

## Long-term trends in bird communities in the northern Alps: consequences of changes in land use?

Frédéric Archaux<sup>1</sup> and Jacques Blondel<sup>2</sup>

Long-term changes of bird communities were investigated in areas with low-intensity forestry and farming practices in the French northern Alps (Giffre valley) by comparing two point count surveys carried out at the same spots in 1978/1980 and 2001/2002. Logistic regressions were applied to the 49 commonest woodland and farmland species controlling for habitat changes, variability in sampling conditions at the spot scale and year-to-year fluctuations in bird numbers. This analysis revealed that the proportion of declining species was not different between trans-Saharan and resident species, but seven migratory species only were considered in the analysis. The proportion of decreasing species was higher in farmland than woodland species. The overall abundance of woodland species was constant, probably because forest habitats changed little over this time period. Farmland specialist species decreased whereas generalist open species remained stable, with the exception of white wagtail *Motacilla alba*. These trends are probably a response to the intensification in farming practice following greater mechanisation. The proportion of decreasing species among farmland birds did not differ between the Giffre valley, France and Europe, showing that the situation of farmland birds is not safer in alpine habitats.

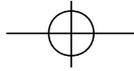
Keywords: long-term monitoring, alpine birds, point counts, climate warming, farming intensification.

<sup>1</sup>CEMAGREF Domaine des Barres, F-45290 Nogent-sur-Vernisson, France; <sup>2</sup>CNRS/CEFE 1919, route de Mende, F-34293 Montpellier Cedex 5, France; email: frederic.archaux@cemagref.fr

Long-term monitoring programmes have shown a general decline of European farmland bird populations over the last 10 to 30 years following agricultural intensification (Marchant et al. 1990, Krebs et al. 1999, Donald et al. 2001, Julliard 2001). Conflicting evidence about population trends of trans-Saharan migratory species reports either an overall decline (Berthold et al. 1986, Böhning-Gaese & Bauer 1996, Berthold et al. 1998) or overall stability (Marchant 1992, Julliard 2001, Dombrowski & Golawski 2002). Data on changes of bird communities over the last decades are unfortunately lacking in France since the national monitoring program STOC (French Common Breeding Bird Census) only began in 1989 (Julliard & Jiguet 2002). Causes of long-term trends of many species are not

fully understood, although it is often recognised that habitat transformation, such as urbanisation, wetland drainage or agricultural intensification, represents a major threat to bird populations (e.g. Tucker & Heath 1994, Pain & Pienkowski 1997). Few studies investigated long-term trends of bird communities in less extensively transformed areas over the last decades, where bird populations should be expected to have changed less dramatically.

Long-term changes in mountain bird communities were studied in the French northern Alps, by comparing two point count surveys carried out in 1978/80 and in 2001/02 at the same census spots. Our aim was to investigate trends in the changes of bird communities, considering potential habitat and climate changes. We



tested whether trans-Saharan migrants and farmland species declined over the study period more than resident species and woodland species.

## Material

### Study sites

The 25 km × 19 km study area (French Alps, 46° 5' N, 6° 44' E) was located in the upper Giffre valley, 20 km northwest of Mont-Blanc. The altitude ranged from 620 m to 3099 m a.s.l. Climate is seasonally fairly extreme with hot (16 °C in July), rainy summers (370 mm) and cold (−2.3 °C in January), snowy winters (c. 100 days a year with snow cover and 164 days with temperature below 0 °C). The area is one of the most rainy places in the French Alps throughout the year: mean yearly precipitation is 1330 mm at low elevations, reaching 3000 mm at 2500 m. Yearly mean temperature is c. 6.9 °C at 1040 m a.s.l. (French Meteorological Office data).

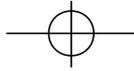
The regional economy is based on tourism, timber and cheese production. About half of the area is covered by forests at elevations ranging from the valley bottom to 1800–2000 m. Mixed stands of beech *Fagus sylvatica* and spruce *Picea abies* represent the main woodland type, with spruce becoming dominant with increasing humidity. A lowland mixed forest of spruce, European and speckled alders *Alnus glutinosa* and *A. incanata* and common oak *Quercus robur* grows along the Giffre stream. At higher elevations, hornbeam *Carpinus betulus* and a few stands of European larch *Larix decidua*, which are more or less mixed with spruce, and pure beech can be found in places depending on elevation, exposure, humidity and forestry practices. Agricultural areas are almost exclusively used as pastures for rearing dairy cattle. Vegetation cover above the tree line consists of patches of green alder *Alnus viridis*, moors and alpine pasture (see Desmet 1982 for a thorough description of habitats).

### Bird censuses

Large-scale bird censuses were carried out in the whole upper Giffre valley at two periods, in 1978/80 and 2001/02. Counts followed the EFP technique (Echantillonnage Fréquentiel Progressif; Blondel 1975, Blondel et al. 1981). The EFP technique is a 20-min point

count method of all birds heard or seen regardless of distance from the observer, estimating species richness regardless of their abundance. Census spots were randomly selected in representative habitat types in 1978/1980 and the same census points were used in 2001/2. Counts were carried out during the 4 hours following sunrise, under favourable weather conditions (i.e. no wind, no rain). Census spots were separated from each other by at least 150 m to avoid double counting of the same individuals. Censuses were evenly spread over the breeding season to give each species, either resident or migratory, the same probability of being detected. A total of 828 counts were carried out, 109 in 1978, 207 in 1980, 316 in 2001 and 196 in 2002: 120 census spots were sampled twice (once in 1978 or 1980 and once in 2001) and 196 census spots sampled three times (once in 1978 or 1980, once in 2001 and once in 2002). Three trained ornithologists were involved in the two series, one in 1978, 1980 and 2001 and two in 2002. Because between-observer variation may bias the results (Sauer et al. 1994, Kendall et al. 1996), we tested for possible observer effects by making simultaneous counts. All observers carried out 35 additional censuses in 2001 and 2002, independently recording birds at the same time and at the same spot. There was little and mainly random difference between observers allowing for the comparison of the 1978/80 and 2001/02 censuses. For instance, one pair of observers carried out 20 simultaneous 10-min counts, recording 57 species: a difference between observers in the number of occurrences greater than 2 was found for only 6 species (c. 10 % of species: cuckoo *Cuculus canorus*, willow tit *Parus montanus*, white wagtail *Motacilla alba*, wren *Troglodytes troglodytes*, song thrush *Turdus philomelos* and goldcrest *Regulus regulus*).

Species were classified according to their migratory status (trans-Saharan migrants or residents) and breeding habitat (farmland or woodland) following Cramp & Perrins (1985–1994). Mediterranean migrants (black-cap *Sylvia atricapilla*, chiffchaff *Phylloscopus collybita*, robin *Erithacus rubecula*) were included in the resident category because (1) there is no current evidence that those species are more adversely affected than resident species and (2) there is a continuum in migratory strategies between strictly Mediterranean migrants and strictly residents species in the valley (Desmet 1982). Farmland species included birds linked to pastures and meadows (farmland specialists, e.g. whinchat *Saxicola*



*rubetra* and yellowhammer *Emberiza citrinella*) and species linked to open habitats (farmland generalists, e.g. black redstart *Phoenicurus ochruros* and house sparrow *Passer domesticus*). Species related to alpine meadows such as wheatear *Oenanthe oenanthe* or alpine accentor *Prunella collaris* were recorded in few censuses because most census spots were located under the tree line, and accordingly were not considered in the analyses. Scrubland and woodland species were combined in the same category. Swift *Apus apus*, cuckoo, fieldfare *Turdus pilaris*, ring ouzel *Turdus torquatus* and citril finch *Serinus citrinella* could be assigned unambiguously neither to the farmland nor woodland categories. These species were therefore used to test whether long-distance migrants decreased more than resident species, but not to test whether farmland species decreased more than woodland species.

#### Climate and habitat changes

Daily weather data were collected from 1977 to 2002 by the French Meteorological Office at Chamonix about 20 km southeast of the study site. For each of the four seasons (March to May, June to August, September to November and December to February), mean temperature and total precipitation were calculated. We tested for long-term changes in these seasonal climatic variables by linear regressions and ANCOVA.

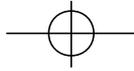
Habitat features (vegetation type, main height of vegetation and vegetation cover) were defined in a radius of 100–150 m around the census spots in 1978/80 and 2001/02. For both periods, all census spots were classified into seven vegetation types including alpine pastures and woodland habitats depending on dominant tree species (speckled alder, common oak, hornbeam, beech, spruce, mixed beech and spruce stands). For simplicity, only the dominant tree species was considered, except for the widespread case of mixed spruce and beech stands. The few mixed stands of spruce and European larch were included in spruce stands. Simultaneous estimations of main vegetation height carried out by different observers provided consistent results, ensuring that observer effects were small. Vegetation cover was quantified as the percentage cover of the woody strata above 4 m (classified as more or less than 25 % of the total area). Regional changes in habitats and in farming practice over the last 20 years are based on data of the French Forestry Inventory Office and of the

Agricultural Statistical Office from a slightly larger area than the study site.

