, these proportions were 55% and 18%, respectively. Overall, around 6% of intraspecific relationships were significantly negative. Donald & Fuller (1998) found that 18 of 57 British bird species had shown range and population size changes in opposite directions over this same time period, although their measure of range change in each case was based on comparison of only two values (species distributions given by Sharrock 1976 and Gibbons, Reid & Chapman 1993). A related analysis tested for intraspecific abundance–occupancy relationships in 20 species of forest songbirds censused in north-western Ontario, Canada (Venier & Fahrig 1998). All of these relationships were positive, and 16 (80%) were significant. However, these differ from the standard way of plotting intraspecific relationships in that each data point refers to abundance and occupancy of sites in different landscapes, rather than in the same landscape at different times (see the Introduction).

Plainly, published studies reveal that significant, positive, intraspecific relationships are far from universal. However, for many of the species in these data sets and others, failures to find significant abundance–occupancy relationships may in part reflect the comparatively narrow range of variation that has been observed in either variable; local abundances and geographical distributions may be quite stable over long periods.

#### ANATOMY OF INTRASPECIFIC ABUNDANCE–OCCUPANCY RELATIONSHIPS

Beyond the fact that most intraspecific abundance–occupancy relationships tend to be positive, rather

little is known about their essential anatomy or structure. Most studies report whether positive relationships exist, but they do not take the logical next step and examine details of the form of such relationships. This is a common problem with macroecological patterns, although structural details may form an important link between pattern and mechanism (Gaston & Blackburn 1999). Most such information in the literature on intraspecific abundance–occupancy relationships derives from recent studies of birds in Britain. However, even here few analyses have been performed. Some isolated observations are as follows.

(i) Because they may often be quite weak, positive intraspecific abundance–occupancy relationships do not necessarily imply that year-to-year changes in abundance and occupancy are themselves always positively correlated. Increases in density from one year to the next can be associated with either increases or decreases in occupancy (Fig. 2). For six species of passerines occupying farmland and woodland CBC sites, Gaston, Gregory & Blackburn (1999) counted the number of between-year transitions in density and occupancy that followed the pattern that would be expected if the two were positively linked (e.g. the number of times that an increase in density between years  $t$  and  $t+1$  was accompanied by an increase in occupancy between those years, or a decrease was associated with a decrease). These analyses showed that most intraspecific year-to-year variation in abundance and occupancy followed a random pattern. If the occupancy of a species increased from one year to the next, its abundance would as likely as not decrease. The single exception was the great tit *Parus major* on farmland sites, for which there were significantly fewer increase–increase or decrease–decrease transitions than expected by chance – opposite to prediction. However, the pattern in the frequency with which changes in abundance and occupancy between years are associated as expected from a positive abundance–occupancy relationship (Gaston, Gregory & Blackburn 1999) is confounded by differences in the strength of the abundance–occupancy relationships for these six species on woodland and farmland; the relationships are always significantly positive on farmland, but never so in woodland. The farmland relationships show a significantly greater number of changes in abundance and occupancy between years in the expected direction than do the woodland relationships (paired  $t$ -test:  $t = 2.65$ , d.f. = 5,  $P = 0.045$ ). Thus, significant positive intraspecific abundance–occupancy relationships are associated with more linked changes in abundance and occupancy (increase with increase, decrease with decrease) between years than are non-significant relationships.

(ii) The association between the strength of positive abundance–occupancy relationships and the

pattern of year-to-year changes in abundance and occupancy is further reflected in an additional association with temporal trends in these variables. The British bird data show that the strength of intraspecific relationships on farmland is related to whether or not a species exhibits temporal trends in density, with the strongest relationships found in species with simultaneous trends in both density and occupancy (Gaston, Blackburn & Gregory 1998). In contrast, and counterintuitively, there is inconsistent support for a similar effect of the range of densities or occupancies.

This outcome may arise because temporal trends in density and occupancy strengthen the mechanistic interaction between the two. For example, if average local densities fluctuate essentially randomly from year to year, then any interaction with occupancy may not be particularly obvious, even if it occurred. This is because there is likely to be a time lag between, say, a drop in overall density and the loss of the species from sites. Evidence for such lags in two British bird species was noted by Hinsley *et al.* (1996). If overall densities recover sufficiently rapidly, levels of occupancy may scarcely fluctuate at all, and not necessarily in direct synchrony. No positive intraspecific abundance–occupancy relationship will result. In contrast, if there is, say, a steady decline in overall densities, the concomitant extinction at local sites is more likely to be realized, albeit after some lag. In this case a positive intraspecific abundance–occupancy relationship will be observed. This idea may also explain why an equivalent association is not seen in woodland CBC sites; many farmland bird species are undergoing significant population declines not mirrored in woodland. As temporal trends in abundance and occupancy in woodland are not so marked, their association with the form of abundance–occupancy relationships may be obscured (Gaston, Blackburn & Gregory 1998).

(iii) British bird data also show that the strength of intraspecific abundance–occupancy relationships seems to be related to the mean occupancy of species: widespread species tend to show stronger relationships. The most probable reason is that when the levels of occupancy attained by a species are high, it is more likely to increase its abundance further by increasing its density than its occupancy because it is difficult for individuals to find the few remaining vacant areas. A positive intraspecific density–occupancy relationship will tend to result (Gaston, Blackburn & Gregory 1998). Species that occupy a small range can adjust to a change in total numbers either by increasing occupancy or total density.

(iv) Underlying the intraspecific abundance–occupancy relationship is a general tendency for individual species to remain abundant or rare at individual sites from year to year (Lawton & Gaston

1989; Bengtsson 1994; Gaston 1994a; although see Bengtsson, Baillie & Lawton 1997). Blackburn *et al.* (1998) examined the concordance of bird species abundances on farmland and in woodland over the period 1968–91. There was significant concordance in both habitats: bird species that were abundant or rare on farmland sites tended to remain so, and likewise for woodland sites. Although concordance does generally decrease over time, this decrease is slow enough that concordance will remain high over many decades (Bengtsson, Baillie & Lawton 1997). High concordance may in part contribute to the tendency for a reasonable proportion of intraspecific abundance–occupancy relationships to appear non-significant: if abundances are not changing sufficiently to disrupt species rank order with respect to them, they may not be varying sufficiently for significant abundance–occupancy relationships to arise (although it is the actual change in abundances that may determine significance, not whether or not it is great enough to disrupt species' rank orders).

#### WHY ARE ABUNDANCE AND OCCUPANCY LINKED WITHIN SPECIES?

Studies to date on the anatomy of abundance–occupancy relationships suggest reasons why these should be more evident among some species than others (i.e. time trends, mean occupancy) but do not explain why these two variables should be linked in the first place. In the extreme, positive intraspecific abundance–occupancy relationships are almost inevitable. Ultimately, there are limits to the area over which a species can spread, and as it approaches or reaches these limits the overall population can increase only if local densities increase. Conversely, as the overall population decreases, in the limit the extent of occurrence must also decline because fractions of individuals cannot be distributed across the landscape to maintain the pattern of occupancy. For many species the extent of between-year variation in local densities may be insufficient for these limiting cases to be of much importance. It therefore becomes less obvious why local abundance and regional distribution should be associated.

