

Quantifying variation in migratory strategies using ring-recoveries

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Abstract

Quantifying variation in migratory strategies using ring-recoveries.— Bird populations have traditionally been labelled as "migrant" or "resident" on the basis of field observations and qualitative interpretations of patterns of ring-recoveries. However, even such a non-systematic approach has identified many intermediate species where only part of the population migrates (partial migrants) or where different components of the population migrate to different extents (differential migrants). A method that would allow a quantitative definition of migratory tendency to be derived for many species would facilitate investigations into the ecological causes and life-history consequences of migratory behaviour. Species or populations could then be placed objectively into the continuum between true residency and an obligate, long-distance migratory habit. We present a novel method for the analysis of ring-recovery data sets that produces just such a quantitative index of migratory tendency for British birds, developed as part of the BTO's *Migration Atlas* project (Wernham et al., 2002). The method uses distributions of ringing-to-recovery distances to classify individual species' patterns of movement relative to those of other species. The areas between species' cumulative distance distributions are treated as inter-species dissimilarities and a one-dimensional map is then constructed using multi-dimensional scaling. We have used the method in example analyses to show how it can be used to investigate the factors that affect the migratory strategies that species adopt, such as body size, territoriality and distribution, and in studies of their consequences for demographic parameters such as annual survival and the timing of breeding. We have also conducted initial analyses to show how temporal changes in the indices could reveal otherwise unmeasured population consequences of environmental change and thus have an important application in conservation science. Finally, we discuss how our approach to producing indices of migratory tendency could be enhanced to reduce the bias that follows from spatial or temporal variation in reporting rates and how they could be made more broadly valuable by incorporating other data sets and recovery data from other countries.

Key words: Migration, Partial migration, Birds, Strategies, Ecology, Demography.

Resumen

Cuantificación de la variación en las estrategias migratorias mediante la recuperación de anillas.— Tradicionalmente, las poblaciones de aves se han definido como "migratorias" o "residentes" en función de las observaciones de campo y las interpretaciones cualitativas de las pautas de recuperación de anillas. Sin embargo, incluso un enfoque no sistemático de estas características ha sido capaz de identificar numerosas especies intermedias, en las que sólo una parte de la población emigra (especies migratorias parciales), o en las que distintos componentes de la población emigran en mayor o menor grado (especies migratorias diferenciales). Un método que permitiera derivar una definición cuantitativa de la tendencia migratoria de numerosas especies facilitaría las investigaciones de las causas ecológicas y de las consecuencias vitales del comportamiento migratorio. De este modo, las especies o poblaciones podrían situarse objetivamente en el continuo entre verdadera residencia y un hábito migratorio forzoso que obliga a recorrer largas distancias. En este estudio presentamos un método innovador desarrollado como parte del proyecto *Migration Atlas* del British Trust for Ornithology (BTO) (Wernham et al., 2002), que permite analizar conjuntos de datos obtenidos mediante la recuperación de anillas y elaborar un índice cuantitativo de la tendencia migratoria

de las aves británicas. Para ello se emplean distribuciones de distancias entre el lugar de anillamiento y el de recuperación, pudiendo así clasificar las pautas de movimiento de especies individuales con respecto a las de otras especies. Las áreas entre las distribuciones de distancias acumulativas de las especies se tratan como diferencias interespecíficas, para posteriormente elaborar un mapa unidimensional utilizando una escala multidimensional. Hemos utilizado este método para analizar varios ejemplos que ilustran cómo puede emplearse en la investigación de los diferentes factores que afectan a las estrategias migratorias adoptadas por las especies, tales como el tamaño corporal, la territorialidad y la distribución; y en los estudios que evalúan sus repercusiones en los parámetros demográficos, como la supervivencia anual y el momento de la reproducción. Asimismo, hemos realizado varios análisis iniciales para demostrar de qué modo los cambios temporales en los índices podrían revelar consecuencias poblacionales originadas por el cambio medioambiental, que de otro modo no podrían medirse, lo que nos permite contar con una importante aplicación en la biología de la conservación. Por último, debatimos de qué forma podría perfeccionarse nuestro enfoque para la construcción de índices de tendencias migratorias, de manera que pudiera reducirse el sesgo provocado por la variación espacial o temporal en la tasa de recapturas, y cómo la incorporación de otros conjuntos de datos y de datos de recuperación de otros países podría mejorar significativamente su validez.

Palabras clave: Migración, Migración parcial, Aves, Estrategias, Ecología, Demografía.

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Introduction

Migratory strategies are frequently described using a classification of species as *migrants* or *residents*. With respect to the birds of Britain & Ireland, such a scheme can separate species that clearly always migrate long distances (such as Swallow *Hirundo rustica* and Swift *Apus apus*) from others that are rarely found to venture more than a few kilometres from their breeding areas (such as Blue Tit *Parus caeruleus* and Dunnock *Prunella modularis*). However, between species that do not migrate at all and species that can be considered to be obligate migrants there are many "partial migrants". A "partially migrant" species can be defined conservatively as one in which different individuals in a single breeding population have different migratory strategies. Partial migrants might then include species in which almost all individuals migrate long distances, while a minority remain close to their breeding areas, and species in which only a minority leave the breeding grounds. Although such mixed strategies have long been recognized, the classification of migratory behaviour has usually been an *ad hoc* process, making qualitative use of records of greatly reduced winter numbers, of observations in overseas wintering areas and of any ring-recoveries that have occurred. Because the range of migratory strategies is, in reality, a continuum, such a simple classification cannot describe it in full.

Recoveries, recaptures and resightings of ringed birds provide an invaluable tool in research into migration, allowing the locations of individuals at (at least) two points in time to be determined. As part of the research underpinning the British Trust for Ornithology's *Migration Atlas* project (Wernham et al., 2002), we investigated more rigorous methods for interpreting ring-recovery data than had been used previously. One aim was to develop a quantitative method for the definition of migratory tendency, i.e. a method by which we could identify where each species lies in the continuum between true residents and true migrants. As well as allowing us to classify strategies objectively, a quantitative system of this kind would allow us to conduct statistical tests to explore the ecological and life-history causes and consequences of variations in migratory tendency.

In this paper, we introduce our new approach to describing a species' migratory behaviour quantitatively, examine some first results of applying the technique to the birds of Britain and Ireland and explore how it might be used further in order to shed light on the evolutionary, ecological and life-history causes and consequences of migration. We also show how the method can be adapted to investigate changes in migratory strategy over time and variation between the strategies of different populations. Our aim here is to provide an overview of the approach and its potential value, describing what it tells us about patterns of migration across species and asking what evidence it can contribute to comparative studies in evolution and ecology.

Methods

Quantifying migratory strategy

We used the differences between the patterns of distances moved by individuals of different species between their breeding and wintering areas to reveal each species' migratory tendency relative to that of each other species. Data from the literature on the biology of all species that breed in Britain and Ireland were used to identify *seasons* (at a resolution of a half-month) during which the majority of birds could safely be assumed to be on their breeding grounds and in the wintering areas that form the end-point of their migration in the non-breeding season: the remaining periods represented conservative definitions of the spring and autumn passage "seasons" (see Wernham & Siriwardena, 2002 for details). Recoveries of dead, ringed birds that had been ringed in each species' breeding season and recovered during its winter season were then extracted from the BTO's data archives. Live recaptures and resightings were omitted to avoid the problems caused by the potentially large spatial and temporal variations in sampling effort and the absence of movements under 10 km from the database (see Wernham & Siriwardena, 2002). Problems with bias due to spatial and temporal variation in sampling effort are also likely to affect dead recovery data, but will not be as extreme because they depend on reporting by the general public rather than by specialist ringers or observers, whose activities are likely to be highly concentrated in reserves and other "hotspots", rather than diffuse across habitats frequented by humans. Only birds ringed as adults were included so that movements that could have incorporated an element of natal dispersal were omitted. Recoveries that were not considered to incorporate accurate timing information or that were otherwise potentially compromised by irregular ringing or finding circumstances were also omitted (details of the criteria for inclusion are given in Wernham & Siriwardena, 2002). Reasonable recovery sample sizes were required to produce reliable frequency distributions, so analyses were restricted to the 91 species for which 20 or more suitable recoveries were available.