#### Analyses of bird changes

Species-specific habitat models were constructed by logistic regressions for species occurring in at least 40 of the 828 counts, corresponding to at least c. 5 % of all censuses carried out both in 1978/80 and 2001/02. Forty-eight out of 97 species could not be included in the analyses because they were either too scarce (46 species) or linked to water habitats (grey wagtail *Motacilla cinerea* and dipper *Cinclus cinclus*, see final list of species in Table 2). As independent variables, we included census point, main vegetation type, main vegetation height, vegetation cover, date, time of the day and year. Census point and vegetation type were categorical variables with 316 and 7 character states respectively. Vegetation cover was defined as a two-level categorical variable (below or above 25 % vegetation cover). Date and time of day were included as quantitative variables in linear and quadratic forms to account for (1) varying species detectability with time of day and advancement in the breeding season (Ralph & Scott 1981, Boulinier et al. 1998) and (2) possible quadratic relationships between date or time of day and the probability of presence for any given species. Time of day was converted into time after sunrise. In order to separate year-to-year fluctuations in species occurrence from long-term changes, we defined contrasts for the year variable (having four states 1978, 1980, 2001, 2002). The first two contrasts were 1978 v. 1980 and 2001 v. 2002, expressing year-to-year fluctuations of bird numbers. A third contrast opposed the two periods 1978/80 versus 2001/02, expressing long-term changes in bird populations (actually the long-term change in the logit of the species' probability of occurrence).

In order to minimise the problem of multiple testing when considering assemblages of species, we used the Akaike's information criterion AIC for model selection because this procedure does not rely on statistical tests of null hypotheses (Anderson et al. 2000). We followed a step-by-step backward selection of the explanatory variables. The variables census spot and year were always kept in the models and the AIC value was calculated at each step. The model giving the lowest AIC value at the end of the selection procedure was used to measure the long-term change for each of the 49 species



studied. The regression coefficient corresponding to the third contrast of the year variable (1978/80 v. 2001/02) measured the species-specific long-term change in frequency of occurrence, controlling for sampling conditions (date, time of day), habitat changes and yearly fluctuations of bird populations. A species was considered as (1) declining when the regression coefficient was significantly negative, (2) increasing when it was significantly positive or (3) stable otherwise.

## Results

### Climatic changes

Yearly ambient temperatures increased significantly by 1.3 °C between 1977 and 2001 ( $R^2 = 0.37$ ,  $n = 23$ ,  $P < 0.01$ ). There was a near-significant difference in climate change between seasons (ANCOVA,  $F_{3,92} = 2.53$ ,  $p = 0.06$ ): warming was stronger in spring (+ 2.5 °C) than in summer (+ 1.2 °C, see Fig. 1), autumn (+ 0.1 °C) or winter (+ 1.8 °C). The number of days below 0 °C per year decreased significantly from c. 180 in the late 1970s to 140 in the late 1990s ( $R^2 = 0.64$ ,  $F_{1,22} = 38.8$ ,  $P < 0.001$ ). Precipitation varied considerably over the period depending on season and year, but there was no significant long-term trend between 1977 and 2002 in any season ( $n = 23$ ,  $R^2 < 0.07$ ,  $P > 0.23$ ). Weather conditions were not unusually bad during the 1978/80 and 2001/02 breeding seasons, nor during the preceding

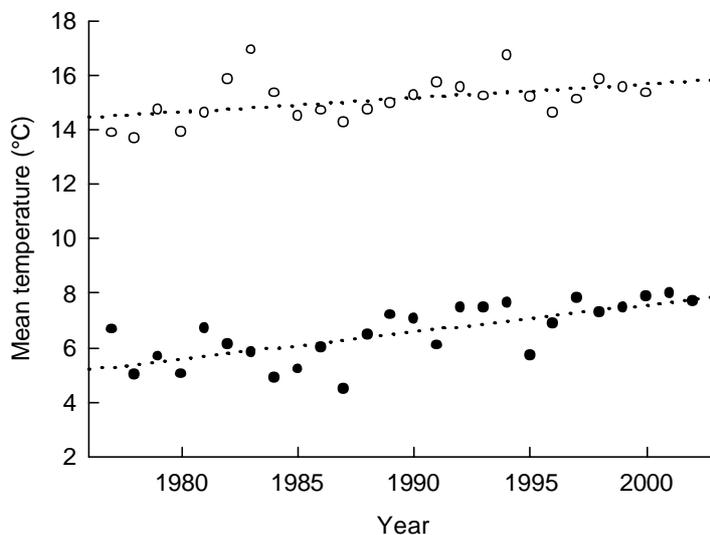
**Table 1.** Change in key indices of agriculture between 1988 and 2000 on the study area (French Agricultural Office data). When considered together, these give a measure of agricultural intensity.

Agricultural index	Number 1988	Number 2000
Farms	312	170
Cattle	3135	3068
Goats	388	329
Sheep	2446	1175
Tractors over 55 hp	77	139
Hay balers and presses	14	43

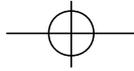
winters, when considering both temperature and precipitation.

### Habitat changes

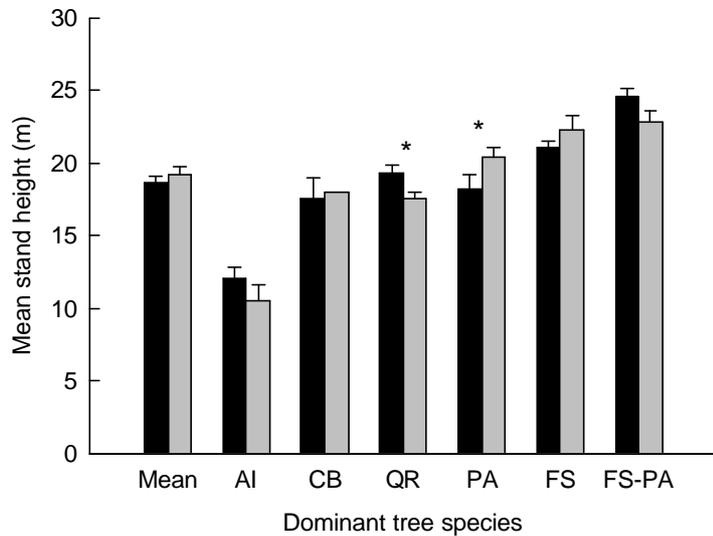
The number of farms almost halved between 1988 and 2000 (Table 1) and the average farm size increased accordingly from 22 ha to 35 ha. There is no information about changes in area of alpine meadows between 1980 and 2002 but other farmed areas decreased from 6800 ha in 1988 to 5850 ha in 2000 (-14 %) in the study area. Numbers of cows decreased by only 2.1 % between 1988 and 2000, but the numbers of sheep and goats almost halved. No data on changes in forest area are available at the scale of the valley but forest area increased at the regional scale by 3 % from 45 600 ha to 47 600 ha between 1984 and 1995. Since 1984, spruce



**Figure 1.** Long-term trends in spring and summer mean temperature in the French northern Alps (French Meteorological Office data). Open circles: summer (regression,  $n = 24$ ,  $R^2 = 0.20$ ,  $p = 0.03$ ), filled circles: spring (regression line,  $n = 26$ ,  $R^2 = 0.51$ ,  $P < 0.001$ ).



**Figure 2.** Change in mean stand height ( $\pm$  s.e.) in the Giffre valley between 1978 and 2001 for all stands (Mean) and for each dominant tree species (AI *Alnus incanata*, CB *Carpinus betulus*, QR *Quercus robur*, PA *Picea abies*, FS *Fagus sylvatica*, FS-PA *F. sylvatica* and *Picea abies*; \*  $P < 0.05$ ).



has been slowly replacing beech in mixed stands, leading to more or less pure spruce stands: areas dominated by spruce increased from 60 % of all woodlands in 1984 to 66 % in 1995, whereas areas covered with mixed beech-spruce decreased from 34 % in 1984 to 26.5 % in 1995. As a result of land abandonment, areas covered by early-successional trees such as *Alnus* or *Fraxinus* species increased from 6 % in 1984 to 7.5 % in 1995. Overall mean tree height estimated in the census spots did not significantly differ between the two periods, averaging  $18.3 \pm 6.7$  m ( $\pm$  s.d.) in 1980 and  $18.9 \pm 7.0$  m in 2001 (Fig. 2,  $t_{427} = -0.95$ ,  $p = 0.34$ ). Mean stand height slightly decreased for common oak and slightly increased for spruce but it did not significantly change for all other tree species (Fig. 2).

### Bird changes

A detailed list of the effects of the explanatory variables included in the final logistic models for each species is available on request. Here, we focus on the long-term trends. Species that remained stable, increased significantly or declined significantly are given in Table 2. Of 49 species in the analysis, 13 increased and 17 decreased significantly over the observation period.

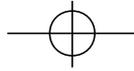
The proportion of decreasing species did not differ significantly between migratory and resident birds (4/7 v. 13/42, Fisher's Exact Test,  $p = 0.21$ ). However, a significantly higher proportion of decreasing species was observed among farmland birds than woodland species (9/13 v. 7/31, Fisher's Exact Test,  $P < 0.01$ ). The pro-

portion of declining and increasing farmland species was only marginally different (2 v. 9 out of 13, binomial test,  $p = 0.07$ ). However, all farmland species that did not decrease were generalist species, i.e., not breeding exclusively in farmland, whereas decreasing species were farmland specialists, apart from the white wagtail (Table 2). The proportion of declining and increasing woodland species was similar (9 v. 7 out of 29, binomial test,  $p = 0.80$ ).

### Discussion

In contrast to evidence suggesting that trans-Saharan migrants declined more than resident species over the last decades (Böhning-Gaese & Bauer 1996, Berthold et al. 1998), we found that trans-Saharan species were not more adversely affected than resident species in the Giffre valley between 1980 and 2002. Three trans-Saharan migrants, swift, redstart *Phoenicurus phoenicurus* and garden warbler *Sylvia borin*, showed stable populations between 1978 and 2002. However, this result has to be carefully interpreted since only seven migratory species were included in the analysis.

