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Extent of recent polewards range margin shifts in Finnish birds depends on their body mass and feeding ecology

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Global warming would predict that, all else being equal, species should shift their range margins polewards, and that a failure to do so could be detrimental for a population. A polewards range margin shift has been documented previously in the Finnish avifauna. Here, I showed that the polewards range margin shift of 116 Southern Finnish bird species was larger for small-bodied species and differed according to their feeding ecology, but not to their migration ecology. Species foraging in wet habitats had experienced strong range margin shifts as compared with other feeding ecologies. For 53 species, population trends for 1983–2005 were available. I found no evidence that those feeding ecological groups that showed a relatively small shift in range margin had experienced low population growth or a population decline. Instead, I found some evidence that the long-term trend in population numbers varied across migration ecologies after correcting for changes in their Finnish breeding range. The results suggest that those processes that cause a shift in the range margin of birds are not involved in the recent changes in bird abundances.

1. Introduction

The scientific community is reaching a consensus that human-induced climate warming is occurring, and that this climate warming is changing the phenology and distribution of animals and plants worldwide (Intergovernmental Panel of Climate Change 2007). A decline in population numbers due to climate change has been documented in a Dutch population of Pied Flycatchers *Ficedula hypoleuca*, where birds have not advanced their arrival date despite recent springs getting warmer (Both *et al.* 2006). In addition, there is evidence that climate warming in spring induces earlier egg laying in Finnish Black Grouse *Tetrao tetrao* populations, causing their chicks to hatch before the summer food peak of insects (which has not changed), possibly explaining the decline in Black Grouse population size (Ludwig *et al.* 2006). These case studies provide great insights into how climate change may, by affecting individual reproduction, cause a population decline. However, we arguably need 'rule-of-thumb' information about which characteristics make a species more sensitive to climate change in order to properly evaluate the ecosystem consequences of climate-induced biotic change.

One population-level change expected under a climate-warming scenario is a poleward shift in the distribution of organisms (Parmesan *et al.*

2000). Birds may be particularly likely to show such a shift, because they disperse readily and should therefore be able to change their breeding locations rapidly in response to a shift in the temperature isoclines across years. Here, I explore whether a classification by avian functional groups (*sensu* Alerstam 1982) provides insight into understanding which species show a population-level response to climate change. From a conservation biological point of view, a decline in population numbers is of particular concern. Potentially, those functional groups that do not shift their range margin consist of species that are declining, and would therefore be of particular management concern. I therefore also study whether long-term changes in abundance are related to functional groups.

2. Material and methods

2.1. Data compilation

The Finnish range size and northern range margins of 116 bird species with a predominantly southern distribution in Finland were measured by Brommer (2004). The range margin of these species was measured as the median latitude of the ten northernmost 10 × 10 kilometres grid cells in two consecutive Finnish atlases of breeding birds, reported for 1974–1979 in Hyytiä *et al.* (1983) and for 1986–1989 in Väisänen *et al.* (1998). Finnish range size was estimated as the number of occupied grid cells in both these atlases.

Out of the 116 species considered, the trend slope describing the change in their abundance for the period 1983–2005 was calculated for 53 species by Väisänen (2006). Abundance was based on yearly line transect counts carried out over the whole of Finland. Details on locations of the transects and methods used are provided by Väisänen (2005). The slope of a trend decribed a percentage change in species abundance during this period and was estimated as a linear trend using the Trends and Indices for Monitoring data (TRIM) software (Pannekoek & van Strien 2004), correcting for overdispersion and auto-correlation across the yearly indices (Väisänen 2005, 2006). To my knowledge, this is the largest dataset available of the long-term trends in population numbers of Finnish birds that is comparable across species, because it has both been gathered and analysed using the same procedures.