The pattern of migratory movements by each species was interpreted through frequency distributions with respect to distance. Obligate migrants would be expected always to move large distances, true residents always to move only short distances and partial migrants to be recovered at a range of distances. Therefore, a left-skewed frequency distribution, showing a preponderance of short-distance recoveries, would suggest a more resident species (fig. 1C) while a right-skewed distribution, showing that long-distance movements dominate, would suggest an obligate migrant (fig. 1A). A partial migrant would have an intermediate frequency distribution of numbers of recoveries with distance (fig. 1B). The variation in migratory strategy could hence be quantified using the exact shape of the frequency distribution of distances moved.

We constructed movement distance frequency distributions in two ways that differed in the definition of what constitutes a "long distance". The "absolute" method considered that a given distance is equally meaningful for each species, i.e. that a species in which the whole population moved 10,000 km was more migratory than one in which all birds moved 2,000 km. To produce *absolute* distributions, the interval between zero and the approximate maximum distance travelled by a passerine (10,000 km: a Swallow movement) was divided into 100 equal segments, such that recoveries of each species were assigned to quantitatively similar categories; any recovery at a distance of more than 10,000 km was assigned to the maximum distance category. The "standardized" method defined long distances on a species-specific basis, as the maximum over which the species had been recorded to move, i.e. it considered species where more individuals migrate over distances approaching the species' maximum to be more migratory than species that rarely move distances close to the maximum. To produce *standardized* distributions, the interval between zero and the maximum distance moved by each species was divided into 20 equal segments, such that recoveries were assigned to categories that varied by species, in terms of absolute values, but were a fixed percentage of the maximum distance (5%) in width.

Each of the two approaches described above has its strengths and weaknesses, and each emphasizes a different aspect of a species' migratory behaviour. The "standardized" method allows the distance that constitutes "a long way" to vary between species. This means that two species that differ in the absolute distances that they move but that have similar proportions of their populations stopping to over-winter, say halfway to their most distant wintering areas, will be regarded as equally partially migrant. This should clearly be a desirable property in an index of migratory behaviour (differences in absolute distances moved can be tested independently). A problem with the standardized approach is that it relies on the existence of unusually distant recoveries of truly resident species to generate a left-skewed frequency distribution. These are rare, by definition, in resident species and large recovery samples must often exist before they are found. In their absence, maximum movement distances could be small, indicating no real migration at all but generating a frequency distribution suggesting a partially migrant strategy. The "absolute" method aids the detection of truly resident species by allowing them to have extremely left-skewed distributions but could hinder the detection of species with truly partially migrant strategies when the absolute distances moved are small. However, the use of a large number of divisions of the interval between zero and the maximum distance should maximize the sensitivity of any comparison of "absolute" distributions. Neither the standardized nor the absolute type of frequency distribution provides a clearly superior measure of migratory behaviour, so we analysed the two in parallel and interpreted the results in the light of their properties.

Once frequency distributions of each type had been produced for each of the 91 species considered, they were converted into cumulative proportions of the sample (fig. 1D, 1E) as in the first step in a Kolmogorov–Smirnov test of the homogeneity of two frequency distributions (Sokal & Rohlf, 1995). This removed any effect of sample size on differences between distributions. The difference between each pair of species was then quantified by calculating the area between the cumulative frequency curves of the two species (fig. 1F). A matrix of "dissimilarity" coefficients was thus generated between each species and each of the others. We used multi-dimensional scaling (MDS; Everitt, 1978; Kruskal & Wish, 1978; Manly, 1986) to express the differences between species in terms of a single index for each of the "standardized" and "absolute" methods. MDS finds the orientation of a set of points, in a specified number of dimensions, that distorts the original between-point distances as little as possible. The distortion of the original dissimilarities in producing a fit with the required dimensionality is measured using a quantity called "stress": values of around 0.05 or less are generally considered to indicate a good fit of the derived locations to the original dissimilarities (Kruskal & Wish, 1978).

The dissimilarity matrices derived from the *standardized* and *absolute* frequency distributions were analysed using the MDS procedure of SAS (SAS Institute, 1996). Each analysis allowed only a one-dimensional fit (i.e. the expression of the differences between distributions in terms of values on a single linear scale). Because the distributions concerned were generally simple and of a standard shape (sigmoid and asymptotic), differences between them could be readily interpreted as differences in the species' tendencies to migrate. The "stress" measures for one-dimensional MDS solutions indicated an acceptable fit for both the standardized and absolute approaches to index calculation (0.061 and 0.025, respectively).

Testing the causes and consequences of migratory behaviour

For the purposes of the *Migration Atlas* project, the indices were used to place each species in a simple, objective classification according to migratory tendency (Wernham & Siriwardena, 2002). In addition, we conducted a range of exploratory, comparative, multi-species analyses designed to investigate some of the physical, social and ecological factors that might influence or be affected by the choice of a migratory strategy. These analyses were intended to illustrate the potential of the method: there are a number of caveats and unresolved analytical issues that would have to be addressed before definitive results could be produced.

We analysed the variation in each of the absolute and standardized indices of migratory tendency between species by testing it against vari-