We observed (1) a higher proportion of decreasing species among farmland birds than among woodland species and (2) a general decline among eight farmland species that breed primarily in farmland (farmland specialist species), whereas only one of five generalist species of open habitats decreased (Table 2). Most studies dealing with long-term trends of farmland species in



**Table 2.** Summary of long-term trends (LTT) between 1978 and 2002 for 49 study bird species in relation to migratory status (MS: R resident, M trans-Saharan migrant) and breeding habitat (BH: W woodland, Fs farmland specialist, Fg farmland generalist). See text for details on the calculation of the LTT. \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

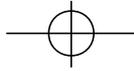
Species	MS	BH	LTT (s.e.)	Species	MS	BH	LTT (s.e.)
Woodpigeon	R	W	1.89 (0.42)***	Long-tailed tit	R	W	0.73 (0.41)
Cuckoo	M		-2.02 (0.49)***	Marsh tit	R	W	-0.06 (0.20)
Swift	M		0.04 (0.27)	Willow tit	R	W	-0.76 (0.34)*
Black woodpecker	R	W	1.27 (0.59)*	Great tit	R	W	-0.21 (0.26)
Green woodpecker	R	W	0.04 (0.24)	Blue tit	R	W	0.67 (0.20)***
Great spotted woodpecker	R	W	-0.17 (0.23)	Coal tit	R	W	1.98 (0.24)***
Barn swallow	M	Fs	-0.76 (0.34)*	Crested tit	R	W	0.76 (0.26)**
Tree pipit	M	Fs	-4.81 (0.72)***	Nuthatch	R	W	0.33 (0.27)
White wagtail	R	Fg	-1.12 (0.31)***	Short-toed treecreeper	R	W	0.03 (0.65)
Wren	R	W	-2.57 (0.34)***	Common treecreeper	R	W	-0.31 (0.36)
Dunnock	R	W	-2.50 (0.39)***	Jay	R	W	0.46 (0.16)**
Robin	R	W	0.35 (0.20)	Nutcracker	R	W	-0.44 (0.23)
Redstart	M	W	7.21 (8.90)	Carrion crow	R	Fg	0.50 (0.22)*
Black redstart	R	Fg	0.91 (0.35)*	Starling	R	Fs	-2.02 (0.58)***
Whinchat	M	Fs	-1.99 (0.63)**	House sparrow	R	Fg	-0.60 (0.77)
Fieldfare	R		-0.27 (0.63)	Chaffinch	R	W	10.90 (21.28)
Song thrush	R	W	0.94 (0.21)***	Goldfinch	R	Fs	-1.28 (0.26)***
Mistle thrush	R	W	0.38 (0.20)	Greenfinch	R	Fg	0.54 (0.68)
Blackbird	R	W	0.46 (0.14)***	Linnet	R	Fs	-2.16 (0.61)***
Ring ouzel	R		1.76 (0.62)**	Serin	R	Fs	-0.96 (0.28)***
Garden warbler	M	W	-0.26 (0.29)	Citril finch	R		12.69 (4.27)**
Blackcap	R	W	1.44 (0.32)***	Bullfinch	R	W	-0.95 (0.23)***
Chiffchaff	R	W	-1.64 (0.31)***	Common crossbill	R	W	0.46 (0.46)
Goldcrest	R	W	-0.79 (0.29)**	Yellowhammer	R	Fs	-11.30 (4.01)***
Firecrest	R	W	-0.84 (0.16)***				

Europe have reported strong declines (e.g. Donald et al. 2001). Alpine habitats are often thought to represent the last strongholds for endangered farmland species due to low-intensity farming practices (Schifferli 2000). However, when comparing the same set of 13 farmland species with previous studies, the proportion of decreasing species is not smaller in the Giffre valley (9/13, this study) than either at the national (9/13 in France; Jiguet 2002) or European scales (7/13 in Europe; Heath et al. 2000). For instance, goldfinch *Carduelis carduelis* remained stable at the French scale and tree pipit *Anthus trivialis*, white wagtail and serin *Serinus serinus* remained stable or even increased in Europe but all decreased in the Giffre valley.

The general decline of farmland species has been linked to the intensification of agricultural practices in Europe (Donald et al. 2001). Several causes have been proposed to explain their decline (reviewed in Schifferli 2000) but the most relevant is probably the reduction in

food supply (Benton et al. 2002) that affects annual breeding success (Wilson et al. 1997, Brickle et al. 2000) and survival rate (Peach et al. 1999). Changes in farming practices in the Giffre valley over the last 20 years are also a likely cause of the decline of farmland species, following rural depopulation, mechanisation and increase in farm size (Table 1). Land abandonment favours scrubland and woodland birds, at the expense of species of open habitats. On the other hand, farming probably became more intensive in the areas still farmed, so that farmland species may be affected by both phenomena. However, woodland areas increased only by c. 3 % over the time period and there is no evidence that scrubland birds increased (e.g. wren, dunnock *Prunella modularis* and chiffchaff decreased), so that intensification might be the more likely cause to the decline of farmland species.

The 31 woodland species showed relative stability as a whole compared to farmland birds, probably because



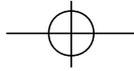
forest areas and mean height of trees did not change significantly over the period. Nonetheless, nine species increased (29 %) and seven decreased (23 %). There is no clear ecological link within and between decreasing and increasing species, suggesting that different birds were affected by different causes. Declines of wren, dun-nock, chiffchaff and bullfinch *Pyrrhula pyrrhula* might be explained by a decrease in forest undergrowth, although precise data on changes in undergrowth are lacking. On the other hand, coal tits *Parus ater* and crested tits *P. cristatus* may have taken advantage of the spatial extension of spruce stands. Large-scale phenomena such as continent-wide habitat transformations or climate warming may also be involved in population trends of many species. The increase of many woodland species, such as woodpigeon *Columba palumbus*, black woodpecker *Dryocopus martius*, song thrush, blackbird *Turdus merula*, blackcap and blue tit *Parus caeruleus* is also found at the national (Yeatman-Berthelot & Jarry 1994, Julliard & Jiguet 2002) and/or European scales (Heath et al. 2000). Furthermore, related species such as thrushes, corvids, tits, treecreepers and gold- and firecrests *Regulus ignicapillus*, often showed the same long-term trend in the valley. Mean annual temperatures increased by 1.3 °C and yearly number of days below 0 °C decreased by c. 40 days between 1977 and 2001. Climate is known to affect bird demography (Møller 1989, Baillie & Peach 1992, Sæther et al. 2000; Thompson & Grosbois 2002), but evidence for a regulating role of climate change on bird numbers remains unclear (Archaux 2003).

Changes in agricultural practice are expected to continue as a result of rural depopulation and mechanisation. Climate warming is predicted to continue in the future (IPCC 2001), calling into question the persistence in the valley of several bird species over next decades. New farming practices in mountain areas should be rapidly encouraged, if we do not want some currently threatened farmland specialist species to become extinct in alpine valleys before long.

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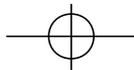
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## Large-scale networks in bird research in Europe: pitfalls and prospects

Franz Bairlein

Large-scale coordinated projects enable much more detailed insights into the pattern and processes of bird life than single-site studies can achieve. However, the success of such networks relies on the adoption of standardised common methods and protocols as well as on training and calibration to secure comparable measurements. This paper describes several of already existing large-scale networks in the study of birds in Europe, devoting particular attention to the recent migration network supported by the European Science Foundation. Owing to the presence of many skilled volunteers, there is an enormous potential for a number of large-scale networks in Europe.

Key words: Migration, populations, conservation, standardization.

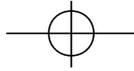
Institute of Avian Research 'Vogelwarte Helgoland', An der Vogelwarte 21, D-26386 Wilhelmshaven, Germany; e-mail: franz.bairlein@ifv.terramare.de

Birds are highly mobile and widely distributed organisms. Consequently, patterns and processes of distribution, abundance, population dynamics, demography and migration must be considered not only by single site-specific approaches but should also be investigated at a large-scale. In the past, a number of projects have aimed at a large-scale continent-wide coverage, making use of the many volunteers available and interested in contributing to science.

In 1934, the first Europe-wide census of white storks *Ciconia ciconia* was organised (Schüz 1936), and these international white stork censuses continue today (Schulz 1999). During these censuses not only are the number of breeding pairs counted, but data on fecundity are also collected. These data, though not gathered in a central data bank, provide an excellent source for large-scale comparisons (e.g. Bairlein 1991, Schulz 1999). Gathering information on the Europe-wide distributions of birds was the main purpose of several other large-scale collaborative projects, of which the following are examples. In 1963, the International Waterfowl and Wetlands Research Bureau (now Wetlands International) started to coordinate the many national waterbird counts at an international level, and these are now conducted all over the world (Rose & Scott 1994,

Scott & Rose 1996, Mooij 1999, Delany et al. 1999). The European Bird Census Council extended the coverage of species, but concentrated on the breeding birds. 'The EBCC Atlas of European Breeding Birds' (Hagemeijer & Blair 1997) is an outstanding example showing the value of such large-scale initiatives. Another European-wide compilation of data emphasised not only the conservation status of birds in Europe, but considerable variation in population changes across Europe (Tucker & Heath 1994). In order to understand the causes and consequences of population changes, however, future work also requires a more extensive approach including demographic parameters. For example, the project 'Monitoring of Raptors and Owls in Europe' (Stubbe et al. 1996, Mammen & Stubbe 1999) combines breeding bird surveys with measures of productivity.

