Patterns of natal and breeding dispersal in birds

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Summary

1. Dispersal is of critical ecological and evolutionary importance for several issues of population biology, particularly population synchrony, colonization and range expansion, metapopulation and source–sink dynamics, and population genetic structure, but it has not previously been possible to compare dispersal patterns across a wide range of species or to study movement outside the confines of local study areas.

2. Using resampling methods, we verified that statistically unbiased estimates of average dispersal distance and of intraspecific variance in dispersal distance could be extracted from the bird ringing data of the British Trust for Ornithology.

3. Using data on 75 terrestrial bird species, we tested whether natal and breeding dispersal were influenced by a species' habitat requirements, diet, geographical range, abundance, morphology, social system, life history or migratory status. We used allometric techniques to ascertain whether these relationships were independent of body size, and used the method of phylogenetically independent contrasts to ascertain whether they were independent of phylogeny.

4. Both natal and breeding dispersal distances were lower among abundant species and among species with large geographical ranges. Dispersal distances and life-history variables were correlated independent of phylogeny, but these relationships did not persist after controlling for body size. All morphometrical variables (wing length, tarsus length and bill length) were not significantly correlated with dispersal distances after correcting for body size or phylogenetic relatedness.

5. Migrant species disperse further than resident ones, this relation was independent of body size but not of phylogeny. A significant positive relation was observed between breeding dispersal distance and long-term population decline among migrants, but not among residents.

6. The species living in wet habitats disperse further than those living in dry habitats, which could be explained by the greater patchiness of wet habitats in space and/or time. This relationship was observed only for breeding dispersal, suggesting that this habitat variable does not impose the same constraint on natal dispersal.

Key-words: body size, comparative analyses, dispersal distances, phylogeny, ring recoveries.

Journal of Animal Ecology (1998) **67**, 518–536

Introduction

The distance moved by animals during dispersal is fundamental to ecology and evolutionary biology. All studies of animal that disperse actively show some individual variation in dispersal distances (Swingland 1983). Many studies of these intraspecific differences have been conducted (Murray 1967; Greenwood & Harvey 1976, 1982; Greenwood, Harvey & Perrins 1979; Gaines & McClenaghan 1980; Waser 1985; Boonstra *et al.* 1987; Trewhella, Harris & McAllister 1988; Berven & Grudzien 1990; Payne 1991; Bengtsson, Hedlund & Rundgren 1994; Stein *et al.* 1994; Dwyer & Elkinton 1995). On the other hand, studies on interspecific differences in dispersal have mainly dealt with sex- or age-specific philopatry (Greenwood 1980; Dobson 1982). Two other issues of importance in the study of dispersal are the rates of movements

between populations, which has been recently reviewed by Nichols (1996), and the distribution of dispersal distances, which is the subject of the present paper.

The distribution of dispersal distances is of fundamental importance for several issues in population biology. It is an essential component of metapopulation and source–sink dynamics (Brawn & Robinson 1996), invasion and colonization (Harrison 1989; Hengeveld 1994; Shigesada, Kawasaki & Takeda 1995), and gene flow and genetic structure (Neigel & Avise 1993). Also, interspecific differences in distribution of dispersal distances have been shown to be critical in species interactions (McLaughlin & Roughgarden 1992; Neubert, Kot & Lewis 1995).

It has been observed repeatedly that long-distance dispersal occurs regularly but at a relatively low frequency (Grinnell 1922; Mayr 1963; Murray 1967). Long-distance dispersal has been shown, on theoretical grounds, to be important in invasion processes (Shaw 1995) and the genetic structuring of populations (Ibrahim, Nichols & Hewitt 1996).

Long-distance dispersal in vertebrates is still poorly understood in spite of its importance (Clobert & Lebreton 1991; Hansson 1991). Detailed field studies are appropriate to measure small-scale dispersal (e.g. Greenwood *et al.* 1979), but they are usually unable to follow individuals that leave the study area (Baker, Nur & Geupel 1995). For instance, field studies on microtine rodents hardly cover more than one hectare while there is reliable evidence that these animals can move several kilometres in a few days (Kirkland 1988; Saucy 1994; Steen 1994). Avian study sites are usually smaller than the distance that a bird can move within a day (Payne 1991; Matthysen, Adriaensen & Dhondt 1995). Such small-scale studies on dispersal are valuable in evaluating the proximate behavioural causes of dispersal (Greenwood *et al.* 1979; Wiggett & Boag 1993), but dispersal outside such local areas can only be studied with a marking scheme operating over a much larger-scale and no such investigation has previously been undertaken. Field studies are usually focused on one or two species resulting in difficulties in identifying general ecological or evolutionary constraints. These issues can be studied by comparing a wide range of species encompassing a diversity of body size, habitats or other ecological variables.

Studies on dispersal distances of a wide range of birds have shown two ubiquitous patterns: the frequency distribution of dispersal distances decreases with increasing distance, and natal dispersal distances are greater than breeding dispersal ones (Newton & Marquiss 1982; Drilling & Thompson 1988; Baillie & Milne 1989; Moore & Dolbeer 1989; Newton, Davis & Davis 1989; Verner, Gutiérrez & Gould 1992; Belant & Dolbeer 1993; Ferrer 1993; Lindberg, Sedinger & Rexstad 1995; Matthysen *et al.* 1995; Wagner *et al.* 1996).

We report here an analysis of interspecific variations in dispersal distances using data on marked British breeding birds from the ringing scheme of the British Trust for Ornithology (BTO). Birds ringed in Britain and Ireland are potentially found anywhere, resulting in no spatial limit to the present study. We did not find any theoretical framework that would have allowed us to formulate specific hypotheses for the present study. This lack of theory on the causal factors that affect the distribution of dispersal distances may be a consequence of the difficulties encountered in the study of dispersal distances mentioned above. Nevertheless, it is possible to formulate a priori some predictions on the variations in dispersal distances expected among bird species. So we tested whether dispersal varies between species occupying differing habitats, diet, social system, population size, geographical range, local abundance, body measurements, life history variables and migratory status. As body size is correlated with a wide range of biological, ecological or physiological variables (Peters 1983), we expected body size to be significantly correlated with dispersal distance, and anticipated the need to correct for body size in our analyses. We used allometric techniques to examine whether correlations persist independently of body size and phylogenetic techniques to test whether correlations persist independently of phylogeny.

Methods

DATA

Raw data on dispersal distances came from the BTO ringing scheme. Distances (to the nearest kilometre) covered by birds between ringing and recovery sites are stored in the data bases. Birds have been ringed by volunteers in Britain and Ireland since 1909. The data on ring recoveries are stored according to the EURING standards (EURING 1979). The data analysed for the present study span the period 1909–94 inclusive. During this period, 24 915 645 birds were ringed, and 492 272 of them (belonging to 405 species) have been recovered (Clark *et al.* 1996). Here we consider only species breeding inland; marine species are mostly colonial and their breeding habitats are linearly distributed making comparisons with inland species problematic, and many of the recoveries of shorebirds are from the tideline where they may have been carried by the sea. We included in our analyses three species of gulls (*Larus* spp.) that breed commonly inland in Britain and Ireland (Gibbons, Reid & Chapman 1993). For species breeding in terrestrial habitats, it has been shown that the probability that a dead ringed bird is found varies spatially (van Noordwijk 1984; Baillie & Green 1987). This point has been raised as a limitation for inferences on dispersal with ringing recovery data (van Noordwijk 1995). However, two points must be considered with respect to the present study. First, ringing recoveries

were made in the same area for all species, so we can expect that spatial variations in recovery rates would be similar for all species, hence conserving any possible interspecific patterns. Second, the bias demonstrated by van Noordwijk (1995) may particularly affect studies with a limited number of sites where birds can be recovered or recaptured. On the other hand, in large-scale studies with a very large number of recovery sites, the bias in the estimates of dispersal distance may be lower than in small-scale studies. This last point requires further evaluation, but in the context of the present study where we focus on interspecific patterns, we do not expect our results to be affected by spatial variations in recovery rates.

The data were screened in the following ways in order to remove spurious effects. First, only birds ringed and recovered during the breeding season were selected; recoveries in the same breeding season as they were ringed were excluded. The breeding season of each species was defined as the period between the beginning of the time when most birds have eggs to the end of the time when most birds have young, and taken from Cramp & Simmons (1977–94). Second, data were filtered to remove heterogeneity as far as possible. Only birds found dead were considered in the analyses, as the spatial distribution of birds controlled (captured, usually in ringers' nets, and released, or identified in the field without being captured) is likely to be biased as field ornithologists tend to catch birds in particular study areas. The following data have been discarded from the analyses: birds that were in poor condition or had an accident when ringed; birds that have been kept more than 24 h during ringing; birds that have been moved or held extensively during ringing; birds that have been intentionally killed by man other than shot; birds that have not been found freshly dead; birds for which the dates and places of ringing and/or recovery have not been recorded accurately (to the nearest 2 weeks for the ringing date, to the nearest 2 months for the finding date, to the nearest 4' for the ringing and finding place); birds whose age was unknown when ringed; birds that had fledged when ringed but whose age was otherwise completely unknown (age code = 2, EURING 1979).