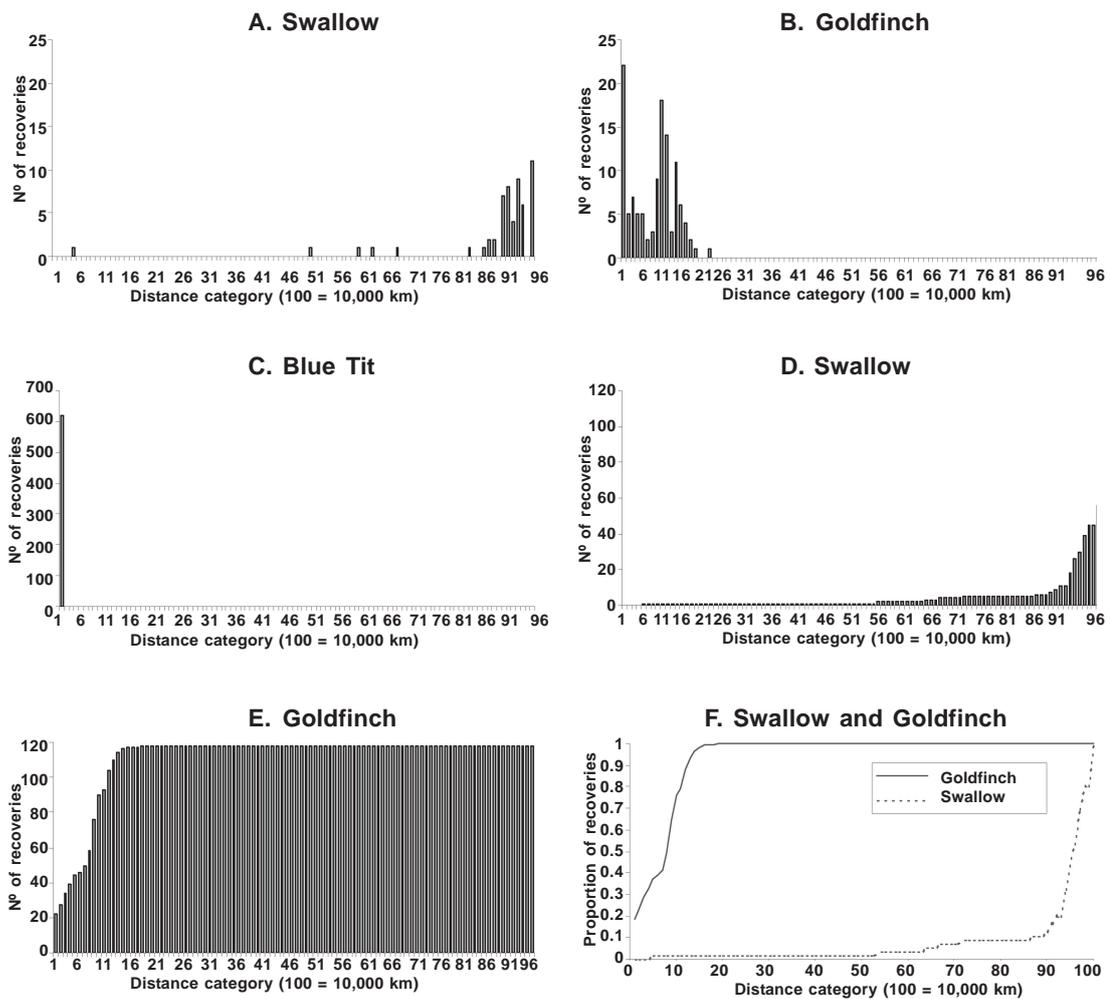


Fig. 1. Producing indices of migratory tendency using the "absolute" method. The graphs show frequency distributions of recoveries with respect to distance category (1–100; ringing to recovery distance): A. Swallow, a migrant; B. Goldfinch, a partial migrant; C. Blue Tit, a sedentary species; D. Swallow, data as a cumulative distribution; E. Goldfinch, data as a cumulative distribution; F. Swallow and Goldfinch, cumulative distributions superimposed to show how the area between the curves provides a quantitative measure of their dissimilarity.

Fig. 1. Elaboración de índices de tendencia migratoria mediante el empleo del método "absoluto". El gráfico indica las distribuciones de frecuencia de recuperaciones con respecto a la categoría de distancias (1–100; distancia entre el anillamiento y la recuperación): A. Golondrina común, migradora; B. Jilguero, migrador parcial; C. Herrerillo común, sedentario; D. Golondrina común, datos expresados como una distribución acumulativa; E. Jilguero, datos expresados como una distribución acumulativa; F. Golondrina común y jilguero, distribuciones acumulativas superpuestas a fin de demostrar cómo el área comprendida entre las curvas proporciona una medida cuantitativa de su disimilitud.

ous key variables using non-parametric tests (table 1). The tests were conducted using general linear models in which the ranks of the species with respect to each index of migratory tendency were either regressed against the ranks with respect to a continuous predictor or compared between the alternative classifications of a categori-

cal predictor. The regression tests were identical computationally to Spearman rank correlations (but were, philosophically, regressions) and the latter comparisons formed Kruskal-Wallis non-parametric analyses of variance (Sokal & Rohlf, 1995). The analyses were conducted using the GLM procedure of SAS (SAS Institute, Inc., 1990). We

used non-parametric methods because we did not know how the indices were distributed and because parametric analyses would emphasize the great variation we found among the more migratory species and the differences between these species and more sedentary ones, rather than the variation among all 91 species considered (see Results). The analyses were then repeated using only subsets of the data: first, using only passerines and birds of prey and, second, using only those species whose recovery sample sizes included 50 or more breeding season-to-winter movements (considering all species, and then passerines and birds of prey alone). In each case, we ran a new comparison of recovery distance distributions and calculated new standardized and absolute indices. Birds of prey and passerines together represent a reasonably homogeneous group of terrestrial species whose migratory strategies are likely to be driven by similar factors. Some relationships might only be detectable using a more homogenous set of species like this. We conducted the tests based only upon larger recovery samples because the shapes of recovery distance frequency distributions are likely to reflect real populations more closely as sample sizes increase.

These analyses considered the data on individual species to be independent measures of the relationships in question, an assumption that is unlikely to be strictly true. It was beyond the scope of our exploratory analyses to conduct formal phylogenetic analyses using independent nodes in evolutionary trees (Harvey & Pagel, 1991). Instead, we included in our analyses a specific control for the potentially confounding effects of phylogeny that controlled for interspecific relatedness at (approximately) the superfamily level (Sibley et al., 1988). "Superfamily", a categorical variable, was added into the general linear models relating the migratory tendency indices (transformed into ranks) to each continuous variable (the latter also being transformed into ranks where appropriate). We present results both including and excluding this control, because the disappearance of a significant difference after the introduction of a control for phylogeny would not necessarily indicate that it had been false: it would merely show that the relationship were confounded with phylogenetic differences. Conversely, any significant effects that are detected only after controlling for phylogeny should not be considered to be less important biologically than effects that are detectable in the presence of phylogenetic variation. Such a pattern would occur where a relationship with migratory tendency is significant within phylogenetic groups but is obscured by the variation between the groups when all species are pooled. Phylogenetic controls were not applied to the analyses using categorical variables because many of the categories in each case were entirely confounded with superfamily. The details of the memberships of the superfamily classifications that we used are given in Appendix 3a of Wernham et al. (2002).

Changes in migratory tendency over time

The quantitative indices of migratory tendency described above could readily be applied to any set of sub-divisions of a population, sample sizes permitting, provided that ring-recovery data can reliably be assigned to the sub-divisions. We carried out a first exploration of variation in migratory strategy over time for each species by dividing the larger data sets used in the analyses described above (40 or more recoveries) into two equal parts (around the median recovery year). A total of 73 species had sufficiently large recovery sample sizes for these distributions to be produced. The "standardized" frequency distributions for the periods both before and after the median year were generated using the species-specific maximum distance across the whole data set (early and late combined). We then tested the significance of the differences between the *early* and *late* recovery distance distributions using Kolmogorov-Smirnov tests (Sokal & Rohlf, 1995) for each species. This rather coarse temporal analysis had the benefit of maximizing the number of species that could be tested. Ring-recovery sample sizes represent the only constraint on how time periods might be chosen to test more specific or complex temporal hypotheses. The results presented here provide only a guide to what is possible and to where interesting changes might have occurred.

Differences between species' breeding and wintering populations

We compared the recovery frequency distributions for the breeding and wintering populations of species present in Britain & Ireland all year to ask whether we could formally identify partial migrants (species whose breeding populations were more migratory than their wintering ones) and species whose British and Irish populations are augmented by winter immigrants. This comparison used standardized and absolute frequency distributions for birds ringed in winter in Britain & Ireland and recovered in the breeding season, in conjunction with the breeding-to-winter distributions used in our other analyses. As previously, tests using absolute distributions will have revealed differences in the absolute distances moved, while those using standardized distributions were sensitive to differences in the proportion of the population that moved. Once again, these analyses were conducted using two-sample Kolmogorov-Smirnov tests (Sokal & Rohlf, 1995). A total of 47 species were considered, all those for which at least 20 suitable recoveries were available from each of the breeding and wintering populations.

Results

Variations in migratory tendency

The range of variation in migratory tendency revealed by the "standardized" and "absolute" forms of

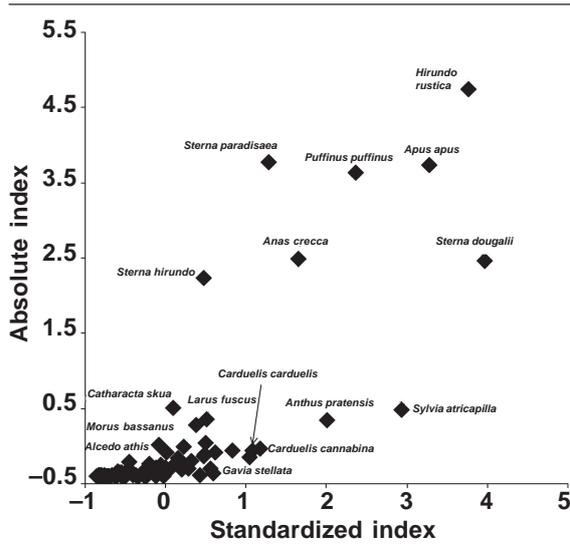


Fig. 2. Plot of indices of migratory tendency derived by the absolute method against those derived by the standardized method. Selected species' data points are identified by their Latin names.

Fig. 2. Representación gráfica de los índices de tendencia migratoria, derivados mediante el método absoluto, frente a los derivados mediante el método estandarizado. Los puntos correspondientes a los datos de las especies seleccionadas se identifican por sus nombres en latín.