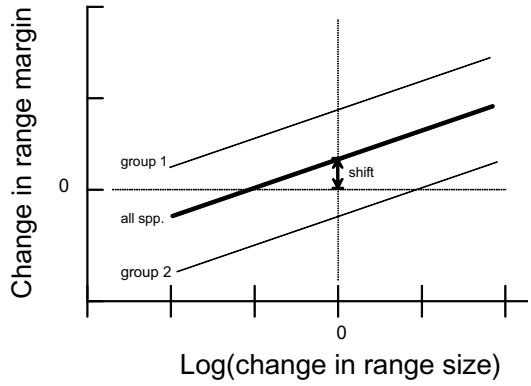

Fig. 1. A schematic illustration of the concept of analyzing a shift in range margin (*sensu* Thomas & Lennon 1999) for different functional groups. The change in the range margins of all species (thick line, 'all spp.') during a certain period of time is positively related to the change in their range sizes during that period. The range-margin shift is the change in range margin if no change in range size would occur, indicated by the intercept in the plotted schematic. This concept of a range-margin shift can be extended to test for differences between functional groups by dividing all species into separate functional groups and testing whether they differ in their range margin shift (intercept of the thin lines).

2.2. Analysis

I modelled changes in the range margin of a species by constructing the minimum adequate model following standard procedures for a Generalised Linear Model (GLM) with normal errors and an identity link (Crawley 2005). The observed change in the range margin needs to be corrected for a change in range size in Finland, because an expansion in Finnish range size will necessary be associated with a change in range margin. Populations that have expanded their range in Finland will tend to have moved their range margin polewards, and *vice versa*. To statistically correct for this relationship, I calculated the change in range size as log(range size in 1986–1989 atlas / range size in 1974–1979 atlas), where the Finnish range of a species is the number of occupied grid

cells in these atlases (as provided by Väisänen *et al.* 1998). Hence, no change in range size in Finland is denoted by a zero [log(1) = 0], with positive values indicating an increase in range size and negative values indictating a range restriction within Finland. In the model, the change in range margin between the two atlases was the response variable, and the log of the change in Finnish range between these atlases was used as a continuous explanatory variable (Thomas & Lennon 1999, Brommer 2004). What is termed here a shift in range margin is the change in range margin assuming no change in range size (i.e., the intercept of the change in range margin; Fig. 1). Note that this concept defines a shift in range margin as a property of a set of species and not of a particular species. In this ANCOVA type of modelling approach, the range margin shift of different functional groups is provided by their least-square means (intercepts of the group-specific lines in Fig. 1).

As a description of functional groups, I included the feeding and migration ecology (*sensu* Alerstam 1982) of each species and, as a continuous covariable, their body mass as provided by Solonen (1994). Species and their assignment to functional groups are listed in the Appendix. I used a modification of Alerstam's (1982) original feeding ecologies, where I grouped shore and/or mire species, species foraging on the bottom of a water mass, fish-eating species, and species foraging from the water surface as 'wetland species' (W). This grouping of the original feeding ecologies was done *a posteriori* of an initial analysis that showed that these four original feeding ecologies grouped in terms of their range-margin response (analysis not shown), and was done because only few species belonged to some feeding ecologies (see Appendix). In addition to this category, I maintained Alerstam's (1982) original categories of terrestrial herbivore species (T), bird of prey (C), insectivorous species (I), granivorous species (G) and omnivorous species (O). Migration ecology was divided into sedentary (N), irruptive/nomadic (I), partially migratory (P), short-distance migrant (S) and long-distance migrant (L).

The GLM was solved using Maximum Likelihood, which is robust to unbalanced data. I constructed the minimum adequate model by starting from the full model with all variables included and sequentially eliminating the non-significant variable with the lowest F statistic (Crawley 2005). F statistics of explanatory variables are based on comparing the likelihood of models with and without that variable. Models were implemented in R.