The analyses of migrant and partial migrant species were complicated by the different timing of migration of different individuals resulting in the recoveries of birds on migration routes late in the breeding season. We chose to be conservative with respect to this problem and discarded all birds which could be suspected to have been ringed and/or recovered on their migration route. The most efficient way to apply this correction was to define a cut-off distance above which the data were discarded (because these birds are most likely to be migrants); this cut-off distance was defined separately for each species. The direction of dispersal was graphically examined against the dispersal distance: this showed that the largest dispersal distances were preferentially directed towards the north–south

axis. The largest dispersal distances were removed as long as their corresponding directions were the closest ones to the north–south axis. This resulted in dispersal movements that were not preferentially orientated in any direction. This method allowed us to define the cut-off distance in a repeatable manner, and to detect the presence of very late migrants (for instance, some birds breeding in northern Europe have been ringed or recovered in late June in Britain, which is their wintering ground); such individuals were a very small proportion of the birds recovered during the breeding season ($< 3\%$). We examined all species with this procedure as, even for strongly resident species (e.g. tits, see Sellers 1984), movements in winter may result in positive bias in the estimation of dispersal distances. Particular care was taken to avoid bias from birds ringed as juveniles in their year of birth (age code = 3, EURING 1979) which are known to be particularly mobile at the end of the breeding season (e.g. da Prato & da Prato 1983; Baker 1993). This was done by examining whether juveniles have significantly larger dispersal distances than birds ringed as nestlings (*t*-test at 0·05 level). If this was the case, then they were excluded from the analyses. This potential source of bias was particularly important for migrants (Baker 1993; see present Discussion). We found that in some species only juveniles ringed early in the breeding season have greater movements than birds ringed as nestlings: this could be explained by the fact that these individuals have more time to explore for future breeding sites, and may have on average a greater dispersal distance than birds born later during the breeding season. In all cases, a category of individuals (ringed either early or late in the breeding season) was excluded if its mean dispersal distance was significantly different from the remaining birds.

Finally, we checked in species which are known to have also migratory movements between Britain and Ireland (e.g. blackbird *Turdus merula* L., song thrush *T. philomelos* L.) that the largest dispersal distances were not preferentially directed towards the east–west axis after removing the north–south migratory movements. We found that no correction was necessary with respect to these longitudinal migratory movements.

After application of the selection criteria, we selected those species with sufficient data (minimum sample size of 10) to estimate the parameters of natal and breeding dispersal separately. Seventy-five species remained (listed in Appendix 1).

Natal dispersal was estimated using birds ringed in their year of birth (either in the nest or as fledglings) and recovered at breeding age; breeding dispersal was estimated using birds ringed at breeding age. Breeding age was determined as the minimum age at first breeding as given by Cramp & Simmons (1977–94). Some species in our sample have a variable age at first breeding (particularly gulls); however, there is evidence from field studies that birds at the minimum age at

first breeding go back to their natal sites though they may not yet breed (e.g. Lack 1966).

Most birds were not sexed when ringed (especially those ringed in the nest) making it almost impossible to define sex categories in this study. In many birds there is a sex difference in dispersal pattern (Greenwood 1980; Greenwood & Harvey 1982); however, here we expected to observe larger interspecific differences than could be measured at the intraspecific level. Another limitation of our approach is that we have no data on the reproductive status of a bird when it is recovered, so we cannot be sure that we really estimate dispersal between a birth site and a breeding site or between two breeding sites. This may be a serious problem for birds that are at breeding age but are not effectively breeding. However, there is some evidence from field studies that such individuals wander around breeding sites during the breeding season, usually waiting for an opportunity to acquire a vacant territory (e.g. Lack 1966). It is therefore likely that such individuals are recovered near their potential breeding sites.

Ecological and life history variables were extracted from Cramp & Simmons (1977–94). The quantitative variables were: mean clutch size, incubation time (in days), age at fledging (in days), age at independence (in days), age at first breeding (in years), modal number of broods per year, adult body mass (in grams), body mass at hatching (in grams), egg mass (in grams), wing length (in millimetres), bill length (in millimetres) and tarsus length (in millimetres). The categorical variables chosen were (see Appendix 1 for details): main food in winter and during the breeding season (animals or plants), social system in winter (solitary or flocking) and during the breeding season (territorial, neighbourhood or colonial), preferred habitat in winter and during breeding (each split into two dichotomous variables: open vs. closed, and dry vs. wet), and migration (treating trans-saharan migrants as migrants and all other species as residents). The extracted variables were from studies conducted in the British Isles when available in Cramp & Simmons (1977–94); otherwise they were from studies conducted on mainland Europe on the same subspecies as occurs in the British Isles. Additionally, data on juvenile and adult survival rates were taken from Sæther (1989). This latter study compiled estimates of survival rates from the literature that mostly were made with enumeration methods, which could result in substantial biases compared to methods based on probabilistic models (Lebreton *et al.* 1992). However, a recent review of the literature showed that when different estimates of survival rates based on different methods were available for the same species, the differences were less than 0·1 (and often less than 0·05), and did not confound interspecific variations (Balmer & Peach 1997).

Variables on population status were taken from some studies conducted at the BTO. Four variables were considered: (i) population size, measured as the number of pairs breeding in Britain and Ireland (Gibbons *et al.* 1993), (ii) geographical range, measured as the number of 10-km squares occupied during the breeding season in Britain (Gibbons *et al.* 1993), (iii) local abundance, measured as the estimated densities on Common Birds Census (CBC) plots (Marchant *et al.* 1990) averaged from 1991 to 1995, and (iv) population trend, as evaluated by the percentage change in estimated density on CBC plots between 1969 and 1994.

ESTIMATION OF PARAMETERS

Dispersal is a complex phenomenon making the development of statistical models difficult (North 1988). Several models are available but their application requires restrictive assumptions (Taylor 1980; North 1985; Tonkyn & Plissner 1991; Porter & Dooley 1993). Our approach was to use univariate parameters to measure the distribution of dispersal distances for each species. One potential problem was the heterogeneity in sample size (n) among species (see Appendix 1). The expected value of the chosen estimator should be, as far as possible, insensitive to sample size, though the variance is expected to increase with decreasing sample size. We performed a resampling analysis with four species for which we had relatively large sample sizes: k birds were randomly selected ($k < n$) and various univariate parameters were then estimated for these k individuals; this was replicated 10 times for each value of k. Performance of the different estimators was then assessed by plotting the estimates against k. Seven parameters of dispersal distances were estimated for each replicate: arithmetic mean, standard deviation (SD), coefficient of variation (CV), minimum, median, first and third quartiles. Distances were $\log_e$-transformed before analysis. Note that the arithmetic mean of $\log_e$-transformed data is equivalent to the $\log_e$-transformed geometric mean of the original data. Analyses were made with SAS (1990).

INTERSPECIFIC COMPARISONS

Three sets of analyses were performed with the estimates of dispersal distance across all species. First, we computed linear correlation coefficients with $\log_e$-transformed continuous variables, and one-way ANOVAs with the categorical variables. Second, we removed the influence of body size on dispersal parameters with linear regressions. The residuals were then analysed in the same way as for the first set of analyses. The two sets of analyses were performed with SAS (1990). Third, to cope with the problem of dependence among species, we computed phylogenetically independent contrasts (PICs) for each variable according to the method described by Felsenstein (1985). Each PIC is associated with a node in the phylogeny and is a measure of the evolutionary diver-

gence between both taxa originating from this node. The phylogeny for the 75 species was built following Sibley & Ahlquist (1990). Sibley & Ahlquist's phylogeny, based on DNA/DNA hybridization, has been repeatedly criticized (Mindell 1992; Sheldon & Bledsoe 1993) but is the only one published that covers all avian families and gives estimates of branch lengths, and it is relatively uncontentious for the birds covered in this paper. Furthermore, some controversial conclusions reached by Sibley & Ahlquist (1990) have been confirmed by several recent phylogenetic studies using alternative methods (review in Avise 1996).

Felsenstein's method can cope with the problem of uncertainty in phylogenetic reconstruction by analysing several phylogenies for the considered taxa but these phylogenies must all contain only dichotomous bifurcations and known branch lengths (Felsenstein 1985). Sibley & Ahlquist (1990) provide a phylogeny of living birds with dichotomous bifurcations and known branch lengths, but several species in our study are not present in their phylogeny. We resolved the branching orders of these species with data from the taxonomy which allowed us to infer the relationships between species, and estimated branch lengths for these inferred dichotomies using information in Sibley & Ahlquist (1990). We used two different hypotheses for the latter step: (i) we took the smallest branch length within the considered genus if available, or the smallest branch length possible (0·1); or (ii) we took the largest branch length within the considered genus if available, or the largest branch length possible (length of the branch to the nearest genus −0·1). This procedure allowed us to evaluate more rigorously the phylogenetic effects, as the phylogeny used in comparative analyses has a critical influence on the results (Felsenstein 1988; Pagel & Harvey 1989). The PICs for dispersal parameters and the continuous life history and ecological variables were computed with PHYLIP (Felsenstein 1993). The categorical variables were mapped along the phylogeny to identify the transitions that occurred along the tree using the criterion of parsimony. Linear correlations were made between PICs to examine the relationships between dispersal parameters and the continuous variables. One-way ANOVAs were computed considering the nodes where a transition in the considered categorical variable vs. the nodes with no transition (Burt 1989). All analyses were made considering successively the two reconstructed phylogenies. We considered as statistically significant only those tests which were significant with both phylogenies.

Results

WITHIN-SPECIES DISTRIBUTION OF DISPERSAL DISTANCES

Most individual birds were recovered on or close to their ringing sites (Figs 1 and 2). Only ringing recover-

ies between breeding seasons were used as a measure of breeding or natal dispersal, depending on the age at which the bird was ringed. This could generate a bias if birds tend to move significantly each year. If so, we should expect a positive relationship between the distance recorded between ringing and recovery and the time elapsed. However, plots of these two variables shows no relationship (Figs 3 and 4), suggesting that once birds have dispersed they tend to stay at the same breeding site. Such site tenacity has been described extensively in birds (Kellner, Brawn & Karr 1992; Peach, du Feu & McMeeking 1995).