Probably the most long-term and most elaborated large-scale approach to studying the biology of wild birds is carried out in the study of bird migration. Thus, I use this example in more detail to emphasise the need and great value of large-scale networks. This does not mean that I ignore the other initiatives, nor does the focus on Europe disregard similar large-scale projects that are carried out in northern America (e.g. Tautin



& Metras 1998, Sauer & Link 1999, DeSante et al. 2001).

### The case of bird migration studies

Migratory birds use a wide geographical range, moving twice a year between breeding and wintering grounds that may be very far apart (Alerstam 1990, Berthold 2001). Thus, the patterns and processes of migration must be viewed and analysed on a large scale. Most of the studies conducted, however, were and still are single site approaches. Many of these studies provide excellent insights into site-specific details of migratory passage and performance. However, they all investigate their own sub-set of species using that area, and use their own procedures and routines in trapping and taking bird measurements, thus making comparisons across a wider geographical scale difficult. Large-scale approaches are still rare, although understanding of natural patterns needs a broader view of spatial and temporal scale (Simons et al. 2000). This is required particularly in the light of the recent theoretical frameworks concerning optimality principles in bird migration (Alerstam & Lindström 1990, Alerstam & Hedenström 1998). Implicit in current theories of migration strategies are two distinct sources of variation encountered by migrants. This is the trade-off between locally experienced performance at a site and the expected performance at future sites (Weber 1999, Weber et al. 1999). Thus, understanding the migration strategy of a species requires data over a wide geographical range in order to learn more about variation between sites and to take global variation into account. Sophisticated networks of study sites can achieve this task. Large-scale coordinated networks can be used (1) to identify migration routes, (2) to evaluate passage, timing and speed of migration, and (3) to evaluate the fuelling strategies of migrating birds. A few examples may illustrate that potential.

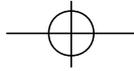
### Large-scale migration approaches

The first ever large-scale network to study bird migration was initiated by the introduction of bird ringing (Bairlein 2001). Already some 30 years after bird ringing was introduced as a tool to study bird movement, Schüz & Weigold (1931) published the first 'Atlas of Bird Migration' compiling more than 6800 recoveries

of some 230 species, and evaluating major flyways across Europe and into Africa. Since then the major migration routes of many bird species have been identified (e.g. Zink 1973–1985, Zink & Bairlein 1995, Fransson & Pettersson 2001, Wernham et al. 2002). However, comparatively little has been explored in greater detail. There is still much room for more detailed and sophisticated analyses to evaluate the spatial and temporal course of migration routes at a higher resolution, and giving special emphasis to population specific migration routes and the differential migration of age groups and sexes (Imboden 1974, Fliege 1984, Bairlein 2001). Notably in Europe, ringing schemes hold hundreds of thousands of recoveries that would repay comparative analysis. For instance, in contrast to previous ideas that migrants move on rather broad fronts, different populations may show more or less parallel migration routes where adjacent populations follow almost the same principal direction but do not merge, as it is exemplified in the chaffinch *Fringilla coelebs* (Bairlein 2001). This has considerable consequences for understanding migration strategies (Alerstam 2001), migratory connectivity (Webster et al. 2002), and conservation (Have 1991, Salathé 1991).

With respect to the identification of migratory routes, there is another even less-explored potential tool, which is the large-scale use of coordinated colour banding. By using marks that can be read at a distance, the number of 'recoveries' can be much increased simply by stimulating the many bird observers to re-sight marked birds and report to a centralised database. There are already several colour banding schemes established (Flamant 1994, Clark 1996, Marchant 1996), but there is still an unused potential. However, all these analyses are constrained by spatial and temporal variation in recovery and re-sighting probabilities, for example owing to human population density, or hunting regulations (e.g. Tucker et al. 1990).

In contrast to the many single-site studies to evaluate passage, stopover behaviour and fuelling for migration, only a few larger-scale and coordinated projects have been organised using a trapping and ringing approach and adopting standardised protocols. In 1961, Operation Baltic began organising regular annual ringing camps along the Polish Baltic Sea coast (Busse & Kania 1970). A similar large-scale ringing campaign was established by Vogelwarte Radolfzell in 1972, named the 'Mettnau-Reit-Ilmlitz-Program' because it included in



its initial phase three study sites covering central Europe: the Mettnau peninsula at Lake Constance, south-west Germany, Reit near Hamburg in northern Germany, and Illmitz at Lake Neusiedl, eastern Austria (Berthold & Schlenker 1975, Berthold et al. 1991). Later, the Illmitz site was closed and instead a site in north-eastern Germany was included (Vogelwarte Radolfzell, pers. comm.). Elsewhere, between 1982 and 1993, the ASIA programme included more than 20 ringing sites in western Central Asia (Dolnik 1985, 1990). The first Europe-wide initiative was launched in 1984 by EURING, the European Union for Bird Ringing, which focused on *Acrocephalus* warblers (Jenni et al. 1994). Between 1988 and 1990, the willow warbler *Phylloscopus trochilus* was the target for a country-wide project in Sweden, including 18 different sites (Lindström et al. 1996). The 'Small Island Project' including 39 different sites in the central and western Mediterranean Sea was launched in 1988 (Spina et al. 1993, Spina & Pilastro 1998). Very recently, the SE European Migration Network covering the eastern flyway across eastern Europe was initiated by Busse (2000). Finally, the new EURING Swallow Project, targeting mainly barn swallow *Hirundo rustica*, covers most countries of Europe and extends even into Asia, southern Africa and North America (Noordwijk & Oatley 1998, Spina 1998). The most widespread and most comprehensive joint project was carried out across Europe and western Africa between 1994 and 1996, supported by the European Science Foundation (Bairlein 1993).

#### The European Science Foundation Western Palaeartic-African Songbird Migration Network – a case study

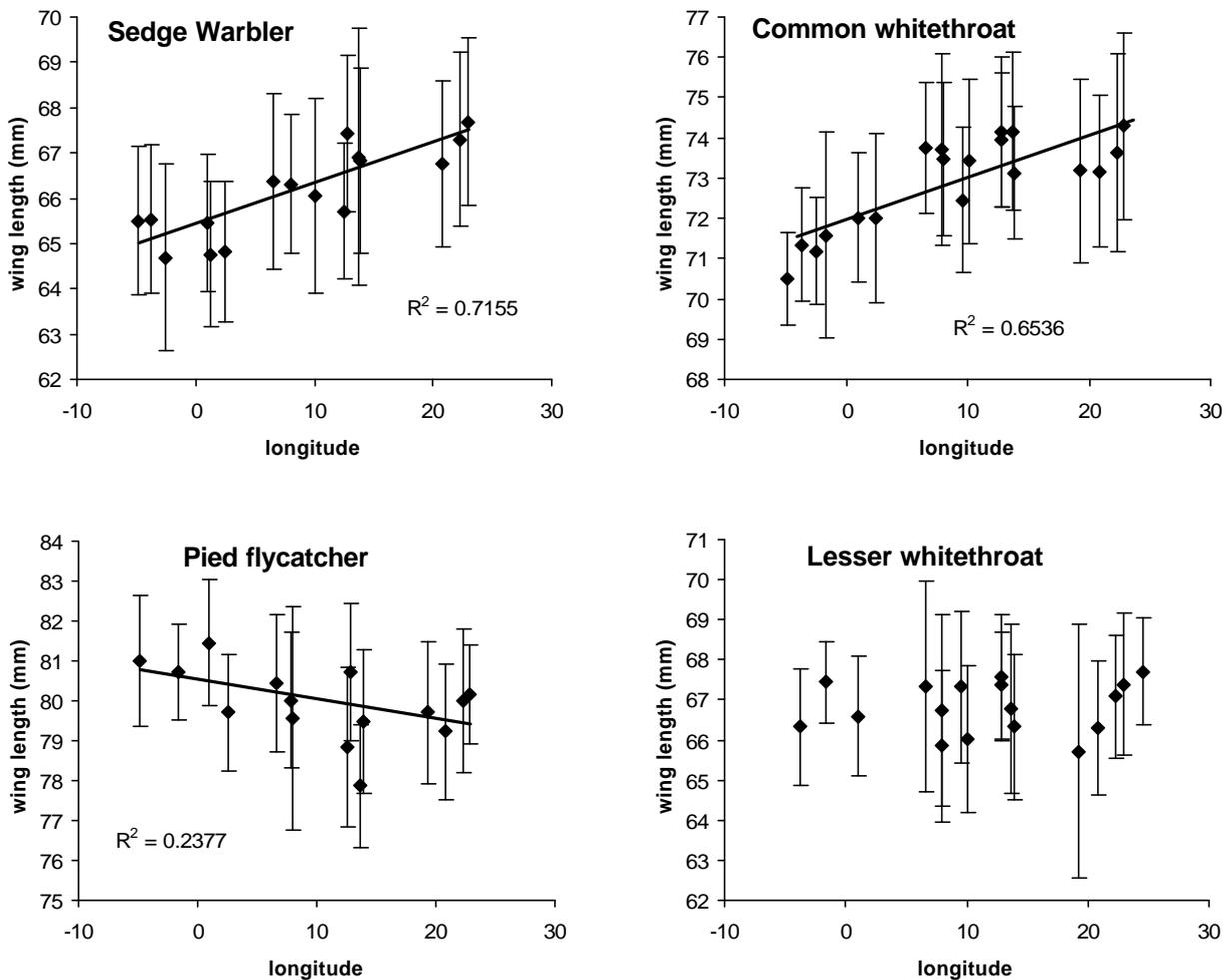
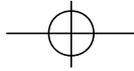
The European Science Foundation Scientific Network on European-African Songbird Migration was launched to create a coherent European project to study the different strategies of migratory songbirds by an integrated collaborative approach (Bairlein 1993, 1994, 1997, 1998). This includes existing national or regional studies and complementary activities within a framework of highly standardised supra-national collaborative work. It aimed to achieve its goals by the comparative analysis of the seasonal and diurnal patterns of occurrence of migrants at the various study sites along the western migration route and on the West African wintering grounds, a comparative analysis of biometric

measurements that are likely to reflect population-specific differences in body features, and the comparative analysis of body mass and fat reserves at the various study sites to learn more about the spatial and temporal patterns of migratory fuelling. The Network achieved its goals by (1) the collaboration and integration of more than 30 research groups from 18 different countries operating more than 50 sites from northern Finland and Sweden across central and western Europe to western Africa; (2) the development and use of a Field Manual of common guidelines, (3) recurrent training and calibration courses to secure standardised measurements; (4) the circulation of Network Newsletters; (5) a centralised database; and (6) several workshops. The amount of data gathered is unique. Between autumn 1994 and autumn 1996 some 400,000 birds of the 34 target species were recorded (Bairlein 1997). Key questions addressed were: (1) What are the routes, timing, and stopover sites used by Palaeartic songbird migrants? (2) Where do they originate? (3) Where do Palaeartic migrants carry out fuelling? (4) What are the ecological requirements at stopover areas? (5) Where do Palaeartic songbirds winter in West Africa?