3. Results

3.1. Range-margin shifts and avian functional groups

Species with a larger body mass showed a smaller range margin shift (Table 1). There were significant differences in range-margin shifts for species that differed in feeding ecology, but migration ecology was not significant (Table 1). The range-margin shifts (i.e., the expected change in range margin corrected for changes in the distribution and for a species' body mass) showed that terrestrial

Table 1. Generalised Linear Model of the change in range margin between the 1974–1979 and 1986–1989 atlases of 116 Finnish breeding bird species. A stepwise backward procedure was used to construct the minimum adequate model, and the dropped variable is shown with the statistic when it was last retained in the model. Model's R^2 = 0.394.

Variable	Coefficient	F statistic	P
Minimum adequate model			
Constant	48.43 ± 11.7		
Log(change in range size)	362.4 ± 46.9	$F_{1, 108}$ = 59.8	<0.001
Body mass (g)	–0.056 ± 0.020	$F_{1, 108}$ = 7.95	0.006
Feeding ecology		$F_{5, 108}$ = 3.73	0.004
Dropped variables			
Migration ecology		$F_{4, 104}$ = 1.19	0.32

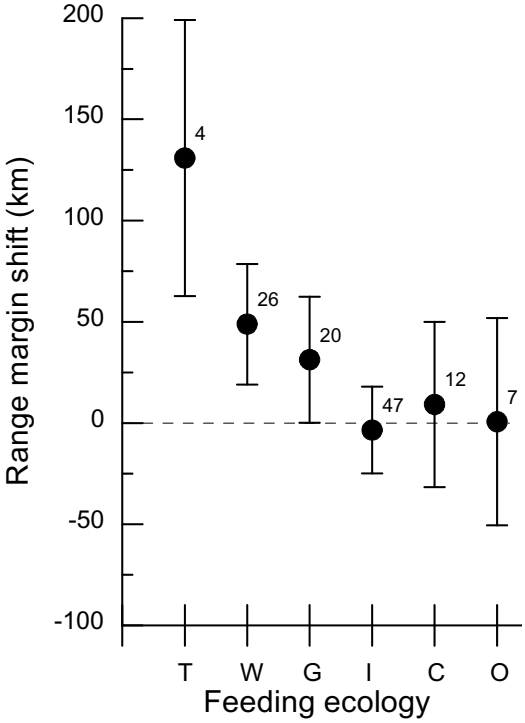

Fig. 2. The range-margin shift (in km) with their 95% confidence interval of 116 Southern Finnish bird species grouped into six categories of feeding ecology (following Alerstam 1982). The range-margin shift is the least-square mean of the change in the range margin between the 1974–1979 and 1986–1989 atlases, corrected for the change in the range size of a species and its body mass (model specified in Table 1). Feeding ecology was: T – terrestrial herbivore; W – wetland species; G – granivorous species; I – insectivorous; C – bird of prey; O – omnivorous. Sample sizes (species per functional group) are denoted next to the plotted least-square mean. The dotted line indicates no shift in range margin.

herbivores and wetland species showed a considerable range-margin shift. Species in the large feeding ecology groups of insectivorous and granivorous species (I and G in Fig. 2) essentially did not change their range margin.

3.2. Changes in abundance and avian functional groups

The logarithm of the change in distribution of a species from the 1974–1979 to the 1986–1989 atlas correlated with the long-term trend in that species' abundance in the period 1983–2005 (Table 2). Hence, changes in the Finnish range, based on atlas data, contains information on long-term trends in abundance. The trends in abundance of Southern Finnish birds was not affected by body mass of a species, and did not vary significantly across feeding ecologies, but there was some evidence for variation across migration ecologies (Table 2, Fig. 3). A direct comparison of the range-margin shift of the different feeding ecologies (Fig. 2) and the mean change in abundance of these functional groups revealed no relationship between range-margin shift and change in abundance ($r = –0.2$, $n = 5$, $P = 0.75$).