We selected four species with large sample sizes to perform the resampling analyses: blackbird ($n = 3372$), blue tit *Parus caeruleus* L. ($n = 784$), greenfinch *Carduelis chloris* L. ($n = 302$), and starling *Sturnus vulgaris* L. ($n = 2376$). Estimates of mean and SD of dispersal distance were unbiased with respect to k, the variance being greater for smaller values of k (Fig. 5). Estimates of other parameters varied substantially with respect to k (CV), or were constant across species (minimum, median, first and third quartiles), and so were unlikely to measure differences among species. We chose to use the mean and SD of natal and breeding dispersal as dispersal parameters. Greenwood & Harvey (1982) suggested that the median should be the appropriate parameter to compare dispersal between species, but this was not the case in our study. This is due to the spatial resolution of the ringing data: in the four species examined above, more than 50% of the individuals were recovered near their ringing site, and as distances are stored in the data bases to the nearest kilometre they were assigned a zero dispersal distance. It may seem surprising that CV (the ratio of SD to mean) varies to a greater extent than mean or SD. However, the variance of the estimate of CV is a function of the variances and covariance of the estimates of mean and SD, and so its variability is increased compared to mean and SD.

All species showed the same pattern of distribution of dispersal distances with the proportion of recoveries declining with distance from the ringing site. However, differences among species were noticeable, particularly the spatial extent of the peak of the distribution, and the importance of the tail relative to the peak. The parameters estimated for each species (mean and SD) represent these variations.

We were able to estimate natal dispersal for all 75 species, and had sufficient data to estimate breeding dispersal for 69 of these species. Among the latter, 61 species had a greater mean natal dispersal distance than mean breeding dispersal distance (see Appendix 1). For the eight other species, the mean estimates were very similar and the difference was certainly due to sampling variations. Breeding and natal dispersal distances covary to a great extent, so the interspecific variation is much more important than the intraspecific one that we were able to measure. Nonethe-

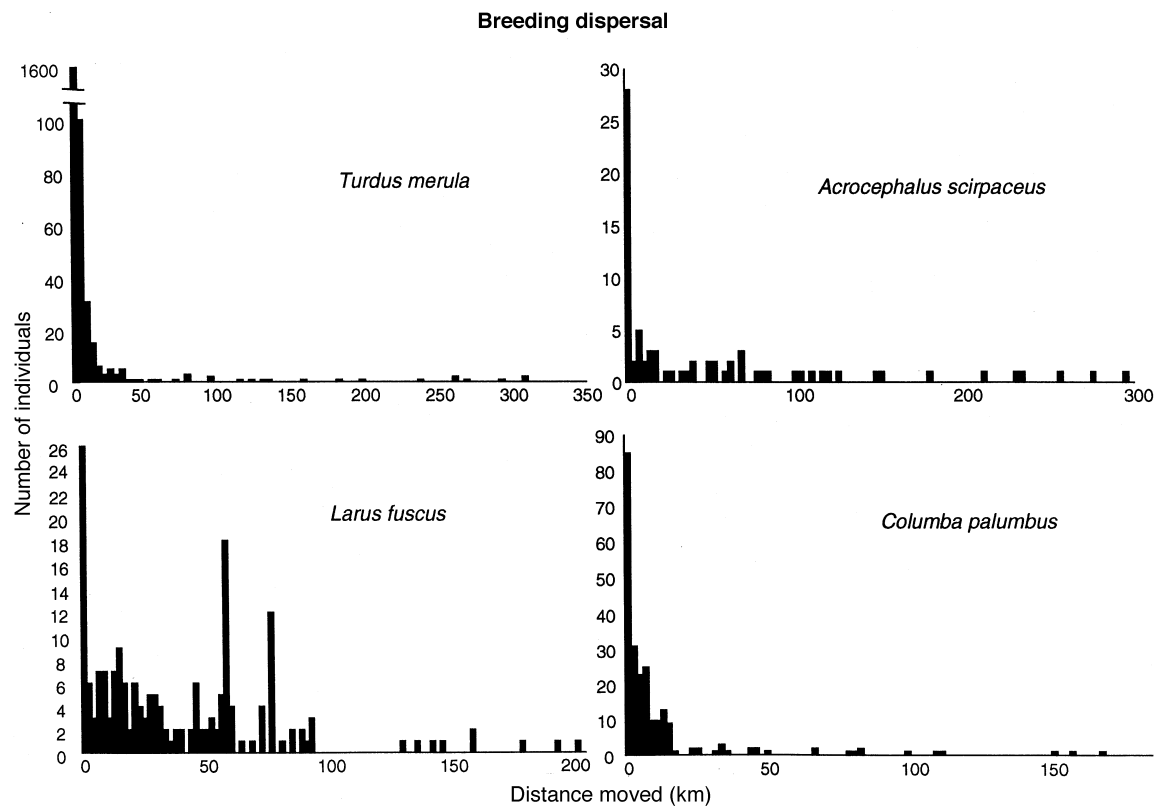**Fig. 1.** Frequency distribution of breeding dispersal distances of four species of birds in Britain.

Natal dispersal

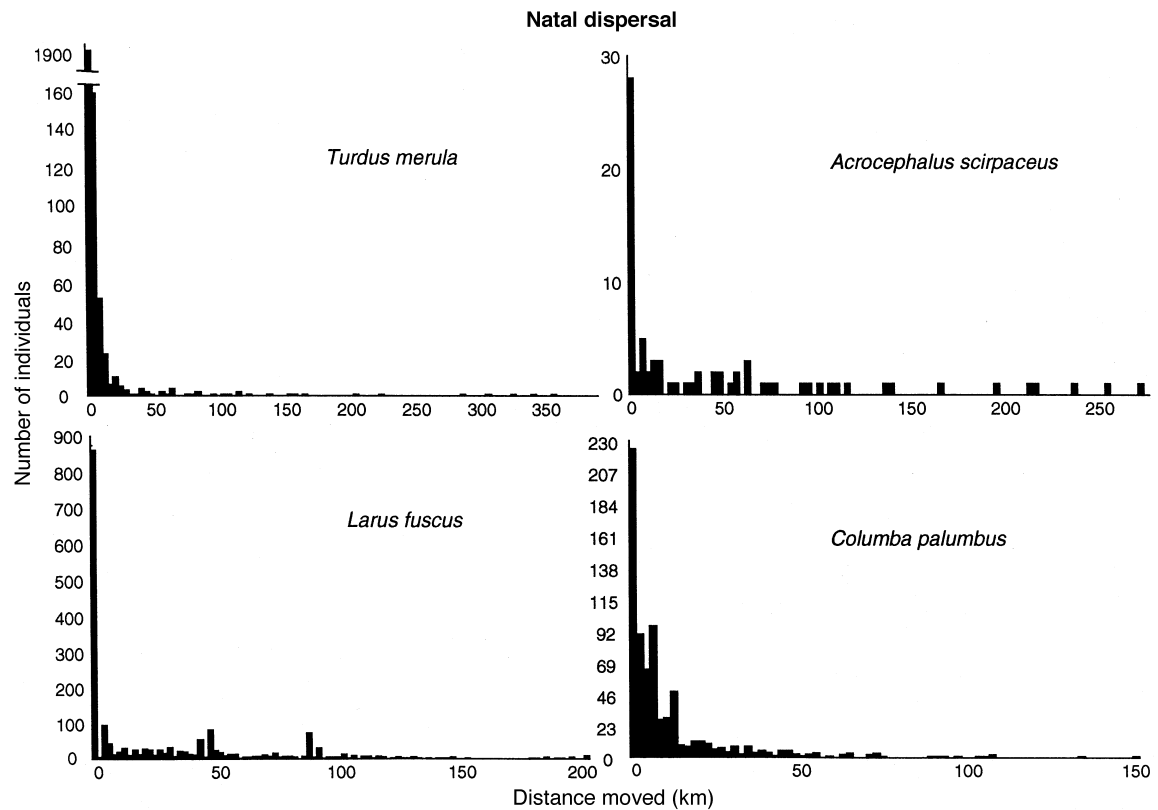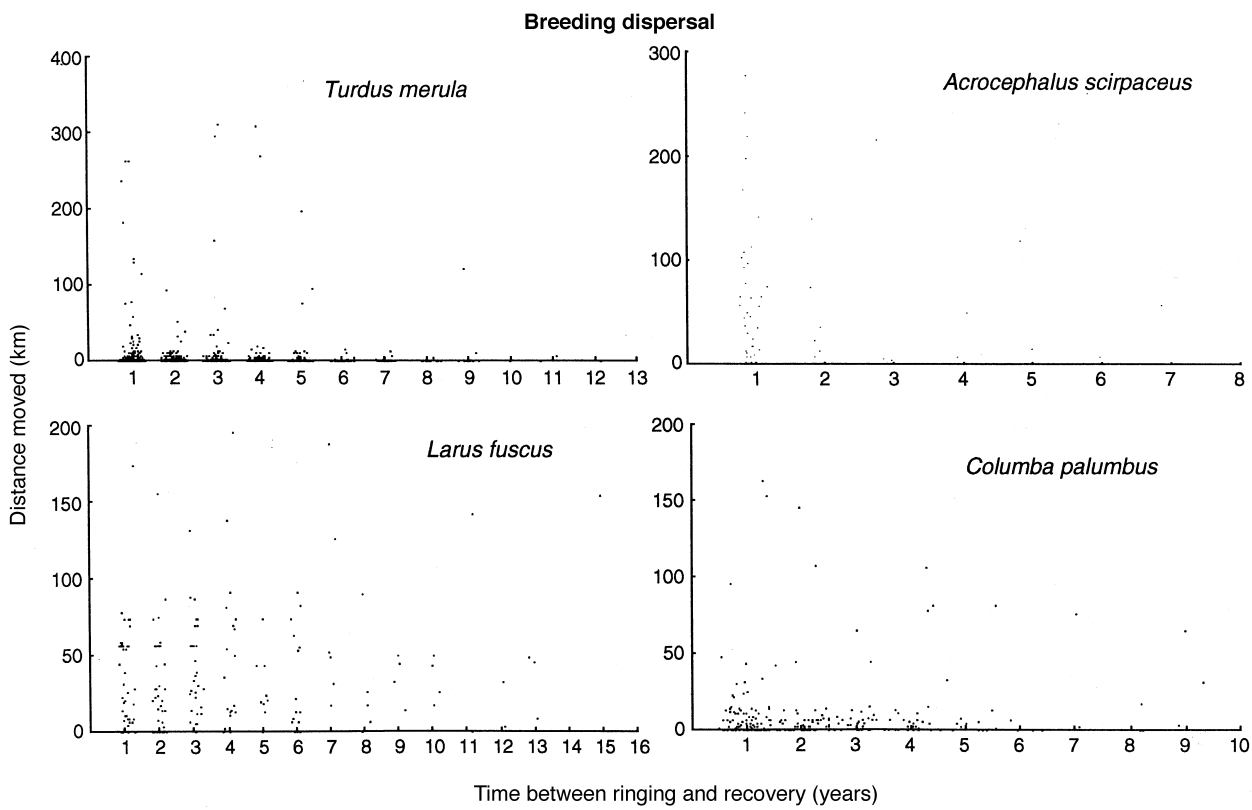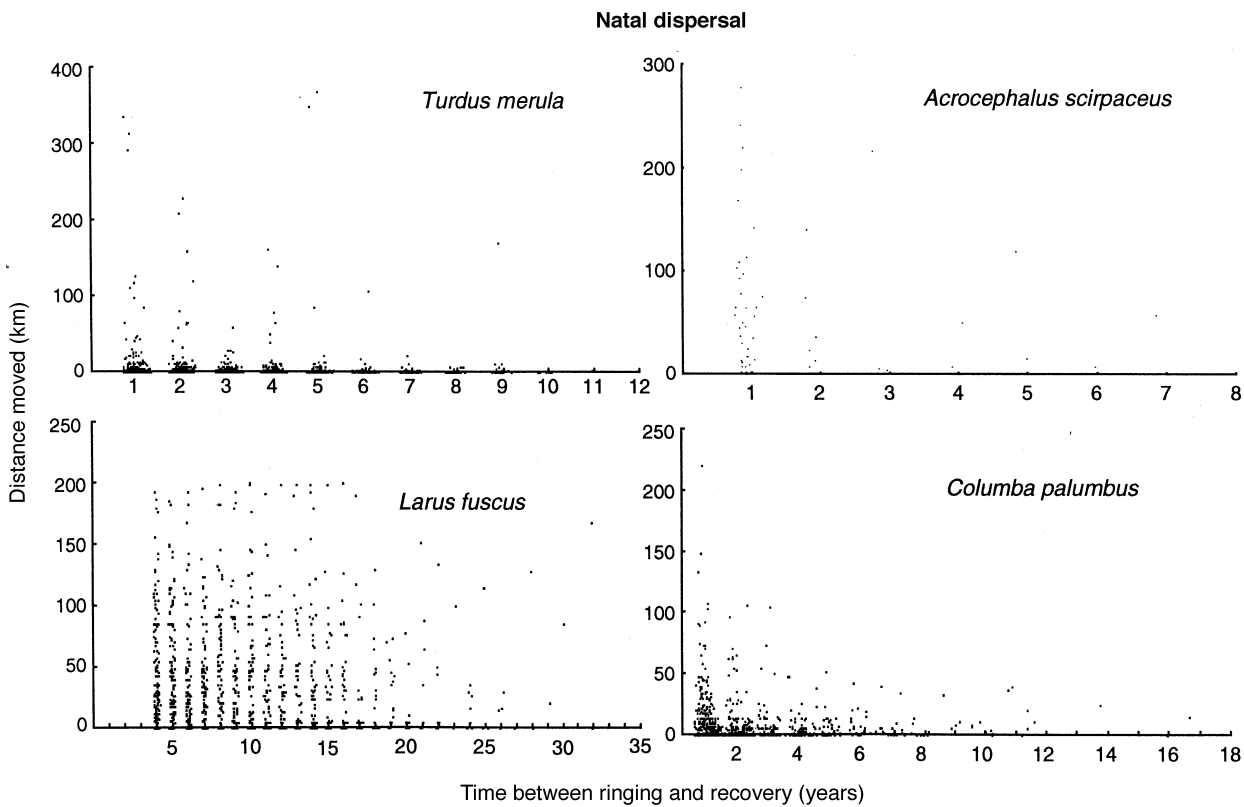**Fig. 2.** Frequency distribution of natal dispersal distances of four species of birds in Britain.