Seven mechanisms can be postulated as possible determinants of positive intraspecific relationships between abundance and occupancy where they do occur, although most of these have been discussed primarily in the context of interspecific relationships (for references see Gaston, Blackburn & Lawton 1997). These can be classified very broadly as statistical, range position, resource, and population dynamic explanations, although they are not necessarily mutually exclusive or even independent (some may simply constitute different levels of explanation from others).

*(i) Statistical explanations*

The first explanation for positive intraspecific abundance–occupancy relationships that needs to be considered is that they do not actually exist, but are instead an artefact of inadequate data. If levels of sampling effort are insufficient, then a species will tend to be recorded from fewer localities when it occurs at low densities than when it occurs at high ones, even if it actually remains equally widely distributed. If census data were of sufficient quality, there would be no pattern to explain.

This seems highly unlikely as an explanation of observed patterns in their entirety. One of the advantages of using data on British birds is that the abundances and distributions of these species are so well known. Moreover, the hypothesis makes two predictions. First, for species showing no intraspecific abundance–occupancy relationship census data should be of higher quality than for species showing a positive one. There is no evidence that this is the case. For example, we do not see how the same farmland observers should census the shy jay *Garrulus glandarius* (L.) so accurately (no significant abundance–occupancy relationship) but its conspicuous relative the magpie *Pica pica* (L.) so poorly (strong significant positive abundance–occupancy relationship). Secondly, the strongest intraspecific abundance–occupancy relationships should be observed for species that generally occur at low densities, and are therefore disproportionately likely to be overlooked at any given site. Again, there is no evidence that this is the case, there being no significant correlations between the strength of relationships and mean density for species in either farmland or woodland habitats (Gaston, Blackburn & Gregory 1998).

Turning from patterns of occupancy revealed by sampling to the real underlying patterns of occupancy, positive intraspecific relationships between abundance and occupancy are expected from very many statistical distributions of individuals across landscapes, including Poisson distributions and highly aggregated ones such as the negative binomial (Wright 1991; Hartley 1998). The distributions of individuals of bird species do not tend to be described by a Poisson model (Hinsley *et al.* 1996; Venier & Fahrig 1998) but rather are aggregated in space in the same way as most other animal species (Taylor, Woiwod & Perry 1978, 1979; McArdle, Gaston & Lawton 1990). Presumably, different intraspecific abundance–occupancy relationships might arise as a consequence of different patterns of variation in aggregation across species, and differences in the nature of the aggregation with density. However, the extent to which this is strictly a mechanism for abundance–occupancy relationships, rather than essentially a restatement of the relationship in another form, is questionable (Gaston,

Blackburn & Lawton 1998). If we accept that spatial aggregation determines abundance–occupancy relationships, then logically we must seek mechanistic explanations for patterns in the spatial aggregation of species (and hence, by implication, the abundance–occupancy correlation). Unfortunately, the patterns and determinants of aggregation are generally poorly understood, particularly at the large (geographical) scales of relevance to most observed abundance–occupancy relationships (for discussion see Perry 1988; McArdle & Gaston 1995). To argue that spatial aggregation explains abundance–occupancy relationships is simply to supplant one poorly understood pattern with another.

*(ii) Range position explanations*

Abundances and patch occupancy are widely believed, on average, to decline towards the edge of the geographical range of a species (Shelford 1911; Kendeigh 1974; Hengeveld, Kooijman & Taillie 1979; Hengeveld & Haeck 1981; Brown 1984; Lawton 1993; Safriel, Volis & Kark 1994). This being so, as the spatial position of the range edge shifts through time, the levels of abundance and occupancy within a region might potentially be seen to rise and fall in broad synchrony, as these become more or less typical of the core (or periphery) of the range.

A prediction of the range position model is that positive abundance–occupancy relationships should be shown more often in those species for which the position of a region is changing most markedly with respect to its wider geographical range, as the distribution of the species either expands or contracts. This is supported by the tendency for stronger abundance–occupancy relationships to be observed in species undergoing temporal trends in both density and occupancy. These trends would be expected as the range edge of a species approached or receded from the sites at which these variables were censused.

Other patterns provide less support for the range position hypothesis. First, while the majority of British bird species show significant positive abundance–occupancy relationships, only a small minority are undergoing changes in distribution that are sufficient to alter significantly the position of Britain with respect to their wider geographical range. Secondly, it is not at all clear that declines in abundance and occupancy towards range limits are general features of species' distributions: while some studies claim to have shown this pattern (McClure & Price 1976; Hengeveld & Haeck 1981, 1982; Brown 1984; Bart & Klosiewski 1989; Svensson 1992; Tellería & Santos 1993; Maurer 1994; Brown, Mehlman & Stevens 1995; Curnutt, Pimm & Maurer 1996), others have not (Rapoport 1982; Brussard 1984; Carter & Prince 1985; Wiens 1989). Of parti-

cular relevance here, Blackburn *et al.* (1999) failed to find evidence that abundance declines towards the range edge in Britain for most of the 32 species of passerine birds they examined. There are several methodological reasons why no such relationships might be forthcoming in these data (Blackburn *et al.* 1999), but their absence is equally likely to be genuine. That is not to say, however, that these species do not become rarer in other terms towards their range edges in Britain. They may, for example, be more patchily distributed close to edges, but attain average densities in those patches that they do occupy (see also Carter & Prince 1985, 1988). Nevertheless, if densities do not, on average, decline towards range limits in British birds, the range position mechanism is unlikely to produce a positive density–occupancy relationship.

Finally, the range position hypothesis unnecessarily raises the question of why abundance and occupancy decline towards range limits.

### (iii) Resource explanations

A positive intraspecific abundance–occupancy relationship could arise if there were temporal variation in the amount of resources available to a species. Year-to-year variation in food supply, for example through the effects of weather conditions on insect or fruit production, could cause concomitant variations in the distribution and abundance of many British farmland or woodland bird species. This variation could be either in the abundance ('resource availability'; Hanski, Kouki & Halkka 1993; Gaston, Blackburn & Lawton 1997) or the variety ('niche breadth'; Brown 1984) of resources utilized. Species showing no significant abundance–occupancy relationship may then be those utilizing relatively invariant resources, or that are able to switch between resources.

The distribution and abundance of all species are obviously affected by resources. Synchronous population cycles of specialist predators (or those of restricted diet) and their prey, for example, clearly demonstrate how the availability of a resource can affect the population of a species dependent on it. We know of no case, however, where an abundance–occupancy relationship has been plotted for a species showing such resource-driven population dynamics. Venier & Fahrig (1998) claim that their study of intraspecific abundance–occupancy relationships of birds in Canada provides support for this mechanism. Recall that each point in their intraspecific plots refers to abundance and distribution in a different landscape. They argue that, as a result, the positive relationships they observe are likely to be consequences of variation in aspects of the habitat, not of the species. The most obvious candidate is resource availability. Nevertheless, there are many other factors that can vary between landscapes (e.g. density-

dependent habitat selection, habitat connectivity), so landscape differences in abundance and distribution alone provide no evidence for the primacy of explanations based on resource availability.