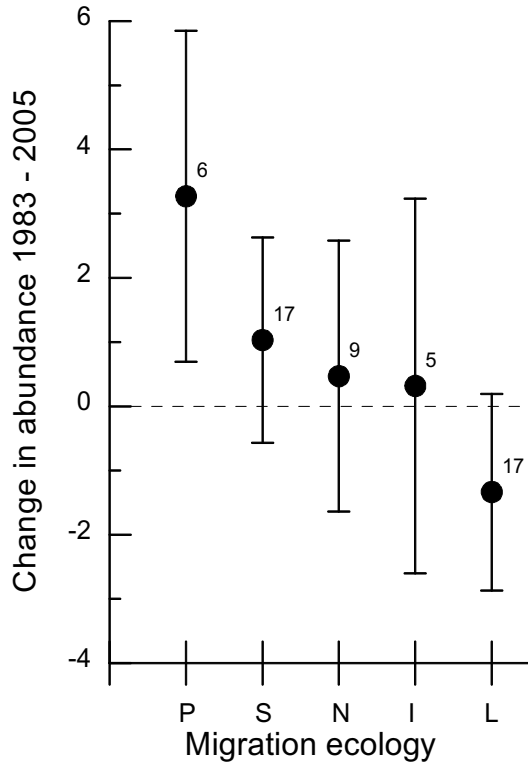

Fig. 3. Least square mean (with 95% confidence interval) in the trend of population abundance during 1983–2005 of different migration ecologies (see Table 2). Migration ecology was divided into partially migratory (P), irruptive/nomadic (I), sedentary (N), short-distance migrant (S) and long-distance migrant (L).

Table 2. Generalised Linear Model of the change in abundance (% per year) between 1983 and 2005 (Väisänen 2006) for different feeding and migration ecological groups of 54 Southern Finnish bird species. A stepwise backward procedure was used to construct the minimum adequate model, and the dropped variables are shown in the order they were dropped with the statistic when each term was last retained in the model.

Variable	Coefficient	*F* statistic	*P*
Minimum adequate model			
Constant	0.69 ± 0.51		
Log(change in range size)	17.2 ± 7.4	$F_{1, 47} = 5.39$	0.025
Migration ecology		$F_{4, 47} = 2.58$	0.049
Dropped variables			
Body mass	0.0001 ± 0.004	$F_{1, 42} = 0.017$	0.97
Feeding ecology		$F_{4, 43} = 1.68$	0.17

4. Discussion

4.1. Range-margin shifts

While the avifauna of Southern Finland has, on average, shifted its range margin polewards (Brommer 2004), I showed here that not all species have done so to the same degree. Two factors (out of the three considered) appeared important predictors for whether the range margin of a species had shifted. First, a smaller body mass facilitates range margin shifts. Small-bodied birds have a short generation time and a high reproductive rate, which may allow such species to effectively track changes in their environment (Saether 1988, Saether *et al.* 2002). Second, the range-margin shift depends on the feeding ecology of a species. In particular, species of wet habitats had experienced a pronounced range-margin shift polewards. In addition, herbivorous terrestrial species had shifted their range margins considerably, but this functional group consists of only four species. In contrast, the three most common feeding ecological groups (granivorous and insectivorous species and birds of prey) showed no appreciable shift in range margin. Range-margin shifts are not related to the migration ecology of a species.

The approach taken here, to understand changes in the distribution of Finnish avifauna, is descriptive, and differences in range-margin shifts between the functional groups analysed here may be due to various factors. Climatic warming is one process that predicts an overall polewards shift in the distribution of animals and plants as they follow the shift in temperature isoclines (Parmesan *et al.* 2000). A response to climatic warming may conceivably differ across avian feeding ecologies, because the different food or foraging habitats may show specific responses to climatic warming. For example, warming may be particularly beneficial for birds that forage in water or in wet habitat, because the time of ice cover in these habitats during Finnish winters would have shortened, and warming may allow easier access to water in more northern localities. Clearly, however, also other large-scale environmental changes can cause such a pattern. For example, intensification of agriculture may have led to eutrofication processes that have especially increased the productivity of northerly water bodies, which may have allowed birds to breed more readily in northerly regions.