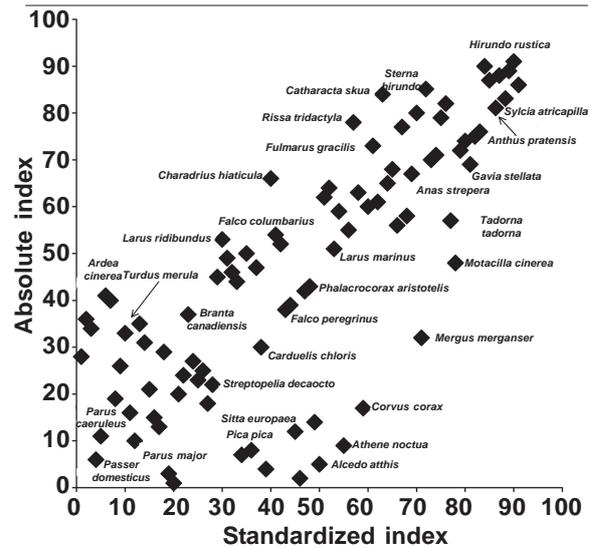


Fig. 3. Plot of indices of migratory tendency derived by the absolute and standardized methods, transformed into ranks. Selected species' data points are identified by their Latin names.

Fig. 3. Representación gráfica de los índices de tendencia migratoria, derivados mediante los métodos absolutos y estandarizados, transformados en rangos. Los puntos correspondientes a los datos de las especies seleccionadas se identifican por sus nombres en latín.

our index is illustrated in figure 2. Each index shows a gradient from more migratory (highly positive values) to more sedentary (highly negative values), so that the concentration towards the bottom left of the graph (especially along the "absolute" axis) shows a large number of species with comparatively sedentary strategies. Obligate long-distance migrants can be seen to form a group discrete from more resident species, especially with respect to the absolute index (more positive index values, towards the top right of figure 2). Most of the variation in strategy therefore separates the few long-distance migrants with sufficiently large sample sizes for analysis from the majority of relatively non-migrant species. Within the broad group of "migrants", there is also greater variation in index values than there is among the more resident species.

The uneven spread of species in figure 2 and, in particular, the proximity of genuine partial migrants such as Goldfinch *Carduelis carduelis* and Linnet *C. cannabina* to the "sedentary" species cluster suggested that examining the relative indices for each species as they are presented was unlikely to be very informative. The index values were, therefore, transformed into ranks, generating a clearer picture

of the relative positions of each species (fig. 3). These ranks then formed the basis for statistical tests examining the causes and consequences of migratory strategies. Figure 3 shows that the position of most species in the rank order of most to least migrant tends not to be dissimilar in terms of the two indices. The bias in the sample of species towards relatively sedentary species means that only a small proportion of the variation in strategy illustrated in figure 3 is made up of obligate migrants, so partial migrants, such as Meadow Pipit *Anthus pratensis*, and shorter-distance obligate migrants, such as Blackcap *Sylvia atricapilla*, can be found towards the "highly migrant" end of the range.

Correlates of migratory tendency

Body size (length, wingspan, wing length and weight) was a significant predictor of migratory tendency only for passerines and birds of prey (table 2). The significant results with no control for phylogeny suggested that larger species were less migratory, but the opposite pattern was found in the four results that were significant after the control was added (table 2).

Body shape had a clearer relationship with migratory tendency: more migratory species tended to have larger wing:body ratios and lower wing-loadings, reflecting morphological adaptations to promote efficient long-distance flight (table 2). There were also consistent, negative relationships between population size and migratory tendency (table 2), suggesting that rarer species tend to be more migratory. However, the effect was limited to the results for the standardized index, indicating that it was not related to the distances moved and that it depended on the input of the relatively sedentary species. A concordant, even stronger pattern was found with respect to distribution (number of occupied breeding atlas squares): species with restricted distributions tended to be more migratory (table 2). This variable had significant effects on the absolute indices as well as the standardized ones, especially when all species were included (table 2).

The extent of territoriality was highly significantly related to migratory tendency, with strongly territorial species tending to be less migratory than colonial and solitary or weakly territorial species (table 3). This pattern was stronger in the analyses using absolute recovery distance distributions, suggesting that shorter migratory distances, in absolute terms, are particularly associated with strong territoriality. Nesting habit was also significantly related to migratory tendency, with open-nesting species tending to be more migratory than hole-nesting species by both standardized and absolute approaches, but the pattern was much less clear when passerines and birds of prey were examined alone (table 4).

Of the tests exploring the possible effects of migratory strategy on demography (table 5), one very clear result indicated that more migratory species tend to begin to breed later: six of the eight indices of migratory tendency tested gave rise to such a result and five of these gave rise to similar, significant results after the incorporation of controls for phylogeny. This may be unsurprising because migrants are likely to leave their breeding grounds in autumn because conditions are becoming unsuitable and are therefore unlikely to return until the annual improvement in spring is well advanced. However, a correspondingly strong effect with respect to the lengths of breeding seasons was *not* found, reflecting a tendency for many migrants to finish breeding later as well.

When all species were considered, all the indices of migratory tendency indicated that more migratory species had higher survival rates (table 5). However, this pattern was entirely confounded with phylogeny, so may be more related to factors such as body size than to migratory strategy *per se*. Among the passerines and birds of prey, only one test was significant, but it showed that more migratory species had *lower* survival rates, and this result was robust to the control for phylogeny (table 5).

Changes in migratory tendency

We found significant or near-significant temporal shifts in recovery distance distribution by one or both of the standardized and absolute methods of

calculating frequency distributions for 22 of the 73 species tested (table 6). Of the 51 species for which there was no significant change with time, 23 were species identified as sedentary in tests of the differences between ringing and recovery locations (Wernham et al., 2002). Note, however, that although Mute Swan and Buzzard were classified as non-migratory in the overall analyses, we found significant changes in migratory tendency over time for these species, suggesting that the lack of a clear pattern overall may have masked potentially important temporal variation for some species. More generally, for 14 of the species whose migratory tendency changed over time, the difference found was significant by both methods, the other eight cases involving small shifts in distribution or differences in the short-distance movements undertaken by very sedentary species (table 6). It was commoner for species to have shifted towards shorter than towards longer migratory distances (15 and 5 species, respectively), but there was no clear taxonomic pattern with respect to the direction of the changes (see table 6). Two other species have undergone more complex changes in distribution (table 6), in which the early and frequency distributions were significantly different, but not in ways that can be interpreted as simple changes in the migratory strategy of an average individual.

Differences in migratory tendency between breeding and wintering populations

Breeding and wintering populations differed in migratory tendency in terms of one or both forms of frequency distribution for 31 of the 47 species tested (table 7). Of these 31 differences, ten were significant only when standardized distributions were used while only one (*Mistle Thrush Turdus viscivorus*) was significant only when absolute distributions were used. For 11 species, the breeding population was the more migratory, indicating that the species concerned are partial migrants, but for 20 species it was the wintering one, reflecting that immigrants join resident populations in winter (table 7). Non-significant results could indicate entirely sedentary populations or, hypothetically, British & Irish populations that migrate annually between breeding and wintering grounds within the islands, with no immigration from overseas in either season.

Discussion

Variation in migratory strategy within and between species

Our new, quantitative method has identified a wide range of variation in migratory strategy among the species we were able to test and more would doubtless be added if larger recovery samples were available for a larger number of species. We have produced the first objective and quantitative definition of the strategies intermediate between seden-

Table 1. Variables used in tests of the influences on and of indices of migratory tendency.

Tabla 1. Variables empleadas para determinar las influencias de los índices en y de tendencia migratoria.