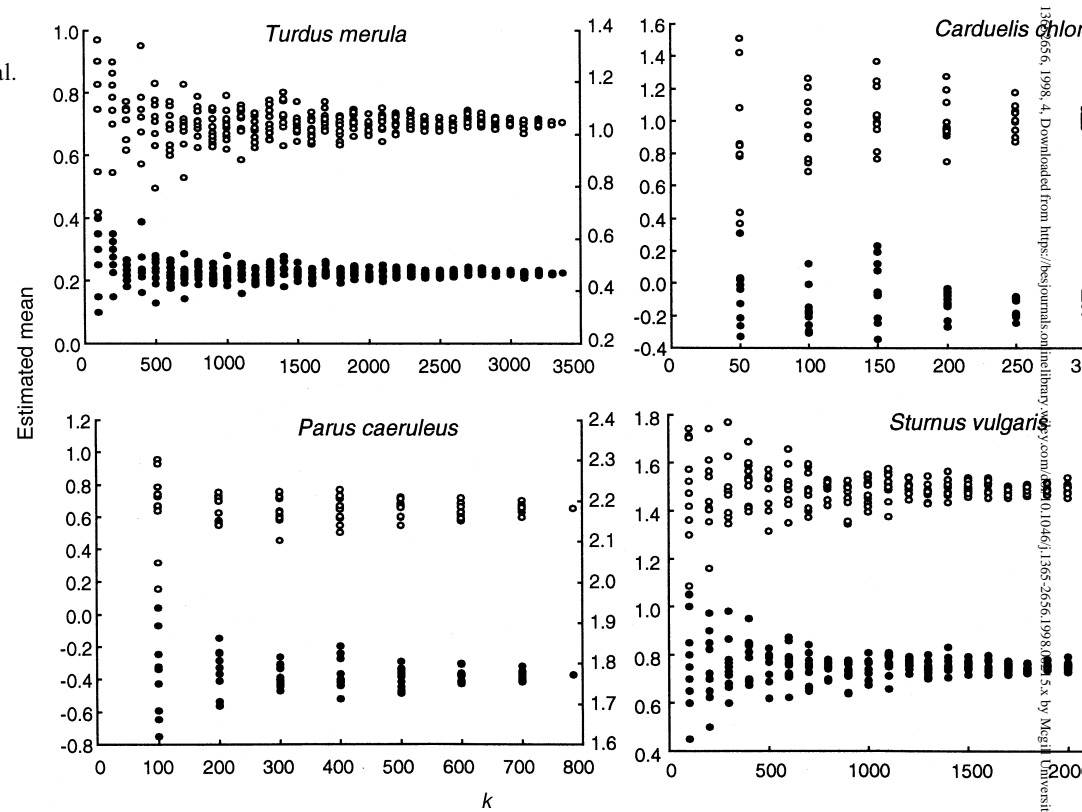## Breeding dispersal

Fig. 3. Distance moved (breeding dispersal) against time elapsed between ringing and recovery of four species of birds in Britain.

Natal dispersal

Fig. 4. Distance moved (natal dispersal) against time elapsed between ringing and recovery of four species of birds in Britain.

Fig. 5. Resampling analysis of dispersal distances of four species (see text for details). Plot of estimated means (filled circles, left vertical axis) and estimated standard deviations (open circles, right vertical axis) against sample size (k). Dispersal distances were $\log_e$-transformed prior to analyses.

less, the distinction between natal and breeding dispersal is relevant for the present study as the difference is consistent across species and the data analysed allowed us to estimate the parameters separately.
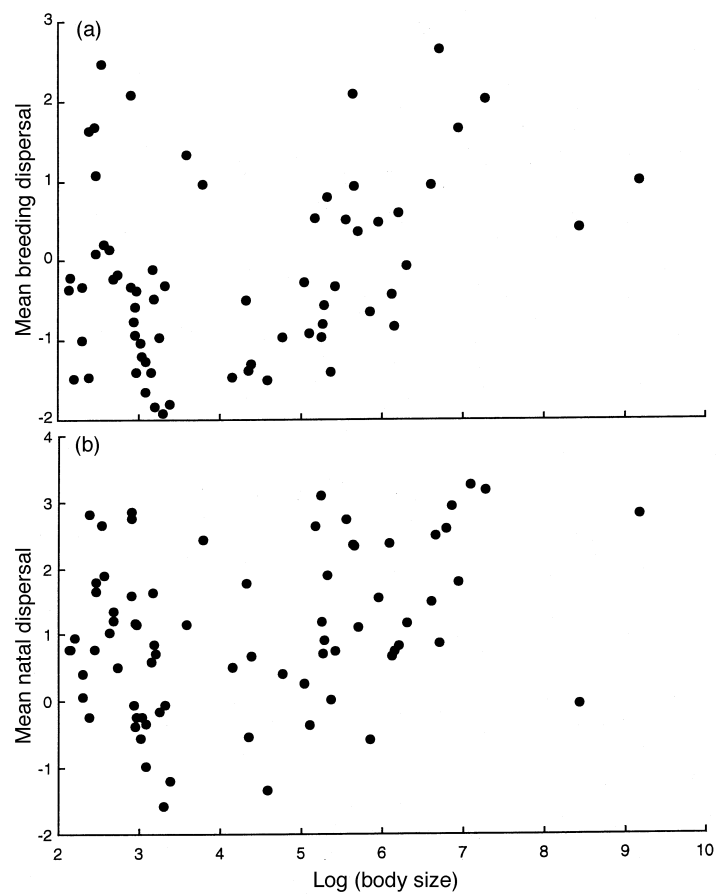
INTERSPECIFIC CORRELATIONS

Cross-species distributions of the mean and SD of log-transformed dispersal distances were normally distributed, so use of cross-species linear correlations and ANOVA was justified. The PICs generated by PHYLIP were also normally distributed and correctly standardized with respect to branch lengths. In the following, we detail the relationships between dispersal distance and the different types of variables, examining successively for each type the simple correlations, correlations after correcting for body size, and correlations after correcting for phylogeny. The former correction was justified by the positive correlation between body size and mean breeding and natal dispersal ($r = 0.298$, $n = 67$, $P = 0.015$, and $r = 0.311$, $n = 75$, $P = 0.006$, respectively). No significant correlation was observed between body size and SD of breeding and natal dispersal ($r = 0.114$, $n = 67$, $P = 0.368$, and $r = -0.152$, $n = 75$, $P = 0.193$, respectively). Plots of mean dispersal distances vs. body size reveal an important scatter with a greater variance for

small body sizes than large ones (Fig. 6). [Esti]mated slopes from these regressions [were …] (SD = 0.079) and 0.214 (SD = 0.077), [for breeding] and natal dispersal, respectively. As the[se slopes were] not significantly different from 0.25, this s[uggests that] the geometric mean of dispersal distance[s scales with] body size with the 1/4 exponent, which i[s commonly] for several ecological variables (Peters 1[983). In the] following, we focus on correlations th[at take into] account the effect of body size or phylo[geny. We do] not present results that correct simulta[neously for] body size and phylogeny as the correlat[ion between] dispersal distance and body size after re[moving the] effect of phylogeny is not significant.