I have here explored the usefulness of Alerstam's (1982) classification of bird ecologies in contrasting different species groups. Nevertheless, the approach outlined here would allow one to contrast also additional classifications of the avifauna in order to find the most important factor(s). One important caveat to the approach taken here is that all species are considered as independent units, whereas many species are phylogenetically closely related. In particular, many species belonging to the same feeding-ecology group are phylogenetically related and are therefore not strictly independent. Comparative approaches can correct for phylogeny (e.g., Bennett & Owens 2002). However, in an ecological analysis as I car-

ried out here, correcting for phylogeny may be overly conservative, because such corrections also take out part of the ecological signal (Westoby *et al.* 1995).

The atlas data used here has an important spatial restriction in that it can only consider the breeding range of birds on a national (i.e., Finnish) scale. Clearly, the birds considered in my analysis occur also south from Finland, and the change in Finnish range need not reflect the change in the overall distribution of a species. For example, a species that has expanded polewards in Finland may only have expanded its northernmost range with no changes in the rest of its distribution, but it may also have shifted its whole distribution northwards.

These two scenarios can only be distinguished by analysing the change in southern range margin of the species considered in this analysis. In general, the southern range margins of bird species have not shifted polewards (Thomas & Lennon 1999, Brommer 2004), although it should be noted that a direct comparison of changes in the northern and souther range margins of the same species, while correcting for range expansion or retraction, is lacking thus far.

4.2. Changes in abundance

The present analysis on trends in abundance during the recent two decades of a subset of 53 out of the 116 species considered, showed that the extent to which a species changed in abundance varies across migration ecologies and not across feeding ecologies. Especially partial migrants had enjoyed a recent increase in abundance. Potentially, this increase may be linked to the climatic trend of warmer Finnish winters in recent decades, which could benefit such a 'mixed' migration strategy. A large-scale, long-term comparison has shown that long-distance migrants are declining more than short-distance migrants and residents (Sanderson *et al.* 2006). This difference is – to some extent – also visible in the Finnish data analysed here, although long-distance migrants did not show a significant decline. An additional finding was that changes in the Finnish range between the 1974–1979 and the 1986–1989 atlases correlated with changes in the abundance of species during a much longer period, extending also after the survey for the second atlas (1983–2005). Abundance and range size of a species are linked (Gaston *et al.* 1997), but it is encouraging to find here that changes in the Finnish range of a species based on atlas data has some predictive power for future trends in abundance.

The finding that feeding ecology was an important factor for understanding range-margin shifts, whereas migration ecology was the only relevant ecological factor explaining changes in abundance, implies that those factors that make a species prone to shift its range margin are not those that cause changes in the abundance of a species. This is further illustrated by the lack of correlation between the shift in range margin of the different feeding ecologies and the change in their mean abundance. This finding is contrary to expected under a climate-change scenario, because, all else being equal, a clear range-margin shift should indicate a good capacity to track climatic change, which should result in a more positive trend in abundance if climate change is indeed the main driver of population-level change.

Unlike other studies that have used a more qualitative measure of changes in abundance (e.g., Sanderson *et al.* 2006), I used data on species abundance based on standardized line-transect counts carried out throughout Finland (details in Väisänen *et al.* 2005). This quantitative approach has the advantage of producing count data that can be compared across species, but has the disadvantage that certain groups are missing (in particular water birds; see Appendix). Hence, this analysis lacks in power, because data on population trends are only available from half of the species whose range margin shift is considered. More studies relating changes in range margins to actual population numbers are needed in order to improve our understanding of whether observed changes in the spatial distribution of organisms indeed have repercussions for their population numbers.

Acknowledgements. My thanks go to all those volunteers who have collected data for the first and second atlas, and to those carrying out line transect counts during the last decades. I hope this work inspires those who are now gathering data for the third atlas! The idea for these analyses traces back to a discussion with Ari Hoffman during his visit to Helsinki in 2006. Patrik Byholm is thanked for help with locating literature. Markus Ahola and two anony-

mous reviewers provided excellent comments that improved the manuscript substantially.