Although the resource availability hypothesis is intuitively appealing, unequivocal tests will be difficult to conduct. There are many components to the resource requirements of an individual species, and these will be hard to combine to provide a measure of resource availability that is meaningful and comparable between time periods (or landscapes). In addition, with so many niche axes along which species may be varying, any test may simply fail to measure the relevant ones (Colwell & Futuyma 1971). This is especially true for migrant species, for which abundance and distribution may be affected by factors changing outside the focal region. In short, we are aware of no study that demonstrates that a positive intraspecific abundance–distribution relationship results from variation in the resources available to the species.

A second resource-based explanation derives from the ideas of habitat selection. It has long been known that some species exhibit density-dependent habitat selection (driven through intraspecific competition), occupying more habitats when densities are high and less when they are low (Kluyver & Tinbergen 1953; Fretwell & Lucas 1970; for a review see Rosenzweig 1991). Such patterns have been observed for a number of British birds (O'Connor 1987). This can give rise to positive intraspecific abundance–occupancy relationships, as explored, with particular regard to marine fish, in MacCall's (1990) basin model (see also Newton 1997; Gregory 1998).

While it is evident that such a mechanism could be important at relatively moderate spatial scales, recent work suggests that it is unlikely to operate at large ones. Tyler & Hargrove (1997), using simulation models, explored the likely validity of ideal free distributions as predictors of species occurrence over large areas. They found that predictions were poor when resources had a fractal rather than a random distribution, and when the scale at which distributions were measured was dissimilar to the maximum movement distance of foragers. This may make it unlikely that ideal free distributions will be appropriate in the circumstances with which we are primarily concerned here, although individuals of many species of birds move sufficient distances in Britain that they are likely to be able to distribute themselves effectively into areas that are unoccupied or occupied at relatively low densities (Paradis *et al.* 1998). Additionally, Tyler & Hargrove (1997) point out that while they may meet some of the assumptions and predictions of ideal free distributions, studies that have marshalled support for the basin model have seldom, if ever, shown fit to the assumption that *per capita* gains or other measures of fitness are affected

by increases in density. However, it remains an open question to what extent, without strict adherence to an ideal free distribution, some form of even approximately density-dependent habitat selection can generate abundance–occupancy relationships.

In sum, while resource issues seem likely to play a role in the determination of intraspecific abundance–occupancy relationships, at present the manner in which they do so remains unclear.

(iv) *Population dynamic explanations*

Alternative explanations for abundance–occupancy relationships have been framed in terms of population dynamic constructs other than the ideal free distribution. In particular, a positive relationship is a prediction of metapopulation structures of the form of the rescue effect hypothesis (Hanski 1991a, 1991b; Gyllenberg & Hanski 1992; Hanski & Gyllenberg 1993; Hanski, Kouki & Halkka 1993). This assumes that immigration decreases the probability of a local population going extinct (the rescue effect; Brown & Kodric-Brown 1977) and that the rate of immigration per patch increases as the proportion of patches that are occupied increases. Here, for many parameter values, a positive relationship between local abundance and number of occupied patches can result.

The significance of such a mechanism rests fundamentally on whether or not species exhibit metapopulation dynamics of an appropriate form. This mechanism seems unlikely to be the most frequent explanation for positive abundance–range size relationships given our present understanding of the proportions of species exhibiting metapopulations. However, there is some evidence for some of the predictions of the rescue effect hypothesis (Hanski *et al.* 1995; Gonzalez *et al.* 1998) and there may be certain taxa for which metapopulation structure is the rule, rather than the exception.

Central to the metapopulation dynamic hypothesis is the concept of a set of discrete sites in the landscape, within which populations are maintained by interpatch dispersal. The idea that habitat is divided into discrete patches is also central to another population dynamic mechanism for abundance–occupancy relationships, the vital rates hypothesis (Holt *et al.* 1997). This mechanism differs, however, in that it is population dynamics within each individual site, rather than interactions between sites, that are hypothesized to forge the link between abundance and distribution. If movement between sites is just sufficient that all potentially occupiable sites are occupied, but is not so great that immigration significantly affects the population supported at a site, then it follows that a species will only persist at sites at which its birth rate,  $b$ , exceeds its density-independent death rate,  $d$ . In other words, as  $b-d=r$ , a species' intrinsic rate of increase

at a site, a site is occupied when  $r > 0$ . A species will occupy more sites when its average  $r$  is high, and fewer when its average  $r$  is lower. In addition, population dynamic theory predicts that the abundance attained by a species at a site will be proportional to  $r$ , assuming constant density-dependence in death rates. Therefore, both the number of sites occupied and mean abundance at those sites will depend on the species' value of  $r$ , and hence on the relationship between birth and death rates across sites. It follows that temporal fluctuations in birth and/or death rates will lead to synchronized variation in both the abundance attained by a species at different sites, and the number of sites occupied. A positive abundance–occupancy relationship will result (Holt *et al.* 1997). There are too few data with which to evaluate the vital rates hypothesis. Collecting these data is not a straightforward task.

(v) *Synthesis*

It should be clear from the above that, as yet, no mechanism proposed to explain intraspecific abundance–occupancy relationships has any significant degree of support. This is due in large part to the relatively recent development of interest in these patterns, prompted mainly by the hope that intraspecific relationships would inform about mechanisms driving the equivalent interspecific relationship, which has a longer history. This hope has been dashed by the realization that all significant mechanisms for positive interspecific relationships can also produce positive intraspecific relationships (Gaston, Blackburn & Lawton 1997). Nevertheless, exploration of intraspecific relationships should continue, for at least two reasons. First, it is not necessarily true that the same mechanism(s) explains intra- and interspecific relationships in any given assemblage, although obviously it would be helpful if it did. Secondly, intraspecific relationships have implications that make their study of interest in their own right.

PRACTICAL IMPLICATIONS OF  
INTRASPECIFIC ABUNDANCE–OCCUPANCY  
RELATIONSHIPS

The foremost implications of positive intraspecific abundance–occupancy relationships are threefold (Gaston 1999).

(i) *Indexing abundance*

Documenting the presence and absence of species requires less resources and effort than does estimating local densities, and the relationship between densities and occupancies may mean the former can be estimated from the latter, at least in relative terms. Thus the use of positive intraspecific abundance–occupancy relationships has been advocated as a



possible means of reducing the costs involved in measuring relative abundance, particularly for monitoring changes in the populations of some birds (Yapp 1956; Verner 1985; Bart & Klosiewski 1989; Robbins *et al.* 1989; Robbins, Droege & Sauer 1989; Gibbons, Reid & Chapman 1993). Bart & Klosiewski (1989), using data from the breeding bird survey (BBS) in North America, compared the numbers of individuals recorded per survey route with the number of stations per route at which a species was recorded. They found a mean correlation coefficient between the two variables for 190 species of 0.997; changes in occupancy indicated changes in abundance. Not surprisingly, numbers of stations tended to exhibit less temporal change than number of individuals, and data based on numbers of stations had narrower general application. However, for the purpose of measuring broad changes in avian abundance, the results were encouraging.