Factor of interest	Variable(s) used	Categories/derivation	Sources
Potential influences on migratory tendency			
Body size	Length, wingspan, wing length, weight	Averages for adult birds	Snow & Perrins, 1998
Body shape	Wing-loading and wing:body ratio	Weight/wing length and wingspan/body length, respectively	Snow & Perrins, 1998
Social organization	Coarse classification of breeding strategy	Colonial, intermediate, territorial	Snow & Perrins, 1998
Nesting strategy	Type of nest built/used	Open, hole	Snow & Perrins, 1998
Population density	UK population size, no. of individuals		Stone et al., 1997
Distribution	Ubiquity of species within Britain & Ireland	Number of occupied 10 x 10 km squares in Britain & Ireland, 1988–1991	Gibbons et al., 1993
Potential effects of migratory tendency			
Survival	Average adult annual survival rate		Balmer & Peach, 1997; Siriwardena et al., 1998
Timing of breeding	Laying date, length of breeding season	95 th percentile for start of egg-laying, and 95 th percentile for end of breeding season minus 95 th percentile for start for length of season (both British & Irish breeders only)	Campbell

tary residency and an obligate, long-distance migratory habit. Within this spread of strategies (figs. 2, 3), there are interesting patterns with respect to ecology and phylogeny. Many of the most migratory species were waterbirds, waders and seabirds, which reflects both their true strategies and a degree of reporting bias: many are conspicuous or are quarry species at various points along their migration routes, making recovery more likely. The highly migratory position of many seabirds reflects the dispersal of almost all species away from their breeding colonies in winter. We did identify some passerines, such as Swallow and Swift, as being highly migratory, but many migrant passerines (e.g. many warblers) were absent from the data set because ring-recoveries are increasingly scarce further from the British Isles, especially south of the Sahara. Notwithstanding this bias, the pattern in figures 2 and 3 also reflects the frequent occurrence of residency in Britain & Ireland: species such as Greenfinch *Carduelis chloris* and Chaffinch

Fringilla coelebs are far more migratory where a continental climate of harsher winters and hotter summers prevails. Conditions in Britain & Ireland are also mild enough to allow some species that always migrate away from breeding grounds elsewhere to become partial migrants (Lundberg, 1988).

There is a notable group of species off the main diagonal in figure 3, towards the standardized index axis, that includes Yellowhammer *Emberiza citrinella*, Buzzard *Buteo buteo* and Little Owl *Athene noctua*. These are species for which the standardized index suggests that migratory tendency is somewhat stronger than does the absolute index. In practice, these species may demonstrate why the absolute index is needed in addition to the standardized one: their maximum recovery distances are somewhat short, leading to "flat", stretched-out standardized recovery distributions that suggest more partially migratory species-specific strategies than probably exist in reality, at least in terms of the recovery sample.

Table 2. Relationships between indices of migratory tendency and continuous ecological/life–history variables reflecting potential influences on them. Results are shown for indices derived from all species and from raptors and passerines only and from species with 20 or more recoveries and those with 50 or more recoveries within each of these sets. Results (slope parameters and P-values) are presented for both the standardized (Stan) and absolute (Abs) methods. P(phylog) shows the P–value for the same relationship when a control for phylogenetic relatedness was incorporated. Slope parameters from univariate tests are shown unless the test was significant only after the control for phylogeny was applied, when the parameter from the latter is given; where both tests produced significant slopes, slope signs were always the same. * Slopes for which the test with or without a control for phylogeny was significant or near–significant at the 5% level; N. Number of species.

*Tabla 2. Relaciones entre índices de tendencia migratoria y variables continuas ecológicas/vitales que reflejan las influencias potenciales a las que pueden estar sometidas. Los resultados se indican para índices derivados de todas las especies y únicamente de aves rapaces y paseriformes, así como de especies con 20 o más recuperaciones y de aquellas con 50 o más recuperaciones en cada uno de estos conjuntos. Los resultados (parámetros de pendiente y valores P) se indican tanto para los métodos estandarizados (Stan) como absolutos (Abs). P (phylog) indica el valor P para la misma relación tras haberse incorporado un control para la relación filogenética. Se indican los parámetros de pendiente de los tests univariantes, salvo que el test sólo haya sido significativo tras haber aplicado el control para la filogenia en los casos en que se ha proporcionado el parámetro de ésta; cuando ambos tests dieron pendientes significativas, los signos de pendiente siempre fueron iguales. * Pendientes en los que el test con o sin control para la filogenia fue significativo o casi significativo en el nivel del 5%; N. Número de especies.*

Variable		All species				Passerines & birds of prey			
		>20 Recoveries		>50 Recoveries		>20 Recoveries		>50 Recoveries	
		Stan	Abs	Stan	Abs	Stan	Abs	Stan	Abs
N		91	91	71	71	46	46	36	36
Body size									
Length	Slope	–	–	–	–	–	–	0.211*	–0.352*
	P	0.346	0.304	0.212	0.490	0.738	0.628	0.218	0.035
	P(phylog)	0.460	0.159	0.914	0.131	0.138	0.508	0.037	0.399
Wingspan	Slope	–	–	–	–	–	–	0.211*	–0.316*
	P	0.246	0.094	0.114	0.158	0.508	0.891	0.218	0.061
	P(phylog)	0.336	0.273	0.887	0.250	0.124	0.432	0.024	0.519
Wing length	Slope	–	–	–	–	0.139*	–	0.273*	–0.243
	P	0.296	0.126	0.159	0.246	0.356	0.860	0.107	0.154
	P(phylog)	0.429	0.399	0.930	0.368	0.063	0.230	0.006	0.859
Weight	Slope	–	–	–	–	–	–	–	–0.422*
	P	0.251	0.200	0.125	0.253	0.822	0.243	0.503	0.010
	P(phylog)	0.749	0.244	0.728	0.436	0.506	0.524	0.159	0.111
Body shape									
Wing–loading	Slope	–	–	–	–	–	–0.280*	–	–0.480*
	P	0.314	0.313	0.165	0.299	0.362	0.060	0.958	0.003
	P(phylog)	0.516	0.100	0.962	0.293	0.338	0.610	0.163	0.099
Wing:body ratio	Slope	0.259*	0.352*	0.337*	0.357*	–	–	–	–
	P	0.013	0.001	0.004	0.002	0.193	0.303	0.176	0.402
	P(phylog)	0.245	0.030	0.140	0.061	0.259	0.210	0.108	0.937

Table 2. (Cont.)

Variable		All species				Passerines & birds of prey			
		>20 Recoveries		>50 Recoveries		>20 Recoveries		>50 Recoveries	
		Stan	Abs	Stan	Abs	Stan	Abs	Stan	Abs
Population									
Population size	Slope	-0.312*	-	-0.308*	-	-0.432*	-	-0.469*	-
	P	0.003	0.111	0.009	0.099	0.003	0.718	0.004	0.885
	P(phylog)	0.003	0.463	0.058	0.156	0.001	0.654	0.012	0.268
Distribution									
No. atlas squares occupied	Slope	-0.495*	-0.408*	-0.551*	-0.448*	-0.323*	0.261*	-0.313*	-
	P	<0.001	<0.001	<0.001	<0.001	0.029	0.080	0.063	0.150
	P(phylog)	<0.001	0.128	0.001	0.047	0.031	0.352	0.145	0.739

Table 3. Tests of the variation in migratory tendency between species with territorial, weakly territorial or semi-colonial and colonial habits. The categories were compared using Kruskal–Wallis (K–W) tests; N. Numbers of species; MR. Mean rank. (Results are shown for both the standardized and absolute indices.)

Tabla 3. Test de variación en la tendencia migratoria entre especies con hábitos territoriales, territoriales débiles o semicoloniales y coloniales. Las categorías se compararon utilizando tests de Kruskal–Wallis (K–W): N. Número de especies. MR. Rango medio. (Se indican los resultados para los índices estandarizados y absolutos.)