Suomen linnuston viimeaikaiset levinneisyysalueiden muutokset napoja kohti riippuvat ruumiinkoosta ja ravinnonkäytöstä

Maapallon lämpenemiskehityksen myötä – muiden tekijöiden pysyessä vakioina – lajien oletetaan siirtyvän kohti napa-alueita, ja siirtymisen epäonnistuminen saattaa olla populaation säilymiselle kohtalokasta. Suomen linnustolle on aiemmin dokumentoitu tällaisia siirtymisiä. Osoitin tutkimuksessani, että 116 pesimälajillemme siirtymät olivat suurempia pienikokoisemmilla lajeilla ja vaihtelivat ravinnonkäytön ekologian mutteivät muuttostrategian mukaan. Märissä ympäristöissä ruokailevien lajien siirtymät olivat suurempia kuin muilla ravinnonkäyttöryhmillä. Populaatiokoon muutos jaksolle 1983–2005 oli saatavissa 53 lajille.

Niille ravinnonkäyttöryhmille, joiden levinneisyysalueet olivat siirtyneet vain vähän, ei löytynyt viitteitä populaation hitaasta kasvusta tai vähenemisestä. Korjattuani aineistoa Suomen sisäisen pesimäalueen muutoksen suhteen kuitenkin havaitsin, että pitkäaikaiset kannanmuutokset vaihtelivat muuttostrategian mukaan. Tulokseni viittaavat siihen, että lintujen levinneisyysalueen muutoksia aiheuttavat prosessit eivät liity viimeaikaisiin lintujen runsauksien muutoksiin.

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Appendix. Species in alphabetic order with their feeding and migration ecology and weight (Solonen 1994). For 53 species, the change in abundance (Δ Abundance) in Finland in percent per year for 1983–2005 is listed (Väisänen 2006). Feeding ecology (Alerstam 1982): T – terrestrial herbivore; G – granivorous species; I – insectivorous; C – bird of prey; O – omnivorous. In addition, I distinguished species foraging in wet habitat (W), which is a grouping of Alerstam's (1982) original feeding ecologies (in brackets): f – fish eating; b – foraging on the bottom of a water mass; s – shore and/or mire, w – foraging from the water surface. Migration ecology was divided into partially migratory (P), irruptive/nomadic (I), sedentary (N), short-distance migrant (S) and long-distance migrant (L).

Species	Feeding	Migration	Weight (g)	Δ Abundance
Accipiter gentilis	C	P	1,120	
Accipiter nisus	C	P	200	
Acrocephalus arundinaceus	I	L	30	
Acrocephalus dumetorum	I	L	12	
Acrocephalus palustris	I	L	12	
Acrocephalus schoenobaenus	I	L	12	0
Acrocephalus scirpaceus	I	L	13	1.2
Aegithalos caudatus	I	I	8	
Aegolius funereus	C	I	123	
Alauda arvensis	G	S	37	–1.1
Anas clypeata	W (b)	S	600	
Anas platyrhynchos	W (b)	S	1,100	
Anas querquedula	W (b)	L	365	
Anas strepera	W (b)	S	755	
Apus apus	I	L	42	–1.8
Ardea cinerea	W (f)	S	1,040	
Asio otus	C	S	290	
Aythya ferina	W (b)	S	870	
Bonasa bonasia	T	N	350	–1.2
Botaurus stellaris	W (f)	S	1,230	
Bubo bubo	C	N	2,625	
Buteo buteo	C	S	750	
Caprimulgus europaeus	I	L	71	
Carduelis cannabina	G	S	17	
Carduelis carduelis	G	P	18	
Carduelis chloris	G	P	29	8.6
Carduelis spinus	G	I	13	0.3
Carpodacus erythrinus	G	L	23	–1.2
Certhia familiaris	I	P	9	2.2
Charadrius dubius	W (s)	L	40	
Chlidonias niger	W (w)	L	74	
Circus aeruginosus	C	L	615	
Coccothraustes coccothraustes	G	P	53	
Columba livia	O	N	360	
Columba oenas	G	S	275	–2.8
Columba palumbus	T	S	500	2
Corvus frugilegus	O	S	470	
Corvus monedula	O	P	225	6.1
Crex crex	I	L	150	
Dendrocopos leucotos	I	N	108	
Dendrocopos major	I	I	88	1.1
Dendrocopos minor	I	N	24	
Dryocopus martius	I	N	330	4
Emberiza citrinella	G	P	30	–0.6
Emberiza hortulana	G	L	24	–13.2
Erithacus rubecula	I	S	16	1.8
Falco subbuteo	C	L	220	
Falco tinnunculus	C	S	185	
Ficedula parva	I	L	10	
Fringilla coelebs	G	S	22	–0.3
Fulica atra	W (b)	S	520	
Gallinula chloropus	W (s)	S	275	
Garrulus glandarius	G	N	160	1.3