Obviously this approach only works for species that do not occur in all areas. In most cases, exploration of the predictive value of abundance–occupancy relationships for relative abundance has concerned abundances averaged over all sites, whether occupied or otherwise. Nonetheless, some lessons can perhaps be learnt from the study of relationships in which they have been averaged over occupied sites only. Thus, for reasons outlined earlier, the approach is likely to be most effective for species that exhibit a wide range of temporal variation in abundance and occupancy, and hence that are more likely to exhibit reasonably strong relationships between the two. It would also seem likely to be more effective for organisms for which the ratio of generation times to the time frame of interest is greatest. In these cases there will be less likelihood of lags in the response of changes in occupancy to changes in average local density preventing the expression of abundance–occupancy relationships (Gaston, Blackburn & Gregory 1998).

#### (ii) *Harvesting*

The relatively large numbers of studies of intraspecific abundance–occupancy relationships for fish (see References above) reflects the potential significance of this pattern for harvesting. Direct tests usually report a positive correlation between stock area and abundance (Winters & Wheeler 1985; Crecco & Overholtz 1990; Rose & Leggett 1991; Swain & Wade 1993; Swain & Sinclair 1994), although there have been technical difficulties in early work (associated with estimating stock area) and there are studies reporting other outcomes (Marshall & Frank 1994; Swain & Morin 1996). The existence of a positive relationship would have important implications for fisheries management and stock assessment (for a detailed discussion see MacCall 1990; Swain & Morin 1996). In the case of commercial fisheries,

catchability, the proportion of a population captured per unit effort, is expected to decrease with stock area. If stock area is proportional to population size, catchability will increase as abundance decreases.

#### (iii) *Conservation*

As we have already discussed, the existence of positive abundance–occupancy relationships, particularly among species that are in decline, would imply that double jeopardy pertains to individual species, with increases in extinction risk from reductions in abundance being accompanied by increases in extinction risk from reductions in range size, and vice versa (Lawton 1993, 1995, 1996a). The existence and direction of a causal link between local abundance and regional occupancy will determine the degree to which this is actually true. Moreover, the outcome may importantly rest on the manner in which abundances or range sizes are reduced, particularly where human agency is involved, and the mechanism forging the link between them. Thus, if intraspecific relationships are largely a consequence of metapopulation dynamics, then a range reduction that increases the isolation of the remaining inhabited patches (Gonzalez *et al.* 1998) may have a more detrimental effect on population size than would an equivalent reduction of range size where the isolation of remaining patches is not so greatly increased.

### **Interspecific abundance–occupancy relationships**

The tendency for individual species to show positive relationships between abundance and occupancy makes no firm predictions about the form of the same relationship across species (Blackburn *et al.* 1998). On the one hand, if intraspecific relationships are strong, and exhibit some commonality of form, interspecific relationships might seem likely to follow. On the other hand, if the range of temporal variation in the abundances of individual species is small relative to the spread of their mean abundances, then intraspecific relationships may have little influence in generating interspecific ones. Intraspecific relationships are highly variable, and frequently not very strong, and interspecific variation in local abundances tends to be vastly greater than intraspecific variation. However, in the limit, species will vary from those that are in the process of colonizing an area or going extinct from it, and so passing through the origin of the abundance–occupancy plot, to those that are both widespread and abundant. Although species can potentially lie along many trajectories connecting these two points, these limits alone perhaps make it likely that interspecific abundance–occupancy relationships will be positive in some broad form. This is indeed the case.

PATTERNS IN INTERSPECIFIC  
RELATIONSHIPS

Positive interspecific abundance–occupancy relationships have been documented for a wide variety of taxa (plants: Gotelli & Simberloff 1987; Collins & Glenn 1990, 1997; Boecken & Shachak 1998; spiders: Pettersson 1997; grasshoppers: Kemp 1992; Collins & Glenn 1997; scale insects: Kozár 1995; hoverflies: Owen & Gilbert 1989; bumblebees: Obeso 1992; Durrer & Schmid-Hempel 1995; macro-moths: Inkinen 1994; beetles: Nilsson, Elmberg & Sjöberg 1994; bracken-feeding insects: Gaston & Lawton 1988; frogs: Murray, Fonseca & Westoby 1998; birds: Gaston & Blackburn 1996b; Collins & Glenn 1997; mammals: Brown 1984; Collins & Glenn 1997; Johnson 1998a). In Britain alone, such relationships have now been documented for vascular plants (Rees 1995; Thompson, Hodgson & Gaston 1998), macro-moths (Quinn *et al.* 1997), butterflies (Hanski, Kouki & Halkka 1993), birds (Fuller 1982; Hengeveld & Haeck 1982; O'Connor & Shrubbs 1986; O'Connor 1987; Gaston & Lawton 1990; Sutherland & Baillie 1993; Gregory 1995; Blackburn *et al.* 1997b, 1998; Blackburn, Gaston & Gregory 1997a; Gaston, Blackburn & Gregory 1997a, 1997b; Gaston *et al.* 1998) and mammals (Blackburn *et al.* 1997b). In a review of published abundance–occupancy relationships, Gaston (1996a) found that around 80% were significantly positive. He concluded that the positive relationship between abundance and occupancy may be one of the general patterns in the study of ecology. Relationships published since this review have almost without exception supported this view.

The positive relationship is remarkably robust (Fig. 3). It has been known for some time that it tends to remain consistent across multiple spatial scales (Gaston & Lawton 1990) and when abundance and occupancy are quantified using a variety of measures. A prime example is provided by the range of relationships reported for British birds. A strong significant positive relationship is found when the total British breeding population size of species is plotted against its geographical range size in Britain; here, an increase in density with range size follows because, on log–log axes, the relationship between population size and range size has a slope of greater than one (Blackburn *et al.* 1997b). The same is true also if breeding abundance and distribution are replaced by wintering figures (Gaston, Blackburn & Gregory 1997b). If breeding and wintering assemblages are split into resident and migrant species, both subsets show significant positive interspecific relationships. A significant positive relationship is found if population size and geographical range size are replaced by species density on local sites and the proportion of these sites that each species occupies (Gaston *et al.* 1998). This is true if

density and occupancy are averaged across the same 4-year period over which population size and geographical range size were estimated, or if density and occupancy are estimated within each of these years individually (Blackburn *et al.* 1998). Indeed, a significant positive density–occupancy relationship is found using data from both farmland and woodland CBC sites for every year from 1968 to 1991 inclusive (Blackburn *et al.* 1998b). Finally, interspecific abundance–occupancy relationships can be examined using bird densities calculated from each individual CBC site. For 137 such sites, the interspecific relationship was positive every single time, and significantly so for 85%.

Such relationships imply that the same species will lie in the tails of the species abundance and species range size distributions for an assemblage. This is largely the case. Seventy per cent of the 5% of bird species with the lowest British population sizes are also among the 5% of species with the smallest British geographical range sizes, while 50% of the 5% of species with the highest British population sizes are also among the 5% of species with the largest British geographical range sizes.