A few examples of analyses of ESF Network data are described below to illustrate the use of large-scale networks to evaluate patterns and processes of bird migration. In all these analyses, only birds caught once as non-moulting first year birds during autumn migration between early August (standardised annual 5-day-period # 43; see Berthold 1973) and mid November (annual pentade # 64) are considered. Other analyses using ESF Network data have been carried out by Schaub & Jenni (2000a,b, 2001a,b).

#### Identifying migration routes

Migratory routes can be directly identified by analysing recoveries and resightings of marked birds. They can also be identified by the use of satellite transmitters capable of being carried by birds. The use of satellite transmitters is still limited by their size and mass but recent developments in their miniaturisation give rise to the hope that even quite small migratory birds such as waders may be equipped with satellite transmitters in the near future (Fuller et al. 1998, Gauthier-Clerc & Le Maho 2001). Besides such direct methods, indirect ones may be used to identify migration routes. These are molecular approaches, the use of stable isotopes and trace



**Figure 1.** Longitudinal variation in wing length (mean  $\pm$  s.d.) in several long-distance migratory songbirds during autumn migration: sedge warbler *Acrocephalus schoenobaenus*; pied flycatcher *Ficedula hypoleuca*; whitethroat *Sylvia communis*; lesser whitethroat *Sylvia curruca*. Only sites with at least 20 birds caught are considered.

elements as biogeochemical signatures (Hobson 1999, Webster et al. 2002), and morphological characteristics. These techniques are particularly helpful in species with low probabilities of recovery, re-sighting or recapture.

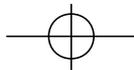
Morphological characters often follow a geographical gradient (Fig. 1) which can be used to track birds of different breeding origin along their migration. As shown in Figure 2, western European garden warblers *Sylvia borin* are shorter winged than birds trapped during autumn passage at more easterly sites and in particular in the eastern central Mediterranean. A similar longitudinal pattern was found in garden warblers in the Mediterranean during spring passage (Grattarola et al.

1999). This gives strong evidence for parallel migration of birds of different origin.

Another attempt to identify migration routes from large-scale network data was made by Pilastro et al. (1998). Using the relative capture frequency of species at different study sites across the western and central Mediterranean, they found significant differences between species which they interpreted as evidence for different migration routes.

#### Timing and speed of migration

Knowledge of timing and the overall speed of migration, including flights and stopovers, is of crucial im-

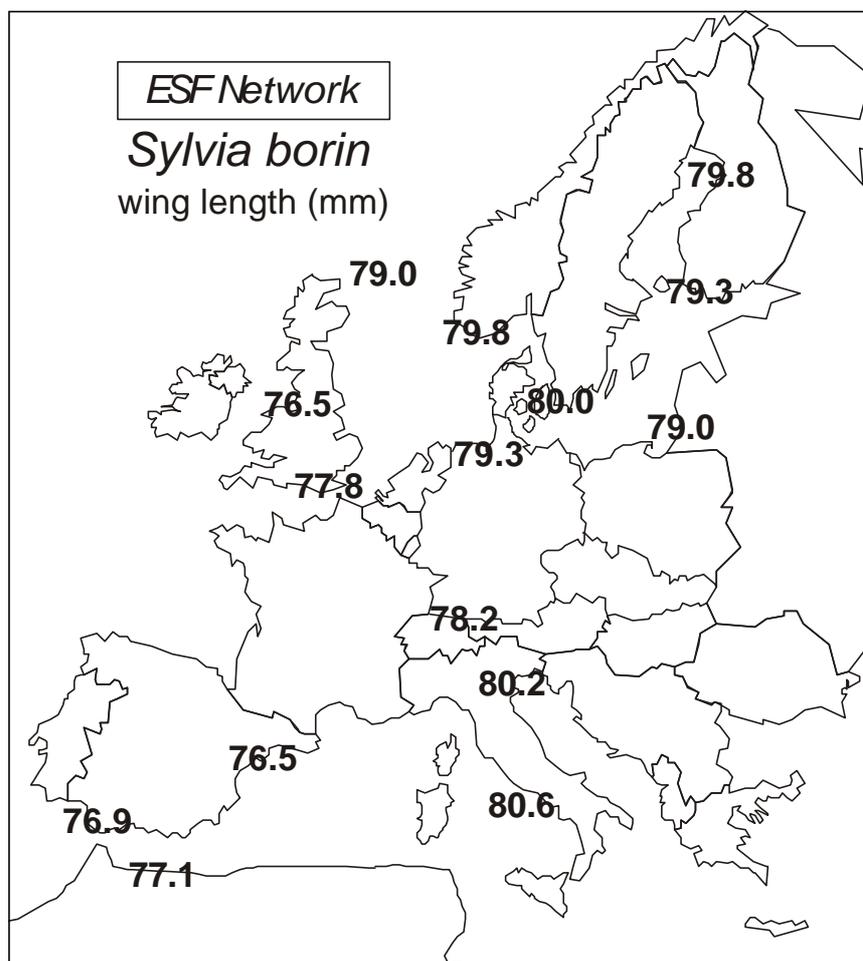


portance for understanding migration strategies. Based on standardised trapping protocols, seasonal patterns of passage at different sites (Fig. 3) can be used to evaluate the timing and temporal patterns of migration across a wide geographical scale. Most of the species targeted by the ESF Network depart from northern and central Europe at quite similar times (Fig. 4). This may indicate that these species rely largely on endogenous timing mechanisms (Berthold 1996). Further to the south, there is a progressively later average passage. Although these patterns need a more thorough analysis, they indicate speed of migration. For example, south of 50° N, the average time lapse at consecutive stopover sites is 21 days per 10 degrees latitude in reed warblers *Acrocephalus scirpaceus* and 31 days/10° in pied flycatchers *Ficedula hypoleuca*. These figures are rather similar to the ones reported by Schaub & Jenni (2001b) calculated on the basis of stopover duration, and to overall migra-

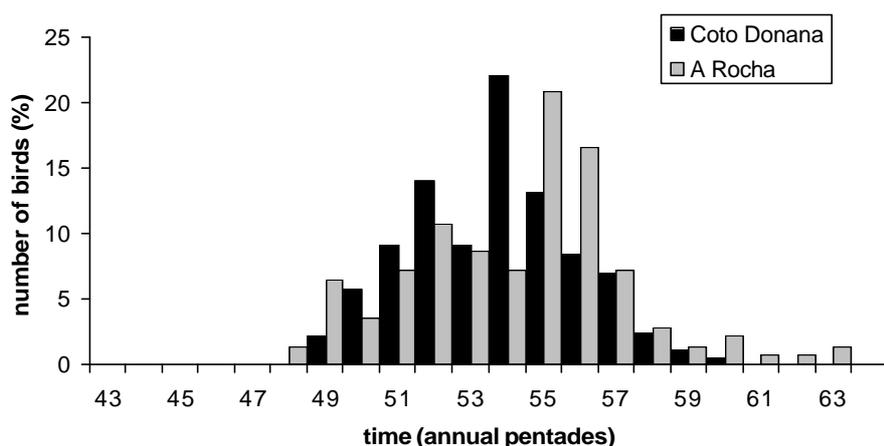
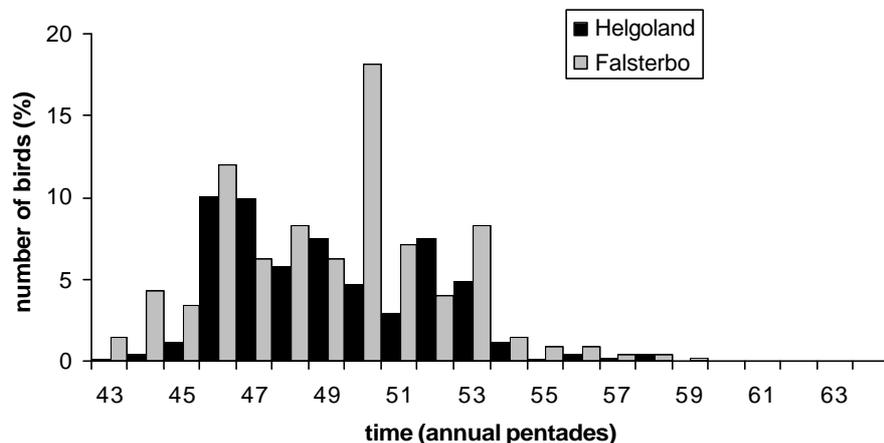
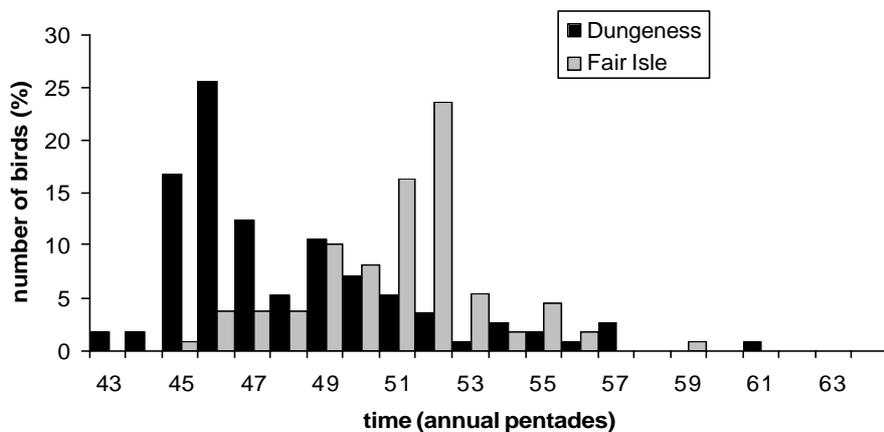
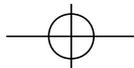
tion speeds derived from the analyses of recoveries of birds ringed in Northern Europe (Hildén & Saurola 1982, Ellegren 1993, Fransson 1995, Bensch & Nielsen 1999). Besides latitudinal variation, there is also some pronounced species-specific longitudinal variation in timing of migration (Fig. 5). North of 50° N, eastern garden warblers and eastern willow warblers start autumn migration later than birds on the British Isles, while the opposite is shown by blackcaps *Sylvia atricapilla*. No significant variation is observed in reed warblers.