Social organization	Standardized				Absolute			
	>20 Recoveries		>50 Recoveries		>20 Recoveries		>50 Recoveries	
	N	MR	N	MR	N	MR	N	MR
All species								
Colonial	32	52.5	28	43.1	32	58.0	28	45.8
Intermediate	17	54.5	11	41.1	17	52.6	11	40.9
Territorial	42	37.6	32	28.1	42	34.2	32	25.7
K–W H (2 d.f.)	7.94		8.69		16.0		14.9	
P	0.019		0.013		< 0.001		< 0.001	
Passerines & birds of prey only								
Colonial	7	23.1	5	16.8	7	21.9	5	13.8
Intermediate	8	27.8	7	24.1	8	29.9	7	26.1
Territorial	31	22.5	24	17.2	31	22.2	24	17.3
K–W H (2 d.f.)	0.985		2.50		2.19		5.02	
P	0.611		0.287		0.335		0.081	

Table 4. Tests of the variation in migratory tendency between species with open- and hole-nesting strategies. (For abbreviations, see table 3.)

Tabla 4. Tests de variación en la tendencia migratoria entre especies con estrategias de nidificación en nido abierto o en agujero. (Para las abreviaturas, ver la tabla 3.)

Nesting strategy	Standardized				Absolute			
	>20 Recoveries		>50 Recoveries		>20 Recoveries		>50 Recoveries	
	N	MR	N	MR	N	MR	N	MR
All species								
Open	74	49.0	60	38.6	74	49.9	60	38.6
Hole	17	33.1	11	22.1	17	29.1	11	21.9
K-W H (1 d.f.)	4.95		5.91		8.60		6.07	
P	0.026		0.015		0.003		0.014	
Passerines & birds of prey only								
Open	29	24.3	25	19.9	29	26.1	25	19.7
Hole	17	22.2	11	15.3	17	19.0	11	15.8
K-W H (1 d.f.)	0.262		1.49		3.03		1.06	
P	0.609		0.223		0.082		0.303	

Our quantitative indices could prove most valuable in exploring intraspecific and interspecific variations in the patterns of movement of species with strategies intermediate between genuine residents like House Sparrow *Passer montanus* and Bullfinch *Pyrrhula pyrrhula* and the long-distance migrants in figures 2 and 3. These species include Goldfinch, Linnet, Puffin *Fratercula arctica*, Tufted Duck *Aythya fuligula*, Oystercatcher *Haematopus ostralegus* and Lesser Black-backed Gull *Larus fuscus*: it is from studying them that new evidence as to how bird migration in general is controlled is most likely to come and quantifying their strategies has been a first step.

The consensus of research to-date is that migratory tendency is under strong genetic control (Berthold, 1996, 2001), although the detail of how the distances individuals move are determined remains unclear. Intraspecific variation in strategy may derive from effects of genetic diversity, dominance or factors related to life-histories, such as age- or sex-specific variation. Our indices do not currently allow these factors to be separated, but physical and social influences, for example, are often confounded and the distinction between "differential migration" with respect to age or sex and socially-mediated "partial migration" may be more semantic than biologically meaningful, because variation in migratory strategy is likely to be correlated with some genetic or demographic variation even if social dominance is the real determining factor (Siriwardena & Wernham, 2002).

Temporal changes in migration patterns

Changes in migratory tendency over time are of intrinsic interest in biology and can have important implications for conservation, for example, as either causes or consequences of variations in abundance. For example, climate change could cause a decrease in the proportion of a partial migrant's population that migrates, making it less vulnerable to hunting pressure overseas, or migration to distant wintering grounds could be density-dependent such that breeding population increases in Britain have little effect on winter abundance. In general, any improvements to our understanding of past influences on changes in abundance would aid the development of conservation policies for the future. There were no clear associations between changes in migratory behaviour and population trends (from Baillie et al., 2001; Gibbons et al., 1993), but our analyses revealed an interesting tendency for migratory movements to have become shorter, as would be predicted of an effect of global warming. Migratory populations or individuals might have begun to migrate shorter distances or the proportion of a population that migrates might have fallen. (Closer scrutiny of the recovery distance distributions would clarify this for each species.) However, examination of the species involved suggests that an effect of global warming is unlikely to be a general explanation: they include several seabirds and waders, but not the partially migrant terrestrial species like Meadow Pipit, Linnet and Goldfinch that might be expected to be respond to a warmer

Table 5. Relationships between indices of migratory tendency and continuous ecological/life–history variables reflecting their potential effects on demography. (For abbreviations, see table 2.)

Tabla 5. Relaciones entre los índices de tendencia migratoria y variables continuas ecológicas/vitales que reflejan sus posibles efectos en la demografía. (Para las abreviaturas, ver la tabla 2.)

Variable		All species				Passerines & birds of prey			
		>20 Recoveries		>50 Recoveries		>20 Recoveries		> 50 Recoveries	
		Stan	Abs	Stan	Abs	Stan	Abs	Stan	Abs
Timing of breeding									
Sample size		88	88	70	70	46	46	36	36
First egg date	Slope	0.465	0.540	0.500	0.540	–	0.283	–	0.318
	P	<0.001	<0.001	<0.001	<0.001	0.282	0.054	0.305	0.056
	P(phylog)	0.002	<0.001	0.002	<0.001	0.634	0.088	0.741	0.252
Length of breeding season	Slope	–0.173	–	–	–	–	–	–	–
	P	0.105	0.303	0.260	0.541	0.986	0.535	0.613	0.793
	P(phylog)	0.079	0.120	0.642	0.595	0.673	0.755	0.096	0.561
Survival									
Sample size		76	76	61	61	40	40	31	31
Annual survival rate	Slope	0.258	0.343	0.338	0.356	–	–	–	–0.480
	P	0.025	0.002	0.008	0.005	0.984	0.603	0.923	0.006
	P(phylog)	0.786	0.744	0.698	0.558	0.742	0.869	0.542	0.078

climate with a simple reduction in migratory distance (table 6). It is also notable that no temporal change was detectable for 51 of the 73 species tested (only half of which were identified as sedentary by Wernham et al., 2002; table 6), suggesting that large and uniform effects of climate change on migratory behaviour have not occurred, although more changes might have been found with larger recovery sample sizes. However, changing migratory distance is just one of several potential responses of bird populations to climate change, and one which, like the others, could be constrained because the behaviours concerned are controlled by endogenous rhythms and photoperiodic cues that are unrelated to climate (Coppack & Both, 2002). It is interesting that a relatively large proportion (9/22) of the species for which significant changes were found were seabirds and we found several complex patterns of change (table 6), which may reflect a tendency for only some parts of the population to become more migratory (for example, young birds or birds from further north). These patterns need further investigation, probably on a species-by-species basis. In fact, because climate change, at least, is likely to affect different species differently, future analyses might best be species-specific. The year around which distributions were divided could clearly have been critical in determin-

ing what temporal changes were revealed and this would be the first parameter to vary in future analyses. Adequately controlled tests, focusing on the species and time periods most appropriate for testing specific hypotheses, are now needed to provide a definitive answer about the possible effects of global climate change on migration patterns. Such research could build on our method and on the results presented here.

Comparisons of breeding and wintering populations

Our analyses provided a formal identification of a range of species as having either partially migrant breeding populations or winter populations that are augmented by immigrants (table 7). Passerines were significantly more likely to fall into the former category (G-test, Sokal & Rohlf (1995): $G = 11.50$, 1 d.f., $P < 0.001$), reflecting the use of Britain & Ireland as a wintering ground by many non-passerines that also breed in the islands. Large numbers of Fennoscandian breeding Blackbirds *Turdus merula* and Chaffinches also winter in the British Isles, joining the breeding populations (Wernham et al., 2002), but these species are unusual. All these patterns are already well-known so, apart from the new, quantitative information that our analyses provide, the more interesting

Table 6. Results of tests of temporal changes in migratory tendency. Species are shown in taxonomic order. Sample sizes (S) refer to total numbers of breeding-to-winter movements that were divided in two around the median recovery years (Y) (19...) shown to produce "early" and "late" data sets. K-S test results (K-S) show significance levels from two-sample Kolmogorov-Smirnov tests as follows: * $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$. Direction (D) indicates the direction of the effects: a minus (-) indicates that movements have become shorter with time and a plus (+) that they have become longer. Differences significant in one analysis only: #. Significant only in the standardized analysis because differences are small in terms of absolute distance; ##. A slight shift towards shorter migratory distances which was detected only by the greater distance resolution in the absolute analysis. Complex effects: ‡. Most recoveries have been in the middle of the range of distances (by both methods), wherein they became less distant after the median year, but other recoveries have been spread throughout the range of distances in both periods and many more minor shifts in the distribution have also occurred; †. Movements before the median year had a bimodal distribution; subsequently, the shorter distance movements became rarer and the longer distance movements more spread out, i.e. commonly both longer and shorter than the previous longer mode.