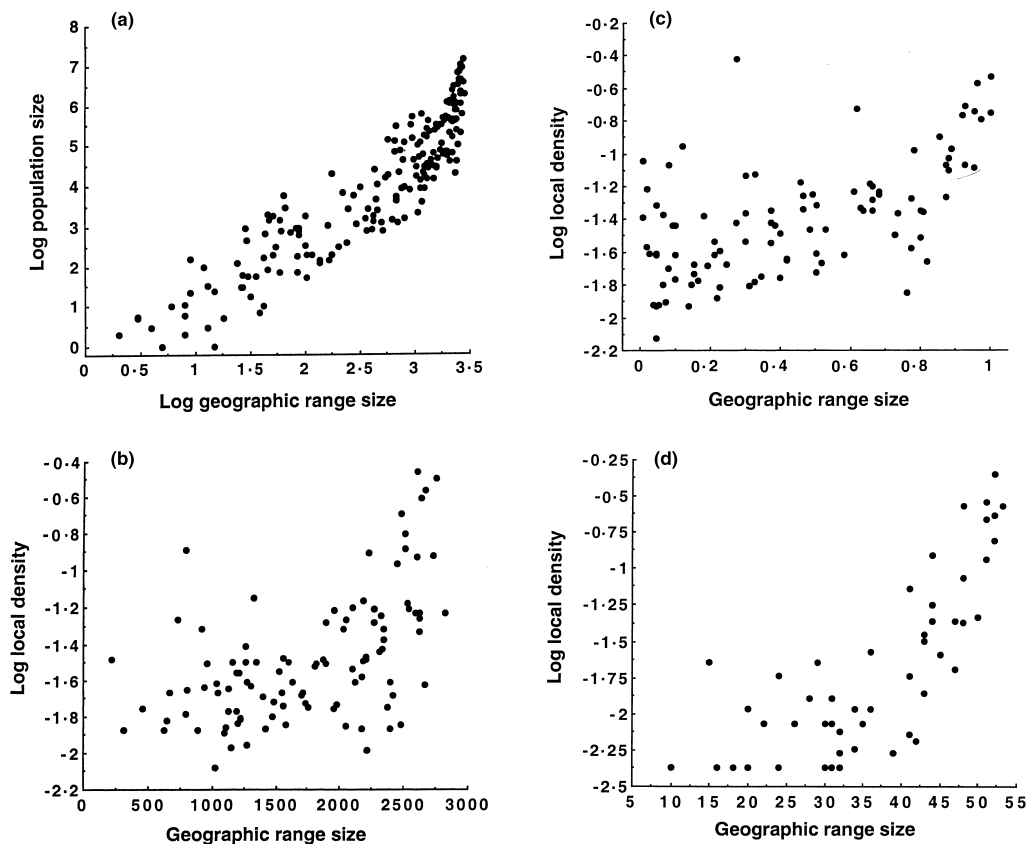
Exceptions to the positive interspecific abundance–occupancy relationship do exist, but are scarce. Gaston (1996a) found that about 5% of the relationships in the literature were significantly negative. Often, the exceptions concern unusual sets of circumstances (Gaston & Lawton 1990; Gaston 1996a; Johnson 1998b). For example, negative relationships can arise when abundance is measured in an area that is highly atypical of the region over which distribution is assessed.

Curiously, while generally reporting positive correlations, studies of interspecific abundance–occupancy relationships that have been conducted for plants have tended to concentrate on quite narrowly defined habitat types. Thompson, Hodgson & Gaston (1998) found that for the vascular plant flora of central England, there was no overall relationship between abundance and occupancy, but that at the level of individual habitat types significant positive relationships were quite common.

ANATOMY OF INTERSPECIFIC  
ABUNDANCE–OCCUPANCY RELATIONSHIPS

A number of facets of the anatomy of interspecific abundance–occupancy relationships have become apparent, particularly with reference to birds in Britain.

(i) For the one data set for which this issue has been carefully dissected, British birds on farmland and woodland CBC sites, the relationship appears to be driven primarily by increases in the maximum abundance that a species can attain at occupied sites. Minimum abundances are, not surprisingly, not related to range sizes across all but perhaps the



**Fig. 3.** Examples of the interspecific abundance–occupancy relationship for birds in Britain. (a) The relationship between  $\log_{10}$  breeding population size (number of individuals) and  $\log_{10}$  breeding geographical range size (number of  $10 \times 10$ -km squares from which a species was recorded in Gibbons, Reid & Chapman 1993);  $r^2=0.83$ ,  $n=193$ ,  $P < 0.0001$  (from Blackburn *et al.* 1997). The slope of this relationship is significantly greater than 1, indicating that the population size of widespread species is higher than expected simply on the basis of their larger geographical distributions. (b) The relationship between local density ( $\log_{10}$  territories per hectare) and geographical range size (number of  $10 \times 10$ -km squares from which a species was recorded in Sharrock 1976) for bird species on farmland CBC plots in the period 1988–91;  $r^2=0.27$ ,  $n=97$ ,  $P < 0.0001$  (from Gaston *et al.* 1998). (c) The relationship between local density ( $\log_{10}$  territories per hectare) and geographical range size (proportion of all sites that the species occupies) for bird species on farmland CBC plots in 1979;  $r^2=0.35$ ,  $n=98$ ,  $P < 0.0001$  (for data sources and methods see Blackburn *et al.* 1998). (d) The relationship between local density (mean  $\log_{10}$  territories per hectare) and geographical range size (number of occupied sites) for bird species on a single farmland CBC site in the period 1988–91;  $r^2=0.60$ ,  $n=51$ ,  $P < 0.0001$  (for data sources and methods see Gaston *et al.* 1998).

most widespread species (Gaston *et al.* 1998). Thus most species are rare at some sites at which they occur, but only the more widespread species attain high densities at others. This pattern results in a roughly triangular relationship between abundance and occupancy when the abundance at every site occupied by each species is plotted on the same axes (Gaston *et al.* 1998). Thus mean density varies with occupancy (Fig. 3) primarily because maximum density does so.

(ii) The relationship tends to become poorer with cruder measures of range size (Table 1). For British birds, the finest scale at which distributions across the whole country are mapped is that of the  $10 \times 10$ -km square on the British National Grid. These fine scale data can be used to derive cruder measures of species occurrence, based on latitudinal or longitudinal extents, or minimum convex polygons (Quinn,

Gaston & Arnold 1996). The strengths of the resultant abundance–occupancy relationships plotted using different range size measures are essentially inversely related to the crudity of this measure (Table 1), as one might expect if, as the measurement scale becomes coarser, the error variance in the estimation of occupancy increases.