#### Identifying migration performance

Most emphasis in recent research on bird migration is given to the analysis of fuelling strategies, as the success of migration is determined by fuel deposition in particular (e.g., Alerstam & Lindström 1990, Bairlein



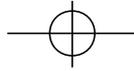
**Figure 2.** Geographical variation in wing length in garden warblers (for clarity, only the mean values are shown).



**Figure 3.** Autumn passage of garden warblers at selected sites along the western European flyway. x-axis: standardised annual 5-day periods; 43 = 30 July–3 August (cf. Bertold 1973). Fair Isle, UK: N = 110; Dungeness, UK: N = 113; Helgoland, Germany: N = 913; Falsterbo, Sweden: N = 467; Coto de Doñana, Spain: N = 1870; A Rocha, Portugal: N = 139.

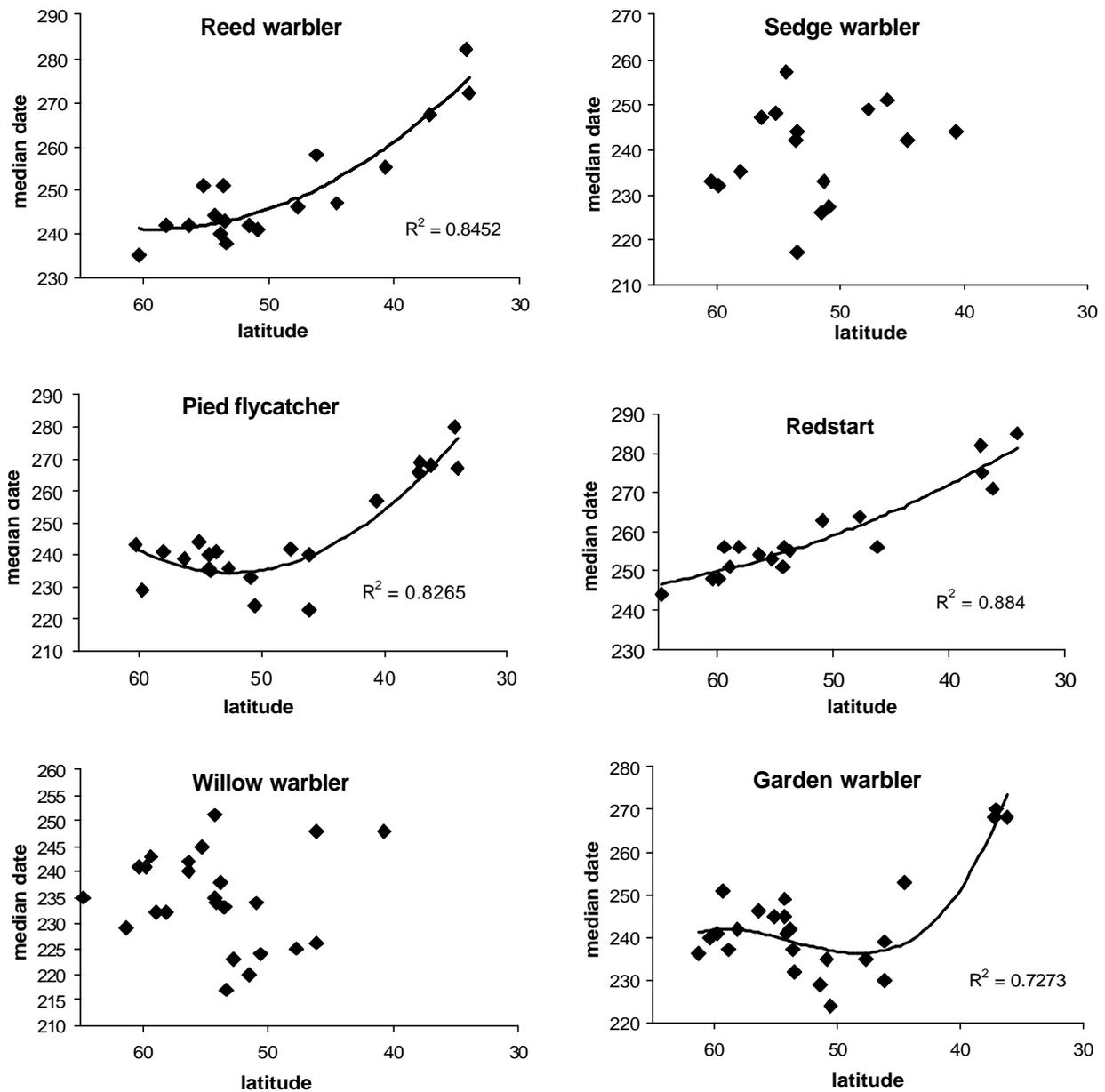
1991, Alerstam & Hedenström 1998, Grattarola et al. 1999, Weber 1999, Weber et al. 1999, Alerstam 2001, Lindström & Lind 2001). As already evaluated by

Schaub & Jenni (2000a,b, 2001a,b) using some data of the ESF Network, large-scale standardised networks of trapping sites enable comparative analyses to be carried

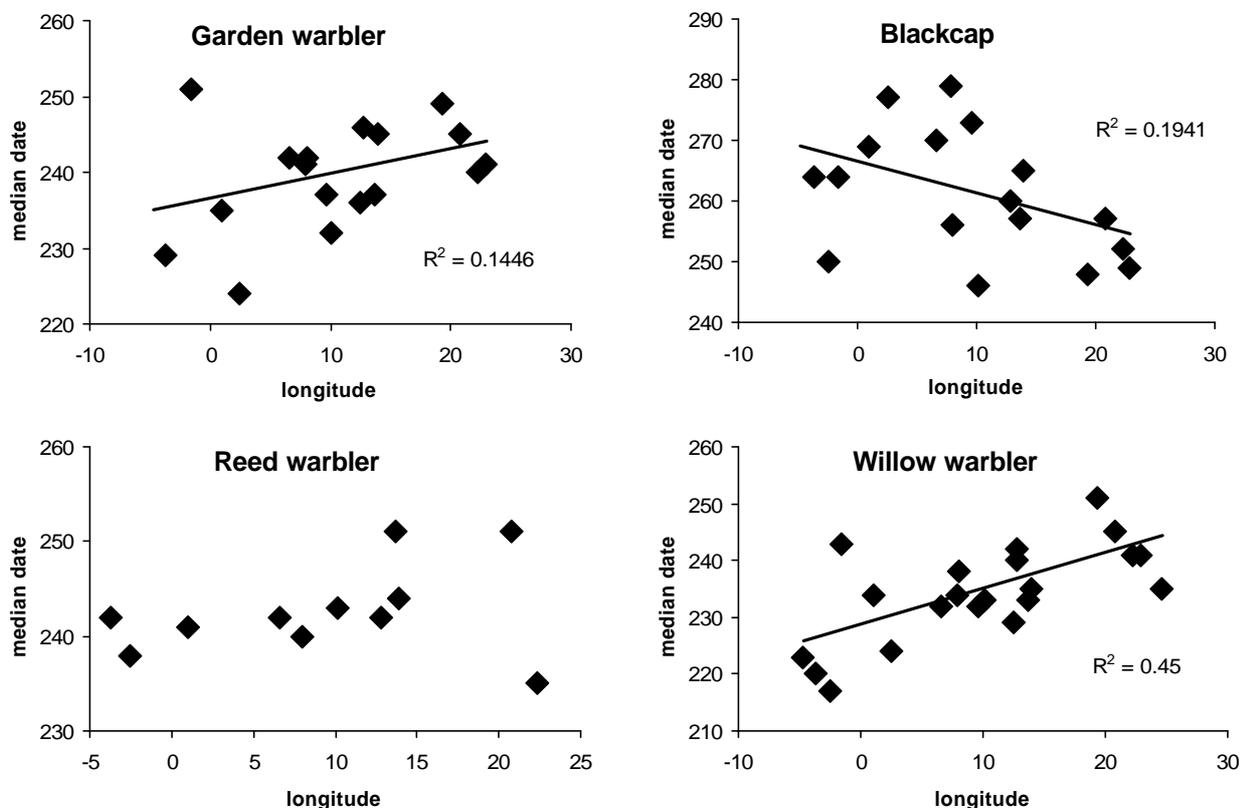
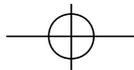


out over a broad geographical scale and on different species. Average body mass and fat score, for example, provide an initial understanding the spatial and temporal pattern of fuelling during migration. In many of the trans-Saharan migrants targeted by the ESF Network, average site-specific body mass during autumn migra-

tion progressively increases across Europe towards the south (Fig. 6), while the opposite trend is observed in species that winter north of Sahara, such as blackcap and chiffchaff *Phylloscopus collybita*. However, these increases are comparatively small, and they would not permit very long flights. Thus, these species do not