After correcting for the influence of b[ody size on] the dispersal parameters, the correlations [between the] life history variables and the dispersal [parameters] were not significant, except for the numb[er of broods] per year with mean breeding and na[tal dispersal] (Table 1). After correcting for phylogen[etic related]ness, three life history variables gave co[rrelations sig]nificant correlations with dispersal par[ameters: incu]bation time with SD of natal disper[sal, clutch] independence with both mean and SD of [natal disper]sal, and age at first breeding with mean na[tal dispersal] (Table 2). For mean natal dispersal, the [correlations] were positive, i.e. an increase in age at i[...]

Fig. 6. Plots of body size vs. (a) mean breeding dispersal ($n = 67$), (b) mean natal dispersal ($n = 75$) for 75 species of British birds. Dispersal distances (km) have been $\log_e$-transformed before computing the arithmetic mean.

Table 1. Correlations between life history and ecological variables, and parameters of breeding and natal dispersal of British birds after removing the effect of body size

| | Breeding dispersal | | | | Natal dispersal | | | |
| | Mean | | SD | | Mean | | SD | |
	r	*n*	*r*	*n*	*r*	*n*	*r*	*n*
Clutch size	−0·035	67	−0·058	67	−0·020	75	−0·164	75
Incubation time	0·141	67	0·010	67	0·240	75	−0·096	75
Age at fledging	−0·142	67	−0·260	67	0·112	75	−0·207	75
Age at independence	−0·035	67	0·090	67	0·107	75	−0·155	75
Age at first breeding	0·232	67	0·008	67	0·138	75	0·041	75
Juvenile survival	0·242	27	0·195	27	0·071	32	0·070	32
Adult survival	−0·019	41	0·113	41	0·007	45	0·252	45
Broods per year	−0·268	67*	−0·076	67	−0·434	75***	0·066	75
Population size	−0·366	67**	−0·126	67	−0·556	75***	0·148	75
Geographical range	−0·421	67***	−0·200	67	−0·384	75***	−0·056	75
Local abundance	−0·144	59	0·022	59	0·054	64	−0·192	64
SD (local abundance)	−0·235	59*	−0·076	59	−0·062	66	−0·231	66*
Population trend	0·121	53	0·076	53	0·150	56	−0·027	56

*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$. *r*: correlation coefficient, *n*: sample size

or age at first breeding during evolution is accompanied by an increase in mean natal dispersal. The correlations with SD of natal dispersal were negative.

Population size and geographical range were strongly negatively correlated with mean natal and breeding dispersal: plots of these correlations reveal different relationships. The relation between population

Table 2. Correlations between life history and ecological variables, and parameters of breeding and natal dispersal of British birds using the method of phylogenetically independent contrasts. t1 and t2 refer to the two phylogenies used to compute the PICs

		Breeding dispersal				Natal dispersal			
		Mean		SD		Mean		SD	
		r	*n*	*r*	*n*	*r*	*n*	*r*	*n*
Body size	t1	0·012	66	−0·260	66*	0·402	74***	−0·467	74***
	t2	−0·237	66	−0·290	66*	0·220	74	−0·144	74
Clutch size	t1	0·089	66	0·019	66	0·172	74	−0·125	74
	t2	0·481	66***	−0·033	66	0·156	74	−0·325	74**
Incubation time	t1	−0·061	66	0·071	66	0·295	74**	−0·381	74***
	t2	−0·207	66	0·030	66	0·160	74	−0·512	74***
Age at fledging	t1	−0·234	66	−0·208	66	−0·024	74	−0·232	74*
	t2	−0·102	66	−0·058	66	0·121	74	−0·169	74
Age at independence	t1	−0·149	66	−0·009	66	0·642	74***	−0·695	74***
	t2	0·009	66	0·173	66	0·371	74***	−0·274	74*
Age at first breeding	t1	0·296	66	−0·155	66	0·415	74***	−0·374	74**
	t2	0·207	66	−0·142	66	0·306	74**	−0·011	74
Juvenile survival	t1	−0·198	26	0·383	26	0·314	31	−0·316	31
	t2	−0·092	26	0·368	26	0·282	31	−0·225	31
Adult survival	t1	−0·187	40	−0·171	40	−0·254	44	0·212	44
	t2	−0·181	40	−0·220	40	0·258	44	0·597	44***
Broods per year	t1	−0·202	66	−0·065	66	−0·181	74	−0·048	74
	t2	−0·077	66	−0·112	66	0·109	74	−0·424	74***
Population size	t1	−0·327	66**	−0·233	66*	−0·794	74***	0·584	74***
	t2	−0·474	66***	−0·217	66	−0·639	74***	0·164	74
Geographical range	t1	−0·329	66**	−0·001	66	−0·601	74***	0·409	74***
	t2	−0·588	66***	0·345	66**	−0·454	74***	0·027	74
Local abundance	t1	−0·328	62**	−0·255	62*	−0·818	66***	0·594	66***
	t2	−0·229	62	−0·506	62***	−0·594	66***	0·052	66
SD (local abundance)	t1	−0·196	62	−0·290	62*	−0·607	66***	0·426	66***
	t2	0·117	62	−0·515	62***	−0·293	66*	0·043	66
Population trend	t1	0·071	52	−0·184	52	0·001	56	−0·001	56
	t2	−0·031	52	−0·249	52	0·205	56	−0·426	56***

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. *r*: correlation coefficient, *n*: sample size (number of independent contrasts)

size and mean dispersal is curvilinear; species that have a large population size have restricted dispersal (Fig. 7). The relation between geographical range and mean dispersal is linear with scatter (Fig. 8). These correlations were still significant after correcting for body size (Table 1), or after the phylogenetic correction (Table 2). Geographic range was weakly negatively correlated with SD of breeding dispersal while population size was weakly positively correlated with SD of natal dispersal. The correlations with local abundance or its standard deviation were not significant after correcting for body size, except for the standard deviation of local abundance with mean of breeding dispersal (Table 1). After correcting for phylogenetic relatedness, local abundance was strongly negatively correlated with mean natal dispersal, while the spatial heterogeneity in local abundance was negatively correlated with SD of breeding dispersal and with mean natal dispersal (Table 2). No correlation was significant with the measure of population trend (Tables 1 and 2).

To investigate the potential relationship between

dispersal and population trend, we made further analyses including population trend taking into account those variables that significantly influenced dispersal parameters (see below). We estimated separately the correlation coefficients between population trend and mean of breeding dispersal for the migrant and the resident species (Fig. 9): the correlation was significant for the migrants ($r = 0.713$, $n = 11$, $P = 0.014$) but not for the residents ($r = 0.230$, $n = 42$, $P = 0.143$). The correlation coefficient for migrants was also significant after removing the effect of body size ($r = 0.724$, $n = 11$, $P = 0.012$), or after correcting for phylogenetic relatedness among the migrant species ($r = 0.722$, $P = 0.018$, and $r = 0.921$, $P < 0.001$, with both phylogenies, respectively, $n = 10$ in both cases). The correlation between population trend and mean of natal dispersal was not significant, either for migrants ($r = 0.389$, $n = 12$, $P = 0.212$), or for residents ($r = 0.264$, $n = 44$, $P = 0.083$).