Tabla 6. Resultados de tests de cambios temporales en la tendencia migratoria. Las especies se indican por orden taxonómico. Los tamaños de las muestras (S) se refieren al número total de movimientos entre la reproducción y el invierno, que se dividieron en dos en torno a los años medios de recuperación (19...), indicados para elaborar conjuntos de datos anteriores y posteriores. K-S test results indica los niveles significativos obtenidos en tests de Kolmogorov-Smirnov para dos muestras según lo indicado a continuación: * $P < 0,1$, ** $P < 0,05$, *** $P < 0,01$. Direction indica la dirección de los efectos: un signo menos (-) indica que los movimientos se han reducido con el tiempo, mientras que un signo más (+) revela que se han prolongado. Diferencias significativas en un único análisis: #. Significativa sólo en el análisis estandarizado porque las diferencias son pequeñas en términos de distancia absoluta; ##. Un ligero cambio hacia distancias migratorias más pequeñas detectadas solo por la mayor resolución de distancia en el análisis absoluto. Efectos complejos: ‡. La mayoría de recuperaciones se encuentran en el centro de la gama de distancias (en ambos métodos), donde llegaron a ser menos distantes después de la mitad del año, pero otras recuperaciones se han dispersado a través de la gama de distancias en ambos períodos y además se han producido más cambios de menor importancia en la distribución; †. Los movimientos antes de la mitad del año tenían una distribución bimodal; posteriormente, los movimientos de corta distancia se convirtieron en más raros y los de larga distancia más dispersos, es decir comunmente tanto más largo y más corto que la moda previa más larga.

Species	S	Y	K-S			Species	S	Y	K-S		
			Stan	Abs	D				Stan	Abs	D
Fulmar	111	84				Roseate Tern	179	69			
Manx Shearwater	61	69	*	*	†	Common Tern	172	78	***	-##	
Gannet	387	68	***	***	-	Arctic Tern	47	80			
Cormorant	2,006	73				Guillemot	1,830	87	**		+‡
Shag	1,745	78	***	**	-	Razorbill	710	81	**	**	+
Grey Heron	462	72				Puffin	143	84	**	**	-
Mute Swan	1,997	83	**		+‡	Stock Dove	92	70.5			
Greylag Goose	114	88.5				Wood Pigeon	559	67			
Canada Goose	1,902	82				Barn Owl	1,207	90			
Shelduck	68	74.5				Tawny Owl	253	85			
Mallard	2,492	70				Kingfisher	82	78			
Pochard	65	82				Swallow	56	68.5			
Tufted Duck	261	78	***	***	-	Meadow Pipit	55	64			
Eider	524	72	***		-#	Pied Wagtail	308	68	**	***	-
Hen Harrier	53	72				Wren	109	82			

Table 6. (Cont.)

Species	S	Y	K-S		D	Species	S	Y	K-S		D
			Stan	Abs					Stan	Abs	
Sparrowhawk	522	85				Dunnock	321	75			
Buzzard	110	82	***		-#	Robin	590	75			
Kestrel	863	82	***		-#	Blackbird	1,525	71	**		-#
Merlin	122	88				Song Thrush	963	64	***	***	-
Peregrine	97	88				Mistle Thrush	89	63			
Moorhen	68	65.5				Blue Tit	621	81			
Coot	48	73.5				Great Tit	308	83			
Oystercatcher	383	77	***	**	-	Jay	129	78			
Ringed Plover	56	67.5				Magpie	91	81			
Lapwing	701	53	***	***	+	Jackdaw	113	72			
Snipe	65	53				Rook	108	71			
Woodcock	277	35				Crow	156	73.5			
Curlew	181	54	**	**	-	Raven	78	76			
Redshank	125	63				Starling	1,433	65			
Great Skua	240	77	**	**	-	House Sparrow	358	66			
Black-headed Gull	1,134	66	**		-#	Chaffinch	154	77			
Common Gull	98	83				Greenfinch	382	75			
Lesser B-b Gull	654	69				Goldfinch	118	71			
Herring Gull	977	73				Linnet	197	65	***	***	+
Great B-b Gull	220	79				Bullfinch	338	73			
Kittiwake	240	80				Reed Bunting	80	79			
Sandwich Tern	1,043	72	**	***	‡						

results may involve the species for which such patterns have not been described before. However, it is important to note that the results for these species, which include Mute Swan *Cygnus olor*, Coot *Fulica atra*, Blue Tit *Parus caeruleus* and Rook *Corvus frugilegus*, may only reflect effects of dispersal or of geographical or habitat differences between the breeding and wintering samples. For example, any dispersal in autumn will have been confounded with movements to wintering grounds and the breeding and winter samples may differ, for example, if the predominant catching methods or types of site for ringing differ markedly between seasons.

Causes and consequences of differences in migratory tendency

Our analyses of some of the potential ecological and life-history correlates of interspecific variation in migratory tendency revealed some interesting patterns. Comparing the results with and without con-

trols for phylogenetic relatedness provides a particularly useful perspective on the taxonomic level at which relationships occur and on the possibility that they are artefacts of other differences between taxonomic groups. With respect to body size, some results indicated that larger species are less migratory, as predicted, but the relationship was detectable only among passerines and birds of prey, related only to the absolute distances that they moved rather than to the proportions of their populations that migrate and was confounded with phylogeny. This result suggests that body size is related to the dichotomy between migrant and resident strategies as either is adopted at the superfamily level. After controlling for phylogeny, i.e. within superfamilies, larger proportions of the populations of larger species tend to migrate. This could indicate that larger species are more likely than their close relatives to move away from their breeding areas, although not necessarily moving very far, perhaps because their size allows them greater mobility.

There were no such apparent contradictions in the results with respect to body shape, but the effect of wing-loading was detectable only with the absolute index for passerines and birds of prey and the effect of wing:body ratio was detectable only when all species were included (table 2). Further, only the relationships between the absolute indices and wing:body ratio were still significant after controls for phylogeny had been added (table 2). The effect of wing-loading on passerines and birds of prey was therefore confounded with phylogenetic variation and was either unimportant or, perhaps more probably, obscured by other factors when all species were included. The wing:body ratio results showed that individuals of relatively longer-winged species tend more often both to go further and to adopt a migrant strategy, but that only the former pattern was robust to phylogenetic variation. This suggests that morphology is related to the absolute distances moved by individual species, but that it is also related to whether species migrate or not at a higher taxonomic level.

The relationships between population size and distribution and migratory tendency (table 2) probably reflect the fact that species near the northern edges of their breeding ranges are more likely to have to move south and west in winter and that the same species tend to be rarer than species that are able to remain in the British Isles all year round. This test does not examine the effect of population "density", however, because different species' populations will be distributed differently in the landscape according to social organization and variations in habitat.

Higher quality individuals of species that are both territorial and migratory tend to arrive on their breeding grounds earlier (e.g. Francis & Cooke, 1986; Møller, 1994; Lozano et al., 1996), probably reflecting a system in which individuals compete for access to high quality territories via arrival times (Kokko, 1999). A logical corollary of this is that residency is promoted by territoriality and that there is a concomitant selection pressure for remaining closer to breeding areas in winter or returning to them earlier in spring. Among all species, our results supported this hypothesis (table 3), but the pattern was much weaker when passerines and birds of prey were considered alone, perhaps because most of these species are territorial. However, it probably also reflects the extent to which social organization is confounded with phylogeny.