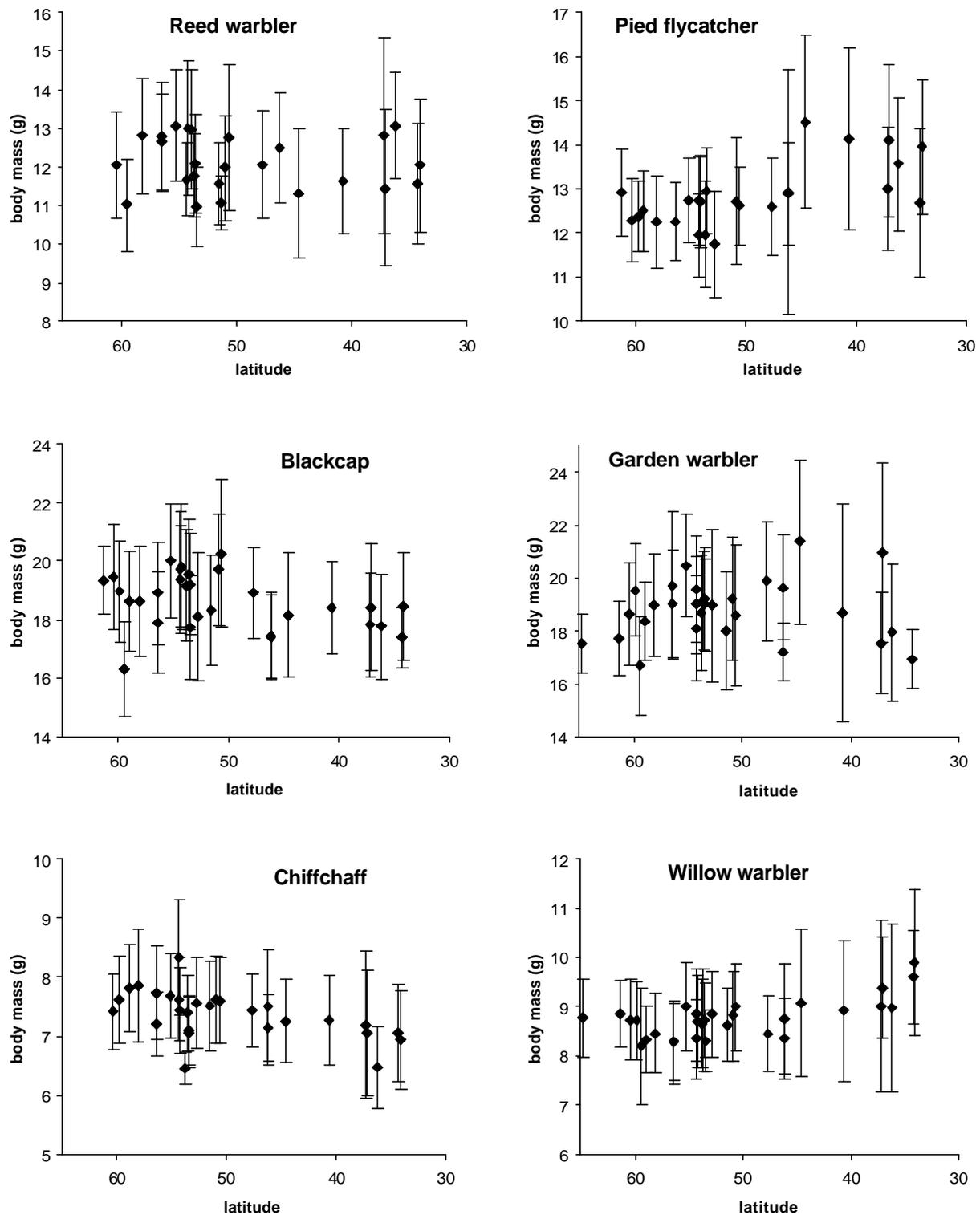
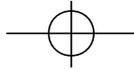
**Figure 4.** Latitudinal variation in timing of autumn passage (median Julian date) in several long-distance migratory songbirds: reed warbler *Acrocephalus scirpaceus*; sedge warbler *Acrocephalus schoenobaenus*; pied flycatcher *Ficedula hypoleuca*; common redstart *Phoenicurus phoenicurus*; willow warbler *Phylloscopus trochilus*; garden warbler *Sylvia borin*. Only sites with at least 30 birds caught are considered.



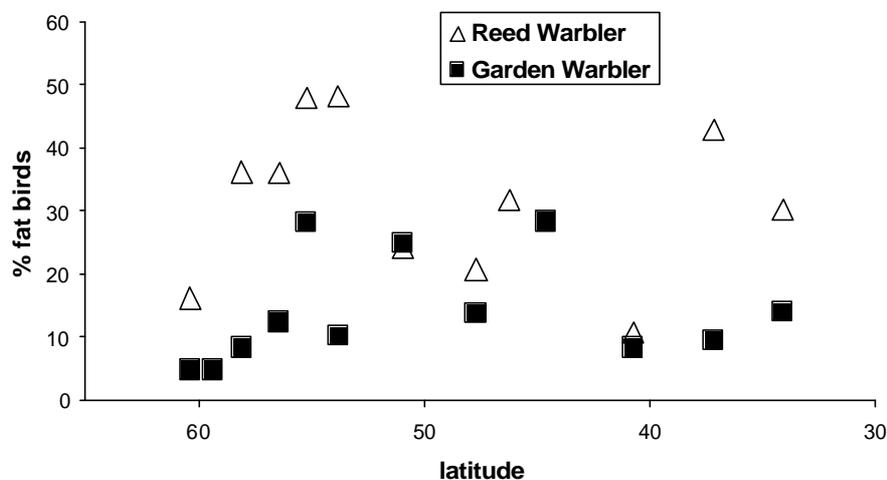
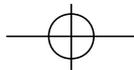
**Figure 5.** Longitudinal variation in timing of autumn passage (median Julian date) in several migratory songbirds: garden warbler *Sylvia borin*; blackcap *Sylvia atricapilla*; reed warbler *Acrocephalus scirpaceus*; willow warbler *Phylloscopus trochilus*. Only sites north of 50° N and with at least 30 birds caught are considered. In both garden warbler and willow warbler birds on passage at Fair Isle (top left data point in each case) are comparatively very late, indicating that the very northern Scandinavian birds are departing late. Without the data from Fair Isle, the  $R^2$ -values are much higher: garden warbler 0.42; willow warbler 0.63.

fatten very much north of the Mediterranean during autumn migration but progressively increase in mass so that they are just sufficiently prepared for the Mediterranean crossing (see also Schaub & Jenni 2000a,b, 2001a). Most of the required fuel to cross the Sahara is then accumulated in northwestern Africa (Bairlein 1991). Moreover, there are species-specific differences in the spatial and temporal pattern of fuelling. Reed warblers do not show a progressive increase towards the South but they already carry considerably more fat farther north compared to garden warblers (Fig. 7). That difference may be related to the predictability of future stopover sites. While garden warblers inhabit bushland, which is rather widespread, reed warblers rely mostly on wetlands with extended reed beds. Their distribution is more patchy and may thus be less predictable. Consequently, reed warblers may accumulate more fuel at

fewer places to be less dependent on future stopover sites. This is also supported by data on stopover duration, with much longer stopover in reed warblers than in garden warblers (Schaub & Jenni 2001b). Similarly, even higher fuel loads in sedge warblers *Acrocephalus schoenobaenus* than in reed warblers during autumn migration are considered to be related to the sedge warbler's more specialised and thus less predictable diet (Bibby & Green 1981, 1983). Predictability of future feeding sites may also be the reason while birds migrating along the eastern European flyway in autumn accumulate more fuel farther north (Bairlein 1991). In contrast to northwest Africa where there are good feeding conditions in an extensive belt of vegetation north of the Sahara, no such extensive feeding opportunities exist in northeastern Africa. Barn swallows *Hirundo rustica* (Rubolini et al. 2002) also show pronounced



**Figure 6.** Latitudinal variation in average body mass ( $\pm$  s.d.) in several migratory songbirds during autumn migration across Europe. Only sites with at least 20 birds caught are considered. Reed warbler *Acrocephalus scirpaceus*; pied flycatcher *Ficedula hypoleuca*; Blackcap *Sylvia atricapilla*; garden warbler *Sylvia borin*; chiffchaff *Phylloscopus collybita*; willow warbler *Phylloscopus trochilus*.