The correlation between population trend and mean of breeding dispersal was close to significance for species living in wet habitats during summer
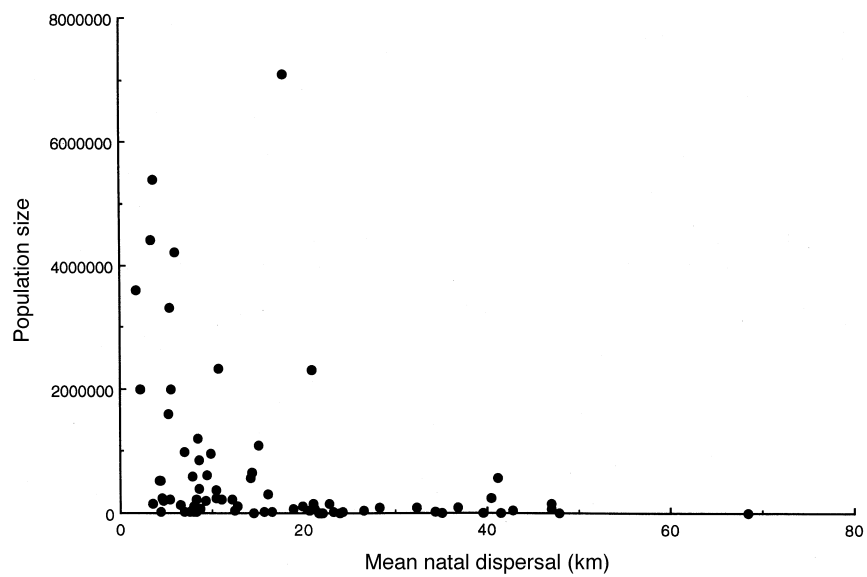
Fig. 7. Plot of mean natal dispersal vs. population size for 75 species of British birds. A similar relationship was observed with breeding dispersal.
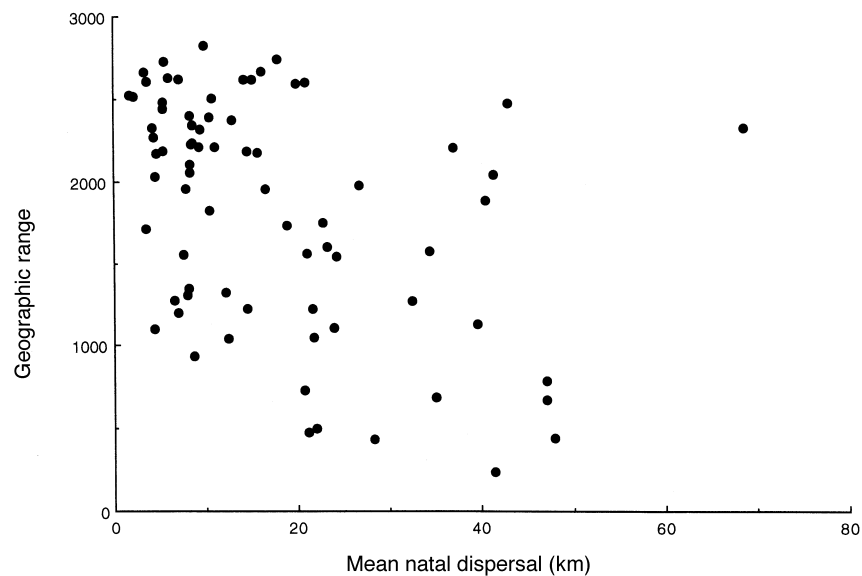

Fig. 8. Plot of mean natal dispersal vs. geographical range for 75 species of British birds. A similar relationship was observed with breeding dispersal.

($r = 0.591$, $n = 10$, $P = 0.072$), but migrant species living in wet habitats (3 out of 10) critically influenced this correlation. Taking into account wet winter habitats gave no significant results. Including population trend along with population size or geographical range in a multiple regression did not yield significant partial correlation coefficients for population trend ($P > 0.05$).

All morphometric variables were significantly positively correlated with means of natal and breeding dispersal ($P < 0.05$) but not after correction for body size ($P > 0.1$). After correcting for phylogenetic relatedness, two morphometrical variables were significantly and consistently correlated with mean natal

dispersal: egg mass ($r = 0.320$, $P < 0.01$, and $r = 0.253$, $P < 0.05$, for both phylogenies, respectively, $n = 74$), and wing length ($r = 0.442$, $P < 0.001$, and $r = 0.243$, $P < 0.05$, for both phylogenies, respectively, $n = 74$).

Migration had a significant effect on all parameters of dispersal (Table 3). The migrant species disperse further than the resident species (class averages in kilometres: migrants, 14.20, $n = 15$, and residents, 7.89, $n = 52$ for mean breeding dispersal; 25.05, $n = 15$, and 16.96, $n = 52$, respectively, for SD of breeding dispersal; 22.76, $n = 16$, and 15.58, $n = 59$, respectively, for mean natal dispersal; 28.23, $n = 16$, and 21.97, $n = 59$, respectively, for SD of natal dis-
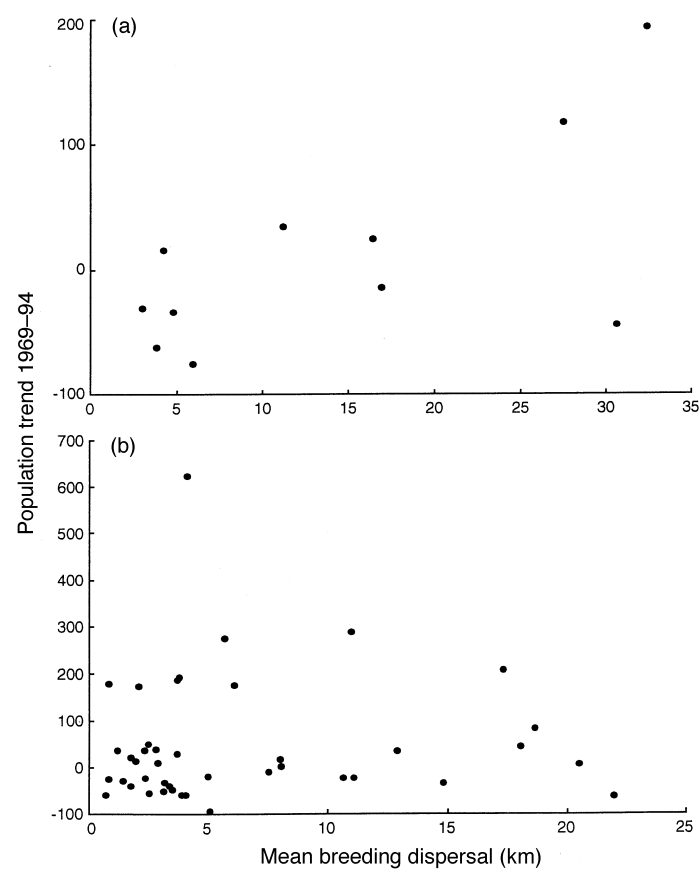
Fig. 9. Plot of mean breeding dispersal against long-term population trend measured by the changes in density on Common Birds Census plots during 1969–94, (a) migrant species, (b) resident species (see results for details on the analyses).

Table 3. Effects of categorical variables on breeding α and natal dispersal of British birds after removing the effect of body size

| | Breeding dispersal | | | | | | Natal dispersal | | | | | |
| | Mean | | | SD | | | Mean | | | SD | | |
	F	d.f.	P	F	d.f.	P	F	d.f.	P	F	d.f.	P
Migration	14·04	65, 1	0·0004	8·97	65, 1	0·004	13·83	73, 1	0·0004	1·17	73, 1	0·283
Summer habitat:												
Open vs. closed	0·28	65, 1	0·600	2·46	65, 1	0·122	1·58	73, 1	0·213	1·24	73, 1	0·270
Dry vs. wet	6·50	65, 1	0·013	2·81	65, 1	0·198	1·66	73, 1	0·419	4·53	73, 1	0·037
Winter habitat:												
Open vs. closed	0·07	65, 1	0·796	2·25	65, 1	0·117	0·72	73, 1	0·399	2·68	75, 1	0·106
Dry vs. wet	7·56	65, 1	0·008	1·89	65, 1	0·174	0·65	73, 1	0·422	5·08	73, 1	0·027
Summer food	0·49	65, 1	0·488	1·07	65, 1	0·305	10·03	73, 1	0·002	1·76	73, 1	0·189
Winter food	5·47	65, 1	0·022	0·38	65, 1	0·539	26·02	73, 1	0·0001	2·62	73, 1	0·110
Breeding social system	2·98	64, 2	0·058	1·96	64, 2	0·149	2·15	72, 2	0·124	4·88	72, 2	0·010
Winter social system	0·19	65, 1	0·663	0·72	65, 1	0·399	2·77	73, 1	0·101	5·21	73, 1	0·025

persal). The dichotomous habitat variables opposing dry vs. wet habitats had a strong effect on mean of breeding dispersal (Table 3): the species living in wet habitats, in summer and/or in winter, disperse further than those in dry habitats (average: 16·04, $n = 17$, and 7·01, $n = 50$, respectively, for summer habitat; 17·83, $n = 14$, and 7·05, $n = 53$, respectively, for winter habitat). The same variables had marginal effects on SD

of breeding dispersal and mean of natal dispersal. Food in winter was also important (Table 3): the species eating mainly animal prey in winter disperse further than those eating mainly plants (average: 10·97, $n = 41$, and 6·67, $n = 26$, respectively, for mean breeding dispersal; 21·13, $n = 49$, and 9·54, $n = 26$, respectively, for mean natal dispersal). Food in summer had a significant effect on mean of natal dispersal

(Table 3). Social system during the breeding season had a significant effect on SD of natal dispersal: average: colonial, 20·81, $n = 10$, neighbourhood, 20·95, $n = 8$, and territorial 15·93, $n = 57$. All ANOVAs computed to test for a relation between evolutionary change in categorical variables and dispersal parameters gave non-significant results ($P > 0·09$).

Discussion

The distribution of animal dispersal distances and the factors affecting it are still poorly known (van Balen & Hage 1989). This study shows that British bird species differ in their breeding and natal dispersal distance distributions and that this variability can be related to ecological and biological variables. The most important variables were: abundance and distribution, some life history traits, whether the habitat is wet or dry, winter food, breeding social system, migration and body size. The phylogenetic analyses revealed that relatedness between species is critical for the evaluation of the importance of these variables on dispersal. Some variables were no longer significantly correlated after the phylogenetic correction, suggesting that the simple correlations were the result of a common heritage through time (Harvey & Purvis 1991). On the other hand, the correlation between age at first breeding and mean of natal dispersal was only revealed after phylogenetic correction. This indicates further the importance of this kind of comparative analysis (Felsenstein 1985).

The present study set out to decipher the interspecific variations in dispersal patterns for British breeding birds. In the following we discuss the results we obtained relative to each studied variable; we emphasize the relationships between dispersal, migration, distribution and abundance in the light of the current ideas on these subjects and previous studies. Finally, we underline the potential contribution of the present study.