Glaucidium passerinum	C	N	61	
Hippolais icterina	I	L	14	–2.3
Hirundo rustica	I	L	19	–2.1
Jynx torquilla	I	L	37	–3.6
Lanius collurio	I	L	29	–0.5
Larus argentatus	O	S	1,050	
Larus canus	O	S	420	
Larus fuscus	W (f)	L	790	
Larus minutus	W (w)	S	129	
Larus ridibundus	O	S	270	
Locustella fluviatilis	I	L	20	
Locustella naevia	I	L	13	
Loxia curvirostra	G	I	41	–3.5
Lullula arborea	G	S	29	
Luscinia luscinia	I	L	27	1.4
Mergus merganser	W (f)	S	1,520	
Mergus serrator	W (f)	S	950	
Milvus migrans	W (f)	L	830	
Nucifraga caryocatactes	G	I	190	
Numenius arquata	W (s)	S	740	–0.4
Oriolus oriolus	I	L	76	–3.6
Pandion haliaetus	W (f)	L	1,500	
Parus ater	I	I	9	–0.2
Parus caeruleus	I	I	11	8.3
Parus cristatus	I	N	12	1.5
Parus major	I	N	19	2.1
Parus montanus	I	N	11	–1.1
Passer domesticus	G	N	32	–3.5
Passer montanus	G	N	23	
Perdix perdix	T	N	350	
Pernis apivorus	I	L	820	
Phasianus colchicus	T	N	1,130	2.1
Phylloscopus collybita	I	S	8	–3.2
Phylloscopus sibilatrix	I	L	10	–3.9
Phylloscopus trochiloides	I	L	7	5.3
Pica pica	O	N	235	0.4
Picus canus	I	N	127	
Podiceps auritus	W (b)	S	560	
Podiceps cristatus	W (f)	S	995	
Podiceps grisegena	W (f)	S	845	
Porzana porzana	W (s)	L	70	
Prunella modularis	I	S	19	0.2
Pyrrhula pyrrhula	G	P	29	3.5
Rallus aquaticus	W (s)	S	95	
Regulus regulus	I	P	6	–0.4
Saxicola rubetra	I	L	17	–2.3
Scolopax rusticola	I	S	300	1.7
Sterna hirundo	W (f)	L	120	
Streptopelia decaocto	G	N	190	
Streptopelia turtur	G	L	124	
Strix aluco	C	N	525	
Strix uralensis	C	N	795	
Sturnus vulgaris	I	S	77	–4.1
Sylvia atricapilla	I	S	20	–0.1
Sylvia borin	I	L	20	1.2
Sylvia communis	I	L	15	0.4
Sylvia curruca	I	L	12	1.5
Sylvia nisoria	I	L	30	
Tringa ochropus	W (s)	S	80	2.8
Troglodytes troglodytes	I	S	10	5.3
Turdus merula	I	S	101	4.1
Turdus viscivorus	I	S	115	5.7
Vanellus vanellus	W (s)	S	205	0.1