(iii) The relationship shows consistencies between different habitats. Thus, using data from the CBC, Blackburn *et al.* (1998) found that the slopes of the interspecific relationships for species censused on farmland and woodland sites were very similar, and that year-to-year variation in the slope value was positively correlated between these habitats. In other words, in years when abundant species occupy a higher proportion of woodland CBC sites, they also occupy a higher proportion of farmland sites. This is presumably a simple consequence of good

**Table 1.** Comparison of the abundance–range size relationship for birds in Britain using different methods to estimate range size (Quinn, Gaston & Arnold 1996) and total population size ( $\log_{10}$  transformed).  $n$  is the number of phylogenetically independent contrasts. All relationships are significant at  $P < 0.00001$ . Range methods are ranked in ascending order according to the amount of variation in abundance which they explain

Range methods	Full model			After removal of outliers/leverage points		
	$n$	$r^2$	Rank	$n$	$r^2$	Rank
Latitudinal extent	107	0.567	6	96	0.669	6
95% latitudinal extent	107	0.338	8	93	0.675	4
Longitudinal extent	107	0.636	5	103	0.672	5
95% longitudinal extent	107	0.406	7	90	0.663	7
Latitudinal $\times$ longitudinal extent	107	0.648	4	104	0.662	8
Minimum convex polygon	107	0.719	3	96	0.797	3
100 $\times$ 100-km squares	107	0.778	2	98	0.835	2
10 $\times$ 10-km squares	107	0.849	1	97	0.900	1

years for common or rare species being the same in both habitat types, and spill-over of individuals from good to poor habitats as abundances increase. This pattern arises despite consistently lower densities being recorded on farmland than woodland sites. A British bird species recorded on a single woodland CBC site in any given year will have a density three to four times higher, on average, than a species recorded on only a single farmland site (Blackburn *et al.* 1998), this difference being a consequence of much of the area of most farmland CBC sites being relatively barren for birds (e.g. crop land).

(iv) The relationship remains stable from one season to another. Thus, the resident species of the breeding and wintering bird assemblages in Britain (i.e. those species they have in common) show a common interspecific population size–geographical range size relationship, such that neither the slope nor the intercept of the relationship differ significantly whether summer or winter data are used (Gaston, Blackburn & Gregory 1997b). However, resident birds do show significantly larger population sizes and geographical range sizes in Britain in winter than in summer. Coupled with the non-significant differences in the winter and summer population size–geographical range size relationships, these results imply that bird species shift up the interspecific relationship from summer to winter, and back down again from winter to summer.

Other interesting regularities arise if migrant species are considered. On average, summer migrants have smaller breeding population sizes ( $F_{1,168} = 6.50$ ,  $P = 0.012$ ) and range sizes ( $F_{1,168} = 7.96$ ,  $P = 0.005$ ) than do residents (see also Greenwood *et al.* 1996), yet summer migrants and residents do not differ in either the slopes ( $F_{1,166} = 1.18$ ,  $P = 0.28$ ) or the intercepts ( $F_{1,167} = 0.003$ ,  $P = 0.96$ ) of their breeding population size–geographical range size relationships. Likewise, winter migrants have smaller breeding population sizes ( $F_{1,156} = 30.3$ ,  $P < 0.0001$ ) and

range sizes ( $F_{1,156} = 30.4$ ,  $P < 0.0001$ ) than do residents, yet winter migrants and residents do not differ in either the slopes ( $F_{1,154} = 0.09$ ,  $P = 0.77$ ) or the intercepts ( $F_{1,155} = 2.47$ ,  $P = 0.12$ ) of their wintering population size–geographical range size relationships. When all species are included, the slopes of the interspecific population size–geographical range size relationship differ between summer and winter (Gaston, Blackburn & Gregory 1997b), but residents and migrants lie on the same line in both seasons. As migrant populations are subject to different environmental pressures to resident populations for around half the year, yet settle on the same interspecific relationship as residents when they arrive in Britain, this implies a commonality in the forces setting this relationship for both groups. What causes this commonality is currently unclear.

(v) The relationship remains reasonably stable from one year to the next. Thus, Blackburn *et al.* (1998) found relatively little interannual variation in the slope, intercept and coefficient of determination for abundance–occupancy relationships for farmland and woodland birds in Britain. In major part, this occurs because abundant and widespread species remain abundant and widespread from year to year, while rare and restricted species remain rare and restricted (see discussion of concordance above). However, the assessment of the amount of interannual variation in these interspecific relationships is necessarily subjective, as there is no baseline against which to compare.

(vi) The relationship is very similar for different groups of organisms in the same area, where estimates of abundance and occupancy are broadly comparable. Thus, Blackburn *et al.* (1997b) found that the slopes of the relationships between overall population size and geographical range size were not significantly different for breeding birds and mammals in Britain, once two outliers were excluded from the mammal data (a similar result was found for the slopes of population size–body

size relationships in these two assemblages; Greenwood *et al.* 1996). However, for a given range size mammals had densities that averaged 30 times higher than those of birds (at comparable masses, non-flying mammal species are about 45 times more abundant than resident bird species; Greenwood *et al.* 1996). The two species outlying the mammal relationship [white-toothed shrew *Crocidura suaveolens* (Pallas) and Orkney vole *Microtus arvalis* (Pallas)] are the only species of terrestrial mammal or bird confined in Britain to offshore islands. They have exceptionally high abundances for their range size, as might be expected if they were exhibiting density compensation in response to species-poor island faunas (MacArthur 1972; MacArthur, Diamond & Karr 1972; Blondel, Chessel & Frochot 1988; Adler & Levins 1994) or if their ranges in Britain could be much larger were they to escape the confines of their current insular habitats.

#### WHY ARE ABUNDANCE AND OCCUPANCY LINKED ACROSS SPECIES?

As mentioned earlier, the mechanisms that can be postulated as explanations of intraspecific abundance–occupancy relationships are essentially the same as those that have been postulated for interspecific relationships, with two further additions. Elsewhere we have examined the assumptions and predictions, and the evidence for, each of these mechanisms in some detail (Gaston, Blackburn & Lawton 1997). Here we simply summarize some of the primary conclusions and direct attention to more recent relevant work.

##### (i) Statistical explanations

Just as for positive intraspecific abundance–occupancy relationships, those assemblages which, beyond all reasonable doubt and independently of sampling, display a positive interspecific abundance–range size relationship refute the sampling hypothesis as an explanation of the pattern (Warren & Gaston 1997; Gaston *et al.* 1998; Murray, Fonseca & Westoby 1998). Sampling biases undoubtedly contribute to many interspecific abundance–occupancy relationships, in some cases perhaps markedly, but equally they fail to explain many, and probably most.

The comments made above about the aggregation mechanism in the context of intraspecific abundance–occupancy relationships apply equally to interspecific patterns, with the additional observation that the probable form of the interspecific relationship is rather difficult to predict a priori on the basis of aggregation. Individual species exhibit different levels of aggregation with changing density,

these changes may be species-specific, and the universe of sites that can be occupied varies between species (Gaston, Blackburn & Lawton 1998). Of these, the most important may be the last. Gaston, Blackburn & Lawton (1998) found that increasing interspecific variance in the value of  $k$  of the negative binomial distribution made little difference to the shape of the abundance–occupancy relationship predicted. The extent to which a species deviates from the predicted relationship may thus depend principally on how the universe of sites actually available to it differs from that assumed for the purposes of the model.

The single mechanism that has been postulated to explain interspecific abundance–occupancy relationships but that does not apply to intraspecific ones, can from one perspective be seen as essentially statistical. This is the phylogenetic non-independence hypothesis. An artefactual positive interspecific relationship between abundance and range size could result from the shared common ancestries of species in an assemblage. Because of their phylogenetic relatedness, species do not constitute independent data points for analysis, inflating the degrees of freedom available for testing statistical significance (Harvey & Pagel 1991; Harvey 1996). If sufficient, this inflation may falsely imply that abundance–occupancy relationships exist when in reality they do not.