The pervasive influence of body size on species' life history and ecology is evidenced by the positive correlations with both measures of dispersal across species. Evolutionary trends towards larger body size have, however, been independent of dispersal which suggests that much of this variation is due to taxonomic differences. Few other studies have explicitly considered the relation between dispersal and body size. Peters (1983) reports that migration distances are greater for larger species but migration and dispersal are distinct processes. Other morphometric variables were correlated with means of breeding and natal dispersal but these disappeared after the body size correction. The fact that egg mass and wing length were correlated with mean natal dispersal after correcting for phylogenetic relatedness is intriguing. It is interesting that Mönkkönen (1995) showed that there is a relationship between wing shape and migration distance but found no relationship between wing length and migration distance. We have no biological explanation for a link between natal dispersal and egg mass or wing length, and cannot exclude the possibility that these relations arose because of type I statistical errors due to the number of tests made.

Some life history traits were strongly correlated with several parameters of dispersal but an allometric relation seems to account for this as these correlations lost significance after the body size correction, except for number of broods per year. Interestingly, Bennett & Harvey (1988) showed there is a negative correlation between the number of broods per year and adult survival among European birds, even after correcting for body size. This is evidence that the number of broods per year is involved in life history trade-offs. Dispersal may also be involved in such trade-offs, which could explain the negative correlation between natal dispersal and number of broods per year once the influence of body size was removed. Correlations with other life history variables may be difficult to characterize because of the small number of species we have here compared to that in Bennett & Harvey (1988). An important result from the phylogenetic analyses is that the correlations between age at independence or age at first breeding and mean natal dispersal were stronger than the cross-species correlations. A close examination of the PICs indicates that this result is mainly due to the contrast between the raven, *Corvus corax* L., and its closest relative in our reconstructed phylogenies, the crow, *C. corone* L. The raven has considerably higher age at independence and mean of natal dispersal than the crow, and as both species are closely related this resulted in a high PIC for this pair of species. PICs for the Corvidae are generally high as there is an important variation in age at independence and mean dispersal distance within this family. If we removed the Corvidae from the phylogenetic analyses, then the correlations were still positive but not significant.

Correlations between population size, geographical range and local abundance on the one hand, and dispersal parameters on the other, are not surprising as dispersal is usually thought to have a critical influence on these variables (Tilman 1994). The relationships here were negative, which we interpret to mean that the species exploiting the most abundant habitats in the British Isles do not need to disperse a long distance to find suitable sites for reproduction. Brown, Mehlman & Stevens (1995) suggested that variations in abundance of North American birds are primarily determined by variation in the distribution of suitable habitats. If the same explanation holds for British birds, then this would corroborate our interpretation of the negative relationship between dispersal distances and abundance. There was no correlation between long-term population trend and dispersal parameters considering all species together, but the correlation was positive and significant when considering the migrant species alone. This correlation

was not influenced by body size or phylogenetic relatedness. Lack of sufficient dispersal, and hence colonization abilities, has been proposed as a causal factor of population decline (Harrison 1991). If so, a positive correlation between dispersal and population trend is expected. This suggests that poor dispersal in some migrant species could have a role in their long-term decline. However, recent investigations showed that mortality outside the breeding season could be the major cause of population decline for several British birds (Baillie & Peach 1992; Peach, Crick & Marchant 1995), indicating that further evaluation of the role of dispersal is necessary.

The negative correlation between dispersal and both species' geographical range size and species' abundance among British birds is entirely new; the non-independence of abundance and range has been widely documented (e.g. Gaston, Blackburn & Lawton 1997). Two studies have also shown life history traits associated with fecundity to be correlated with abundance and range size (Blackburn, Lawton & Gregory 1996; Gaston & Blackburn 1996). Higher rates of offspring production tend to be found in species with higher abundances and larger range sizes, although these relationships often disappear after correcting for phylogeny. Intriguingly, we find that fecundity (measured as broods per year) declines with breeding and natal dispersal across species, and that later development (measured as age at independence and age at first breeding) is associated with greater natal dispersal within taxa. Thus species with limited dispersal tend to be the most fecund and develop earlier; furthermore, they attain higher abundances and larger geographical range sizes. The interrelation between these variables and a suite of other macro-ecological variables is likely to be complex; the role of dispersal in such considerations has until now largely been neglected. It is unclear why some of these patterns are robust to phylogenetic analysis whereas others are not. This implies that some of these patterns may be taxonomic artefacts but the results from different studies are mixed (Blackburn *et al.* 1996; Gaston & Blackburn 1996) suggesting that the power to detect these patterns is low. The significant correlations between dispersal parameters and population size or geographical range after the phylogenetic correction are somewhat intriguing. It is hard to predict that these variables should diverge simultaneously during evolutionary times. This result is in agreement with previous reports of an influence of phylogenetic relatedness between species on the relations between body size and abundance in British birds (Nee *et al.* 1991) or between abundance and distribution (Gregory 1995). Competition within guilds of closely related species may have a critical influence on these phylogenetic relationships (Nee *et al.* 1991; Gregory 1995).

Migration had a strong effect on dispersal parameters, but this needs to be interpreted

cautiously. Migration movements could have confounded the present study; Baker (1993) showed that the redstart *Phoenicurus phoenicurus* L., and the wheatear *Oenanthe oenanthe* L. (two migrant birds) in Britain tend to move significantly along the north–south axis and to a greater extent than the robin *Erithacus rubecula* L., a closely related resident species. Baker (1993) suggested that such postfledging movements have a function in locating a future breeding site, an overwintering site, or in creating a navigational target; some of these explanations could be non-exclusive. We tested the possibility that young migrant birds could be ringed far away from their birth sites by analysing separately the birds ringed in the nest (EURING age code 1) and those ringed in their year of birth but as freely flying (EURING age code 3) for each migrant species. Our expectation, according to Baker's results, was that the mean, and especially the SD, should be greater in the latter category. This was not verified for 15 species out of 16, the exception being the swallow *Hirundo rustica* L. where the 'age 3' birds ringed in August were recovered at a significantly greater distance than all the other birds ringed as juveniles (these birds were excluded for the estimation of the natal dispersal parameters). The other 15 species did not verify our expectation because birds ringed as 'age 3' were a small part of the sample or were ringed mostly early in the breeding season, thus introducing no bias in our analyses. We were quite restrictive with respect to the distances of migrant birds and imposed a threshold so that all distances below it were not preferentially directed in any direction; this threshold varied from 30 km for the turtle dove *Streptopelia turtur* L. to 300 km for the reed warbler *Acrocephalus scirpaceus* L. The distributions of dispersal distances were different between migrant and resident species (see Figs 1 and 2). We consider that our results reveal a real pattern and that migrants disperse further than resident birds, although, as we cannot be absolutely certain that our analytical methods eliminate all migratory movements, this conclusion should be regarded as provisional. British migrant birds differ from resident species with respect to several ecological characters (O'Connor 1981), and this could explain our results. O'Connor (1985) hypothesized that migrant birds in Britain use more intermediate successional habitats compared to residents. Hence, migrants may have an opportunistic settling strategy (Johnson & Grier 1988; Spendelow *et al.* 1995). However, there was variation within the migrants and some species have relatively short dispersal distances similar to most residents (e.g. swallow or house martin *Delichon urbica* L.).

Habitat was an important factor for breeding dispersal with respect to the 'wet vs. dry' feature. Possible confounding interactions with migration seem improbable as only four migrant species use wet habitats in summer, and only three in winter. Furthermore, the effect of 'wet vs. dry' habitat was limited to breed-

ing dispersal. The most sensible explanation of this result is that as wet habitats are more discontinuously distributed in space (patchy distribution of wet areas) or in time (wet areas are less stable) than dry ones, the species requiring a wet habitat to breed need to disperse further. This is supported by the absence of effect of this habitat variable on natal dispersal. The average of mean natal dispersal over the species living in dry habitats in summer (14·90, $n = 57$) or in winter (14·80, $n = 60$) is close to the average of mean breeding dispersal over the species living in wet habitats in summer (16·04, $n = 17$) or in winter (17·83, $n = 14$). This suggests that wet habitats impose a constraint on breeding dispersal but not on natal dispersal.

Food in winter had a significant effect on dispersal parameters, but there is little doubt that this was caused by an indirect effect of migration as all but one migrant species (the turtle dove) eat animal prey in winter.

The present paper reports the first comparative study of large spatial scale dispersal patterns for a taxonomic group of animals. Such studies are critical as parameters on dispersal are usually lacking in population studies (Brawn & Robinson 1996; Kot, Lewis & van den Driessche 1996). We were not able to investigate here the variation in dispersal distances at the intraspecific level, but we characterized interspecific differences. Our findings suggest that several factors critically influence the distribution of dispersal distances, and that it may be relevant to consider these factors in future studies on the costs and benefits of dispersal. Our results should be valuable for other comparative studies in order to evaluate the role of dispersal in several issues of population biology, for instance population synchrony, colonization and range expansion, metapopulation and source–sink dynamics, and population genetic structure.