Whether species build open-cup or hole nests could be an important determinant of migratory behaviour, because nest-holes may be limiting for the latter, potentially providing a selective pressure for residency, shorter migration distances or an early return to the breeding grounds (Von Haartman, 1968; Alerstam & Högstedt, 1981). Our results support the idea that open-cup nesters are less constrained in annual movements by their breeding strategy (table 3). The pattern was weaker when passerines and birds of prey were examined alone

(table 3), suggesting that the pattern across all species could largely reflect more frequent hole-nesting among the passerines and birds of prey included, which tend to be relatively sedentary (figs. 2, 3). Nevertheless, the prevalence of hole-nesting among the passerines and raptors could also be a key factor driving their relatively low average migratory tendency.

Our results suggest that demography is strongly influenced by migratory strategy, in terms of both the timing of breeding and survival: migrants bred later and tended to have higher mortality rates (after controlling for phylogeny; table 5). No effect of laying date was found in the standardized indices for passerines and birds of prey, suggesting that, at least among these species, later laying is associated more with migratory distance than with the selection of migratory strategy. This makes intuitive sense given that a major constraint on the date at which breeding can begin is likely to be travelling time. The effect of survival was also detected with the absolute index, suggesting that species that migrate further tend to have lower survival rates (presumably reflecting the hazards of migration). We also conducted tests of relationships with reproductive effort (egg volume and clutch size) but these were inconclusive, probably because this demographic variable has other components in addition to the ones that we were able to test (Siriwardena & Wernham, 2002).

Many possible influences on, and consequences of, migratory tendency remain to be tested. These tests have not been conducted here either because they would require analyses too complex for an exploratory analysis or because the data needed were not available to us. It would also be useful to re-run our analyses using more formal phylogenetic controls and to investigate possible interactions between the relationships we have found using multivariate analyses.

The potential of the approach: caveats and future work

Analyses of ring-recovery data are generally dependent on the spatial and/or temporal distributions of ringing and recovery effort, depending on the question being asked, and the present study is no exception. Our results refer only to the populations of birds that the relevant ringing and recovery activity has sampled and the extent to which this is representative of the relevant British and Irish population will vary between species, regions and time periods. Specifically, ringing activity will vary spatially with human population density and habitat (proportionally more being conducted in gardens than in mature woodland, for example), and it will also vary over time (both between seasons and in the long term) as catching methods change and particular projects begin and end. The occurrence of recoveries will also vary spatially and temporally because of variation in reporting probabilities. Many species will have a reporting probability close to zero at sea, but it will also vary along migration routes

Table 7. Results of statistical tests for differences between the migratory tendencies of populations using Britain & Ireland in the breeding season and in winter. Sample sizes (numbers of recoveries) are shown for birds ringed in the breeding season and recovered dead in winter ("B-W") and for birds ringed in winter and recovered dead in the breeding season ("W-B"). "K-S test results" show significance levels from two-sample Kolmogorov-Smirnov tests as follows: * P < 0.1, ** P < 0.05, *** P < 0.01. The final column (M) indicates which of the British & Irish breeding (B) or wintering (W) populations appeared more migratory.

Tabla 7. Resultados de tests estadísticos para las diferencias entre las tendencias migratorias de poblaciones de Gran Bretaña e Irlanda en la estación de reproducción y en invierno. Se indican los tamaños de las muestras (número de recuperaciones) para las aves que fueron anilladas en la estación de reproducción y que se recuperaron muertas en invierno ("B-W"), así como para las aves anilladas en invierno y recuperadas muertas en la estación de reproducción ("W-B"). "K-S test results" indica los niveles significativos obtenidos en tests de Kolmogorov-Smirnov para dos muestras según lo indicado a continuación: * P < 0,1, ** P < 0,05, *** P < 0,01. La última columna (M) indica cuáles de las poblaciones reproductoras británicas e irlandesas (B) o invernantes (W) mostraron una mayor tendencia migratoria.

Species	Sample sizes		K-S test results		M
	B-W	W-B	Stan	Abs	
Mute Swan	1,997	722	***		W
Canada Goose	1,902	23			
Teal	38	211	***	***	W
Mallard	2,492	844	***	***	W
Pochard	65	105	***	***	W
Tufted Duck	261	248	***	***	W
Eider	524	103	***		W
Sparrowhawk	522	41			
Moorhen	68	75			
Coot	48	40	**		B
Oystercatcher	383	635	***	***	W
Dunlin	28	25	***	***	W
Curlew	181	38	***	***	W
Redshank	125	60	***	***	W
Black-headed Gull	1,134	1,635	***	***	W
Common Gull	98	86	***	***	W
Lesser Black-backed Gull	654	141	***	***	B
Herring Gull	977	438	**	***	W
Greater Black-backed Gull	220	41	***	***	W
Wood Pigeon	559	105	***		W
Collared Dove	25	72			
Barn Owl	1,207	26	***		W
Tawny Owl	253	30			
Pied Wagtail	308	278	***	***	B

Species	Sample sizes		K-S test results		M
	B-W	W-B	Stan	Abs	
Wren	109	25			
Duncock	321	545			
Robin	590	448			
Blackbird	1,525	3,528	**	***	W
Song Thrush	963	875	***	***	B
Mistle Thrush	89	160		*	B
Blue Tit	621	1,349	**		B
Great Tit	308	529			
Nuthatch	27	29	*		B
Jay	129	69			
Magpie	91	40			
Jackdaw	113	81			
Rook	108	63	**		B
Starling	1,433	6,214	***	***	W
House Sparrow	358	673			
Tree Sparrow	28	72	***		W
Chaffinch	154	664	**	***	W
Greenfinch	382	3,679	***		B
Goldfinch	118	28	***	***	B
Linnet	197	60	***	***	B
Bullfinch	338	270			
Yellowhammer	39	111			
Reed Bunting	80	44			

over land, both due to the population density of potential human reporters and cultural factors such as interest in wildlife and knowledge of conservation

activity in general and ringing in particular. Variations in hunting activity in time and space are also a key influence. As well as determining which species

had sufficient data to be investigated at all, these variations in ringing and reporting will have determined the (sub-) populations that our analyses considered and will also have influenced the shapes of the recovery distance distributions that we used to produce indices of migratory tendency. Some of the biases they have caused may be unimportant because all samples in a given comparison were affected similarly (for example, a temporal comparison where the same spatial fraction of the population was sampled in both periods compared). Others, however, may have had a critical influence on our results (for example, if hunting pressure has changed over time such that a major source of recoveries from a given region that contribute to a temporal comparison cease). Such problems should be taken as a general caveat to our results and will have affected some analyses (such as temporal and breeding–winter comparisons) more than others, but they are not insurmountable.

We have investigated the magnitude of, and variation in, biases such as those described above elsewhere (Wernham et al., 2002) and the results of such studies could be used to develop controls for variations in reporting rate and ringing activity, which could then be used to correct, or to modify, recovery distance distributions. For example, one approach would be to formulate reporting probability profiles with respect to distance along key migration routes and to apply these to the observed recovery distributions. Such profiles could be developed from spatial analyses of ring–recoveries or recaptures, perhaps building on the random–walk approach of Manly & Chatterjee (1993) or the approach for estimating dispersal distances from mark–recapture data developed by Thomson et al. (2003). Other forms of location or distance data could also be added to distributions such as we have used if they could be translated into distance–frequency profiles for individual species or produced as modifiers of the existing frequency distributions. A different approach, in the long term, would be to target ringing activity would to make the spread of sampling effort more even.

Our indices of migratory tendency represent the first attempt to–date to quantify avian migratory strategies. The method has several caveats and further refinements are needed, but nonetheless we believe that it represents a significant advance and that it has already produced useful and interesting results, starting with an objective classification of the migratory behaviour of all British and Irish birds for which sufficient data are available (Wernham et al., 2002). Future applications of the methods, or adaptations of it, could include further comparative studies of the evolutionary influences on migratory behaviour and tests of the effects of temporal changes in climate, habitat or population density on the migratory tendency of bird populations. In addition, more powerful tests of hypotheses are likely to be possible by carrying out comparative analyses on data sets from different ringing schemes or by developing the technique to produce pan–European indices and analyses.

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