A growing number of studies have found that interspecific abundance–occupancy relationships persist when phylogenetic non-independence has been controlled for (macrolepidoptera: Quinn *et al.* 1997; frogs: Murray, Fonseca & Westoby 1998; birds: Blackburn *et al.* 1997b; Gaston, Blackburn & Gregory 1997a; mammals: Blackburn *et al.* 1997b). Thus the relatedness of species does not generate the positive interspecific relationship.

In a related vein, Johnson (1998b) found that for marsupials on the Australian mainland there is a rather weak, albeit positive, interspecific relationship between the local abundance of species and the extent of their geographical occurrences. He then separated the species into two groups, those of recent evolutionary origin and those which are more ancient (assuming that species with no recent extant relations are genuinely old, and do not simply appear to be so because their relatives have gone extinct). When analysed within taxa, the former exhibit a relationship which is both positive and much stronger than that documented across the entire assemblage. The more ancient species, however, exhibit a negative within-taxon relationship. Although the validity of distinguishing between ancient and recently evolved species for separate within-taxon analyses seems questionable, the result is intriguing nonetheless, albeit its probable generality is difficult to judge at present.

*(ii) Range position explanations*

The range position mechanism cannot explain interspecific abundance–occupancy relationships based on data for the entire geographical ranges of species (Brown & Maurer 1987; Gaston & Blackburn 1996b; Murray, Fonseca & Westoby 1998). While its predictions are often upheld for less extensive analyses, controlling for its effects reveals that it cannot explain some documented interspecific abundance–range size relationships (Gaston, Blackburn & Gregory 1997a). This is not to say that the effect does not contribute to many documented patterns, especially in partial analyses ('partial' analyses are performed over areas that embrace the entire geographical ranges of none or only a small proportion of the species concerned; 'comprehensive' ones are performed over areas that embrace all, or a very large proportion, of the extents of the geographical ranges of the species concerned; Gaston & Blackburn 1996c). The extent to which it does will depend upon the proportion of between-species variation in abundances that can be accounted for simply by the position of the area in which those abundances were measured with respect to the centres of the geographical ranges of the different species.

*(iii) Resource explanations*

Intraspecific abundance–occupancy relationships were hypothesized to be driven by variation in resource availability, which could result from variation either in the abundance of resources or in their diversity. However, the effect of variation in resources deriving from these two different sources can be considered separately across species. Interspecific abundance–occupancy relationships may then arise either because widespread abundant species use a greater variety of resources, on average, than narrowly distributed rare species (the resource breadth hypothesis; Brown 1984), or because widespread abundant species use widespread abundant resources (the resource availability hypothesis; Hanski, Kouki & Halkka 1993; Gaston, Blackburn & Lawton 1997).

There have been a host of studies of the interspecific relationships between local abundance and breadth of resource usage and between range size and breadth of resource usage. Unfortunately, in the main these suffer from innumerable statistical difficulties, mostly associated with the problem of dissociating simple sample size effects from genuine differences between the resource usage of common and rare species (for discussion see Gaston 1994a; Gaston, Blackburn & Lawton 1997 and references therein). The evidence for the hypothesis as an explanation for positive interspecific abundance–range size relationships appears to us to be largely unconvincing.

Resource use in British breeding birds has been examined using extensive census and environmental data (Gregory & Gaston 2000). The former came from a volunteer-based survey of 1830 1-km squares in 1996, the latter from ground surveys and satellite imagery. Eighty-five species were considered for study, and 34 land use or environmental variables were used to generate four ordination axes by canonical correspondence analysis (CCA). Niche breadth and position (measures of resource breadth and resource availability, respectively) were derived from these axes using standard procedures. Across all species, none of five measures of abundance and distribution chosen was correlated with niche breadth, whereas four out of five of these measures were correlated with niche position. Repeating the analyses using a method designed to control for phylogenetic non-independence confirmed these general patterns. Birds that tend to utilize resources that are more atypical of the environment tended to be rarer and more thinly distributed, while those utilizing typical resources were common and widely distributed. These results refute the resource breadth hypothesis, but support the resource availability hypothesis.

Although these analyses on British birds support the resource availability hypothesis, little evidence has been garnered from other taxa (but see Arneberg *et al.* 1998). For example, the resource availability hypothesis predicts that widespread species should be those utilizing widespread resources. Quinn, Gaston & Roy (1997, 1998) tested for such a relationship by comparing, separately, the range sizes of butterflies and monophagous macrolepidoptera (moths) in Britain with those of their food plants. Ignoring other constraints on resource availability, widespread species should be those with widespread foodplants. There are indeed positive relationships between host and consumer range size in both groups of insects. However, a positive relationship of some form is the null hypothesis in this case, because consumer species cannot have ranges that are larger than those of their resources. In neither taxon does the smallest range size attained by species of consumer increase with host-plant range size, suggesting no tendency for consumer ranges to be constrained by those of their hosts. Therefore, neither taxon provides evidence that simple resource availability is constraining range sizes, making it less likely that resource availability will shape their abundance–occupancy relationships.

Habitat selection is unlikely to be of major importance in determining interspecific abundance–occupancy relationships for many taxa, but may perhaps play a role for some.

*(iv) Population dynamic explanations*

Recent tests of the metapopulation dynamic hypothesis for abundance–occupancy relationships have

been performed using microcosms. Gonzalez *et al.* (1998) experimentally fragmented a natural miniature moss ecosystem. When dispersal between the moss fragments was prevented, most species in the microarthropod assemblage inhabiting the fragments declined in both abundance and distribution, and many became extinct. These declines caused the collapse of the positive interspecific abundance–occupancy relationship. However, when the patches were connected by habitat corridors, allowing dispersal of animals between patches, the declines in both abundance and distribution were arrested, and the positive relationship between them was maintained. Control patches linked by broken corridors exhibit similar patterns to isolated patches, showing that the effect of corridors is not simply due to the extra area they provide. Thus, the positive abundance–occupancy relationship in this natural microecosystem is maintained by dispersal in a connected landscape, as predicted by the metapopulation dynamic hypothesis (Gonzalez *et al.* 1998).

Warren & Gaston (1997) used laboratory microcosm communities of protists to test the effects of different dispersal regimes on the abundance–occupancy relationship. Positive relationships were present in all treatments, even in those communities where there was no dispersal between patches. The results failed to support the specific hypotheses based on metapopulation dynamics, but suggest that occupancy may be driven by local abundance, combined with a very general (not specifically metapopulation-structured) set of extinction and colonization processes.

In sum, the metapopulation dynamic hypothesis finds equivocal support in the experiments so far performed. Nevertheless, the experimental design in the study by Gonzalez *et al.* (1998) rules out the action of other mechanisms, so that metapopulation dynamics must be generating the relationship in this system, at least. However, Gonzalez *et al.* (1998) themselves point out that the scale of fragmentation and the dispersal distances of the organisms in their system are likely to be appropriate for observing

metapopulation dynamics, and they do not necessarily expect the metapopulation mechanism to pertain at biogeographical scales, where interpatch dispersal is unlikely to be important.