Acknowledgements

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Appendix 1

For each species, the following data is indicated: the sample size (*n*), arithmetic mean (AM), geometric mean (GM) and standard deviation (SD) of breeding and natal dispersal distances (km), respectively, the number of ring recoveries between 1909 and 1994, and the categorical variables used in the analyses. The means and standard deviations are for the untransformed data. Number of categorical variables*

Species	Breeding dispersal				Natal dispersal				Recoveries 1909–94	Categorical variables*								
	n	AM	GM	SD	*n*	AM	GM	SD		1	2	3	4	5	6	7	8	9
Ardea cinerea	4	7·8	7·502	2·4	440	68·4	24·078	84·7	2347	R	C	F	A	A	O	W	O	W
Cygnus olor	497	18·0	2·719	48·0	49	34·3	16·772	35·9	19917	R	T	F	V	V	O	W	O	W
Branta canadensis	365	8·9	1·503	10·8	173	7·0	0·969	10·6	9688	R	C	F	V	V	O	W	O	W
Anas platyrhynchos	328	18·6	5·192	21·6	666	19·9	6·058	21·6	24917	R	T	F	V	V	O	W	O	W
Circus cyaneus	1	—	—	—	18	22·0	10·730	19·4	356	R	T	S	A	A	O	D	O	D
Accipiter gentilis	0				9	41·4	18·839	45·1	93	R	T	S	A	A	C	D	C	D
Accipiter nisus	17	17·3	2·220	36·2	231	15·6	6·654	22·0	3237	R	T	S	A	A	C	D	C	D
Buteo buteo	0				41	24·2	12·096	24·1	547	R	T	S	A	A	C	D	C	D
Falco tinnunculus	27	14·8	1·687	47·4	395	42·8	14·005	58·0	3933	R	T	S	A	A	O	D	O	D
Falco columbarius	1	—	—	—	39	35·1	22·245	23·0	702	R	T	S	A	A	O	D	O	D
Falco peregrinus	1	—	—	—	21	21·7	13·497	10·7	506	R	T	S	A	A	O	W	O	W
Gallinula chloropus	31	4·9	0·525	8·0	38	4·5	0·563	10·3	975	R	T	S	V	V	O	W	O	W
Fulica atra	32	20·5	2·565	25·8	25	23·2	4·444	28·1	1040	R	T	S	V	V	O	W	O	W
Larus ridibundus	110	44·5	7·968	72·5	1478	47·0	10·527	69·2	15582	R	C	F	A	A	O	W	O	W
Larus canus	19	16·6	1·600	34·4	159	21·1	4·731	30·0	1417	R	C	F	A	A	O	W	O	D
Larus fuscus	190	38·2	13·805	37·4	1882	28·2	2·384	40·7	8528	R	C	F	A	A	O	W	O	W
Columba oenas	19	5·6	1·426	6·5	96	10·4	3·035	15·6	368	R	N	F	V	V	O	D	O	D
Columba palumbus	233	10·9	1·805	24·1	718	10·7	2·277	19·3	2501	R	T	F	V	V	C	D	C	D
Streptopelia decaocto	102	4·1	0·570	9·3	37	9·3	2·503	11·5	757	R	T	F	V	V	O	D	O	D
Streptopelia turtur	12	3·8	0·757	6·1	4	8·8	1·300	10·8	209	M	T	F	A	A	O	D	O	D
Tyto alba	24	16·9	2·521	36·3	445	23·9	10·323	36·6	2556	R	T	S	A	A	O	D	O	D
Athene noctua	19	11·1	0·385	41·6	82	14·5	3·267	26·4	415	R	T	S	A	A	O	D	O	D
Strix aluco	24	3·1	0·433	7·4	282	8·3	2·121	13·5	1659	R	T	S	A	A	C	D	C	D
Asio otus	6	4·8	1·668	4·0	38	47·8	15·421	56·9	244	R	T	S	A	A	O	D	O	D
Apus apus	644	10·8	2·630	34·0	30	36·8	11·466	37·1	3139	M	N	F	A	A	O	D	O	D
Alcedo atthis	12	9·5	3·753	10·8	67	21·5	3·175	39·6	726	R	T	S	A	A	C	W	C	W
Picus viridis	19	1·7	0·449	2·5	14	7·6	2·049	10·1	145	R	T	S	A	A	C	D	C	D
Dendrocopos major	30	3·7	0·608	10·4	15	16·5	5·875	19·8	363	R	T	S	A	A	C	D	C	D
Alauda arvensis	15	0·7	0·167	1·9	32	5·5	0·302	23·1	207	R	T	F	V	V	O	D	O	D
Riparia riparia	144	7·7	1·221	13·4	395	20·9	6·650	22·8	15813	M	N	F	A	A	O	D	O	D
Hirundo rustica	76	4·8	0·564	9·4	72	14·1	3·194	28·4	8321	M	T	F	A	A	O	D	O	D
Delichon urbica	191	4·2	0·688	8·3	28	10·4	3·185	12·2	1127	M	N	F	A	A	O	D	O	D
Motacilla flava	14	3·0	0·715	3·8	20	12·5	4·948	11·5	485	M	T	F	A	A	O	D	O	D
Motacilla cinerea	3	—	—	—	20	26·6	15·802	29·5	253	R	T	S	A	A	O	W	O	W
Motacilla alba	47	8·0	0·892	30·5	157	16·1	5·164	23·6	3595	R	T	S	A	A	O	W	O	W
Cinclus cinclus	12	1·2	0·230	3·2	56	8·0	1·678	10·9	485	R	T	S	A	A	O	W	O	W

Appendix 1 (cont)

Species	Breeding dispersal				Natal dispersal				Recoveries 1909–94	Categorical variables*								
	n	AM	GM	SD	n	AM	GM	SD		1	2	3	4	5	6	7	8	9
Troglodytes troglodytes	33	6·5	0·527	14·5	40	8·9	1·170	14·7	1442	R	T	S	A	A	C	W	C	W
Prunella modularis	190	1·4	0·191	8·3	237	2·1	0·380	7·2	4952	R	T	S	A	A	C	D	C	D
Erithacus rubecula	147	8·0	0·359	35·9	409	6·0	0·571	20·2	8219	R	T	S	A	A	C	D	C	D
Phoenicurus phoenicurus	1			—	18	12·2	3·873	11·9	333	M	T	S	A	A	C	D	O	D
Oenanthe oenanthe	6	17·2	0·623	39·2	21	18·9	2·353	28·9	326	M	T	S	A	A	O	D	O	D
Turdus merula	1806	3·2	0·224	20·6	2189	3·3	0·264	20·3	48511	R	T	S	A	A	C	D	C	D
Turdus philomelos	397	4·0	0·253	21·8	779	7·0	0·591	21·6	11318	R	T	S	A	A	C	D	C	D
Turdus viscivorus	89	2·3	0·384	5·8	92	8·3	1·490	17·4	1265	R	T	S	A	A	O	D	O	D
Acrocephalus schoenobaenus	29	30·6	1·097	58·3	70	40·4	6·020	57·8	3400	M	N	S	A	A	O	W	C	W
Acrocephalus scirpaceus	53	32·4	2·935	61·6	77	47·0	5·215	68·6	5336	M	T	S	A	A	O	W	C	W
Sylvia curruca	19	16·4	5·129	21·2	26	32·3	16·886	24·3	396	M	T	F	A	A	C	D	C	D
Sylvia communis	51	11·1	1·145	19·0	89	14·4	2·815	19·0	825	M	T	S	A	A	O	D	O	D
Sylvia atricapilla	64	27·5	8·027	32·0	74	41·2	17·539	37·9	1976	M	T	S	A	A	C	D	C	D
Phylloscopus trochilus	58	16·9	0·816	39·6	79	20·8	2·172	46·3	2329	M	T	S	A	A	O	D	C	D
Muscicapa striata	38	5·9	0·796	12·1	47	12·8	3·377	17·6	398	M	T	S	A	A	C	D	C	D
Ficedula hypoleuca	238	20·6	11·668	17·7	1551	20·6	14·272	16·5	3126	M	T	S	A	A	C	D	C	D
Aegithalos caudatus	32	3·7	0·695	6·1	21	8·3	2·176	8·3	1063	R	T	F	A	V	C	D	C	D
Parus montanus	14	1·7	0·369	3·1	14	4·6	1·063	5·3	204	R	T	F	A	A	C	D	C	D
Parus ater	22	1·2	0·228	3·1	35	9·4	2·597	10·8	878	R	T	F	A	A	C	D	C	D
Parus caeruleus	201	2·3	0·232	10·2	703	5·3	0·796	15·2	17885	R	T	F	A	A	C	D	C	D
Parus major	173	2·5	0·246	12·3	560	5·3	0·797	17·9	7313	R	T	F	A	A	C	D	C	D
Sitta europaea	22	0·8	0·247	1·6	30	6·5	1·803	8·8	305	R	T	F	A	V	C	D	C	D
Garrulus glandarius	76	2·8	0·401	8·1	42	3·5	0·702	6·3	990	R	T	S	A	A	C	D	C	D
Pica pica	33	2·1	0·245	7·5	205	7·9	1·033	18·2	1008	R	T	S	A	V	O	D	O	D
Corvus monedula	51	6·0	0·721	12·8	51	8·6	2·127	11·6	1478	R	C	S	A	V	O	D	O	D
Corvus frugilegus	96	3·1	0·650	4·7	84	8·5	1·964	13·0	1602	R	C	F	V	V	O	D	O	D
Corvus corone	20	3·7	0·925	4·3	206	9·9	3·240	12·8	891	R	T	F	A	A	O	D	O	D
Corvus corax	0				212	39·6	25·835	37·6	545	R	T	S	A	A	O	D	O	D
Sturnus vulgaris	1672	3·4	0·273	19·1	401	9·5	1·100	28·1	37101	R	C	S	A	V	O	D	O	D
Passer domesticus	526	1·9	0·147	22·4	531	1·7	0·206	6·9	5971	R	C	F	V	V	C	D	C	D
Passer montanus	38	5·0	0·284	23·3	54	8·0	0·717	17·5	715	R	C	F	V	V	O	D	O	D
Fringilla coelebs	120	2·8	0·302	9·9	64	3·6	0·787	5·6	5454	R	T	F	A	V	C	D	C	D
Carduelis chloris	283	7·5	0·732	22·1	99	4·2	0·954	6·4	25174	R	T	F	V	V	C	D	C	D
Carduelis carduelis	63	10·6	0·835	20·8	85	11·1	1·663	18·2	1158	R	T	F	V	V	C	D	C	D
Carduelis cannabina	110	3·5	0·393	8·3	147	4·4	0·694	8·8	1852	R	N	F	V	V	C	D	C	D
Carduelis flammea	45	21·9	5·383	25·1	31	22·7	2·139	31·0	1551	R	T	F	A	V	O	D	O	D
Pyrrhula pyrrhula	194	2·5	0·382	5·2	195	4·6	0·852	9·8	3017	R	N	S	A	V	C	D	C	D
Emberiza schoeniclus	79	3·8	0·468	9·3	58	5·4	0·952	13·1	1993	R	T	F	A	V	C	W	O	D