#### (v) Synthesis

The mechanisms for interspecific abundance–occupancy relationships for which tests have been performed for different groups in the flora or fauna of Britain are compiled in Table 2. As yet, we are not in a position to provide a definitive statement as to which determine the patterns for each group. In most cases, there is evidence in support of more than one mechanism. There may be two reasons for this. First, the tests could be inadequate. It is not unusual for tests that claim to support one mechanism to fail unequivocally to rule out the operation of another. As McArdle (1996) has pointed out, we ‘usually start out with many ideas and end up with a few hypotheses but these are usually the ones that are the most difficult to distinguish between.’ Secondly, as with other general ecological patterns, the abundance–occupancy relationship may have multiple causes (Wilson 1988a; Warren & Gaston 1992; Blackburn & Gaston 1996a, 1996b; Lawton 1996b; Gaston, Blackburn & Lawton 1997; Gaston & Blackburn 1999). This is highly likely, given that some mechanisms simply provide different levels of explanation or are not otherwise mutually exclusive, and that some mechanisms may be more appropriate at some spatial scales than others.

#### PRACTICAL IMPLICATIONS OF INTERSPECIFIC ABUNDANCE–OCCUPANCY RELATIONSHIPS

The principal implications of interspecific abundance–occupancy relationships are threefold (Gaston 1999).

**Table 2.** The mechanisms postulated to explain positive interspecific abundance–occupancy relationships for which tests have been performed for different groups of organisms in Britain. 1, sampling artefact; 2, phylogenetic non-independence; 3, range position; 4, breadth of resource usage; 5, resource availability; 6, habitat selection; 7, metapopulation dynamics; 8, vital rates; 9, aggregation (Hinsley *et al.* 1996; Blackburn *et al.* 1997; Gaston, Blackburn & Gregory 1997a; Quinn *et al.* 1997; Quinn, Gaston & Roy 1997, 1998; Gonzalez *et al.* 1998; Thompson, Hodgson & Gaston 1998; Thompson, Gaston & Band 1999; Gregory & Gaston, in press).

	1	2	3	4	5	6	7	8	9
Vascular plants	✓	✓		✓	✓				
Moss microarthropods							✓		
Macro-moths		✓			✓				
Butterflies					✓				
Birds	✓	✓	✓	✓	✓				
Mammals		✓							

*(i) Inventorying biodiversity*

Within an assemblage, both the species abundance distribution and the species range size distribution are strongly right-skewed (Preston 1948; Williams 1964; Anderson 1984a,b, 1985; Gray 1987; Schoener 1987; Pagel, May & Collie 1991; Tokeshi 1993; Gaston 1994a, 1996b, 1998). Most species are locally rare and few are abundant, and most species are narrowly distributed and few are widespread. Combined with the positive interspecific abundance–occupancy relationship, this means that most species only occur in a few places and, critically, are also, on average, amongst the more difficult to find in those places (because of their low abundances). Given that spatial coincidence in the occurrence of rare species often is not high (Prendergast *et al.* 1993; Gaston 1996c; Prendergast & Eversham 1997), this has profound implications for the generation of inventories of biodiversity. Thus the intensity and extensiveness of sampling programmes cannot readily be traded against one another, although a trade-off would be desirable to limit the cost and effort involved. While it will find the rare species at those sites, an intensive programme at a few sites will, because of its limited spatial coverage, inevitably miss many other such species that only occur at other sites. Likewise, an extensive programme over many sites will fail to find many species because they are locally rare and will not be detected by superficial sampling. If these are missed at a few critical sites, they may not be recorded anywhere because of their restricted occurrence. To generate worthwhile biodiversity inventories, then, there seems no choice but to sample extensively and intensively.

*(ii) Conservation*

As mentioned earlier, the existence of a positive interspecific abundance–occupancy relationship implies that, in terms of extinction risk, species face ‘double jeopardy’ (Lawton 1993, 1995, 1996a). Both the magnitude of local abundance and the extent of spatial distribution of a species may contribute independently to its risk of global extinction. Low local abundance increases the likelihood of stochastic extinction (although the dynamics of local density and population size may be very different; Gaston & McArdle 1993), while a narrow geographical range increases the likelihood that all populations will simultaneously be subject to adverse abiotic and/or biotic environmental conditions (Hanski 1982; Diamond 1984; Pimm, Jones & Diamond 1988; Tracy & George 1992; Gaston 1994a; Lawton 1995; Gaston & Blackburn 1996b). There has been little empirical work to discriminate the relative importance of abundances and range sizes to extinction risk (but see Gaston & Blackburn 1996b; Johnson 1998b), and opinion seems divided.

Additionally, positive interspecific abundance–occupancy relationships have implications for methods of identifying networks of priority areas for conservation based on the principle of complementarity (Pressey *et al.* 1993). These methods typically have the objective of determining the minimal set of areas required to embrace all the species in a given taxon (which occur in the region of interest) in at least one area, or some other predefined number of occurrences. If species of restricted occupancy also have lower densities than more widespread species, then such an approach serves to include in a priority area network disproportionately fewer individuals of narrowly distributed species for a given level of occurrence than of widely distributed species, the converse of what is most desirable. The existence of positive abundance–occupancy relationships may itself provide a simple basis on which to set different targets for the representation of rare and common species, to negate this problem.

*(iii) Invasions*

By the same logic applied to their implications for species that are undergoing decline in abundance or range size, positive interspecific abundance–occupancy relationships also have implications for species that are of concern because they are invading areas, and which in so doing may have undesirable consequences. Just as such relationships imply ‘double jeopardy’ for species in decline, so they in some sense imply ‘double trouble’ from species that are on the increase, if these are potential pests or otherwise problematic. The magnitude of local abundance and the extent of spatial distribution may contribute independently to the problem status of a species (and the costs of its control or eradication), and the positive interspecific abundance–occupancy relationship means that individual species tend simultaneously to be undesirable with regard to both.

**Conclusions**

A positive, inter- and intraspecific, abundance–occupancy relationship is a widespread feature of ecological assemblages. Arguably, this pattern constitutes one of the most fundamental in ecology. Yet it has only received attention from ecologists in the last two decades. Probably for this reason, we are still in the process of finding out about the structure of the pattern. Little is known beyond the obvious fact of its existence. The statistics describing the relationship have been conspicuously under-reported, retarding its integration with other ecological patterns (Leitner & Rosenzweig 1997). Several mechanisms have been proposed as its cause, generating initial tests of their assumptions and predictions, but as yet no hint of consensus as to which of these is (or are) the most likely explanation(s) has emerged.



Indeed, arguably several mechanisms are most likely to be acting, depending on the spatial scale of the assemblage, or whether patterns are within or across species. Understanding the processes underpinning this important relationship is undoubtedly growing, but progress is slow. Yet, as we have seen, the positive abundance–occupancy relationship has significant applied implications, affecting the quantities of interest to conservationists, wildlife managers, fisheries and pest management agencies. As abundance and occupancy are fundamental variables in ecology, and the positive relationship between them one of its most robust patterns, more attention to the form, structure and mechanisms underpinning the abundance–occupancy relationship will surely pay rich dividends in a deeper understanding of ecology as a whole.

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