**Figure 7.** Latitudinal variation in the proportion of fat birds (birds with a fat score of at least 5 according to Kaiser 1993) in reed warblers *Acrocephalus scirpaceus* and garden warblers *Sylvia borin* during autumn migration across Europe. North of 50° N, the proportion of fat birds is significantly higher in reed warblers than in garden warblers ( $\chi^2$ -test;  $P < 0.001$ ).

geographical variation in the extent of migratory fuelling during autumn southbound migration.

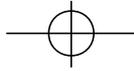
The predictability of future feeding sites must also be considered when trying to understand seasonal patterns of fuelling within and between sites (Fig. 8). In many species later birds during autumn migration carry more fuel than earlier migrants, and this seems to be more pronounced the farther north the site is located. Irrespective of the cues these birds use to judge their delay (Bairlein 2000, Totzke et al. 2000), they are faced a lower predictability of good feeding conditions later during autumn. This may force these late migrants to increase their local rate of fuelling and departure fuel load in order to be less dependent on future stopover sites. These data illustrate that predictability of future feeding places has a considerable influence on migration strategies both within and between species.

## Outlook

Other subjects besides migration deserve large-scale collaborative and coordinated approaches. Tucker & Heath (1994) and Marchant (1992) revealed considerable variation in population changes across Europe. These data, together with atlas data, may enable the identification of areas of particular conservation concern (Greenwood 1999). However, they do not reveal the demographic features of the populations that are prerequisites for understanding the changes in bird numbers and their likely causal factors. Bird ringing at constant effort sites (CES) has been shown as an effective measure for changes in population numbers, pro-

ductivity and survival rates (e.g. Peach et al. 1996, 1998, Greenwood 1999). CES ringing has been recently launched in a number of European countries (Balmer 2003) and it should be elaborated to a European network. Combined with the Pan-European Common Bird Monitoring Initiative (Noble 2003) as central elements of an integrated population monitoring scheme (e.g. Baillie 1990, Greenwood 1999) it will elucidate the causal relationships of population changes better than single site or national approaches.

Climate change is increasingly affecting ecosystems, habitats and species (e.g. IPCC 2001, Walther et al. 2002, Berry et al. 2003, Parmesan & Yohe 2003, Root et al. 2003). Several migratory birds are reacting to increased local temperatures, or to large scale climatic phenomena such as the North Atlantic Oscillation (NAO), with changes in arrival and departure phenologies (e.g. Bairlein & Winkel 2001, Tryjanowski et al. 2002, Buttler 2003, Cotton 2003, Hubalek 2003, Hüppop & Hüppop 2003, Jenni & Kéry 2003). Many species of birds start egg-laying much earlier than in previous times (e.g. Winkel & Hudde 1996, 1997, Crick et al. 1997, Brown & Bhagabati 1999, Crick & Sparks 1999, Dunn & Winkler 1999, Walther et al. 2002, Møller et al. 2004). Several species are currently changing their breeding (e.g. European bee-eater *Merops apiaster*; Todte 2003) or winter distribution (Berthold 1998, Fiedler et al. 2004), which is likely to be related to climate change. Moreover, there is evidence for considerable geographic variation in the impact of global climate change on wildlife (e.g. Hurrell 1995, Forchhammer et al. 2002, Walther et al. 2002, Stenseth et al. 2003,



Bairlein & Hüppop 2004). Consequently, the broad geographic patterns of species richness, bird numbers and the proportion of migrants, for example, are likely to change. Understanding these changes and assessing their consequences require large-scale initiatives and networks (e.g. the European Phenology Network; <http://www.dow.wau.nl/msa/epn/>). Owing to the thousands of skilled volunteer bird watchers and bird ringers across Europe, a bird-based European Climate Assessment Network can contribute significantly to knowledge and understanding of global climate change on wildlife.

However, large-scale networks are subject to a number of biases, for example the distribution of observers, observer skills, variation in field methods, distribution of study sites, etc. Consequently, large-scale networks can achieve their potentials and goals only if they are following a strict standardised methodology, and a common protocol. Another prerequisite is training and calibration to ensure standardisation of measurements and to minimise between-site observer variability which otherwise could hinder proper comparative analyses (e.g. Busse & Kania 1970, Berthold & Schlenker 1975, Bairlein 1994, 1998, Busse 2000).

Some concern must be given towards the design of networks (Marchant 1999). Collaborative surveys are particularly valuable if they include many study sites. However, the selection of sites must be structured and stratified to ensure that sites are as representative as possible. For example, most of the recent larger-scale migration networks are faced with a dominance of coastal sites and comparatively few inland ones. Locality, however, has a considerable influence (Lindström et al. 1996). Coastal sites often attract many birds but may offer less good feeding conditions. In contrast, many inland sites offer adequate feeding but there is often a considerable overlap between local breeding birds and passage migrants.

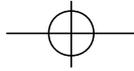
If these basic requirements are met, large-scale networks constitute a unique approach to studying patterns and processes in bird life by comparisons across a wide geographic area and at a much more elaborated level than single-site studies alone could achieve. Provided there is standardisation of methods, training and calibration as well as coordination provided, they could also make use of the many skilled and enthusiastic volunteer bird watchers.

There are several European institutions and initiatives in the study of birds (e.g. European Union for Bird

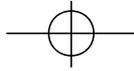
Ringling, European Bird Census Council, Wetlands International, Pan-European Breeding Bird Initiative, Constant Effort Ringing) which already operate large-scale networks. It would be worthwhile to link several of these projects into a more coherent and collaborative pan-European approach by creating Euro-Monitoring (Gibbson & Marchant 1999) under the umbrella of the European Ornithologists' Union (see <http://www.eou.at>).

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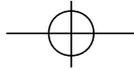
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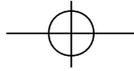
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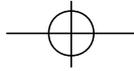
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## The phylogeographic differentiation of the European robin *Erithacus rubecula* on the Canary Islands revealed by mitochondrial DNA sequence data and morphometrics: evidence for a new robin taxon on Gran Canaria?

Christian Dietzen<sup>1</sup>, Hans-Hinrich Witt<sup>2</sup> and Michael Wink<sup>1</sup>

Sequences of the mitochondrial cytochrome b-gene (1125 basepairs) of the European robin, *Erithacus rubecula*, from the Canary Islands, Spain, revealed new insights into the systematics and the phylogeography of this taxon. Additionally, a range of morphological measurements was investigated by using discriminant function analysis. Genetic and morphological data show no differences between robins from the western Canary Islands and mainland Europe and these populations should be retained within the nominate form *E. r. rubecula*. Sequence data revealed well defined haplotypes and distinct genetic distances between *E. r. superbus*, both from Gran Canaria and Tenerife. *E. r. superbus* from Gran Canaria takes a more basal position and birds from Tenerife are more closely related to *E. r. rubecula* than are birds from Gran Canaria. Statistical analysis of measurements also showed significant differences in wingtip shape. We propose to treat the robins from the Canary Islands as a superspecies containing *E. [r.] rubecula* (western Canary Islands and Europe), *E. [r.] superbus* (Tenerife) and *E. [r.] canariae* (Gran Canaria).

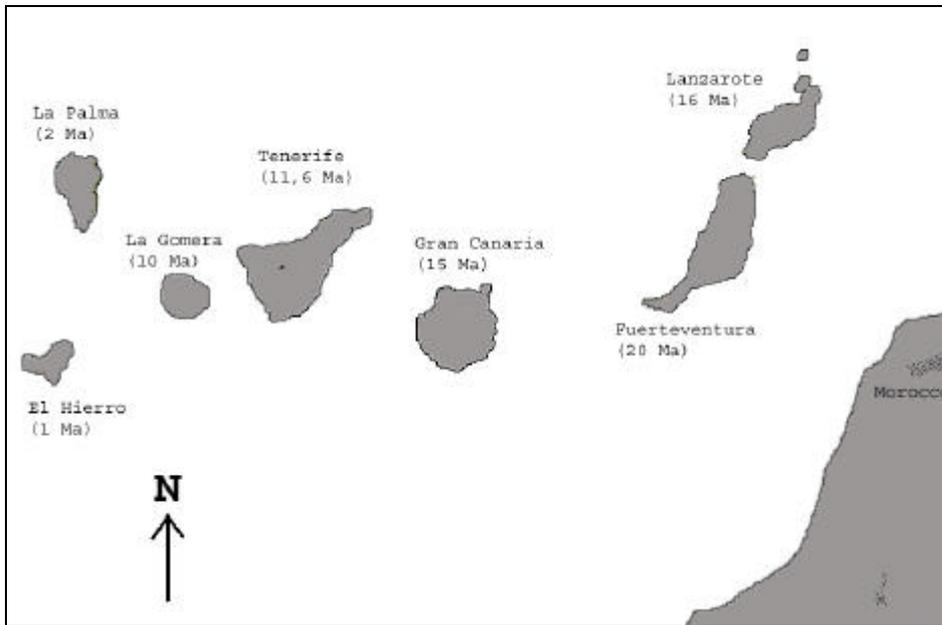
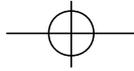
Key Words: Phylogeographic differentiation, mitochondrial cytochrome-b sequences, Canary Islands, *Erithacus rubecula*, morphometrics.

<sup>1</sup>University of Heidelberg, Institute of Pharmacy and Molecular Biotechnology, Im Neuenheimer Feld 364, D-69120 Heidelberg, Germany; <sup>2</sup>Forsthaus Kornberg, D-34621 Frielendorf, Germany; <sup>1</sup>email: christian.dietzen@urz.uni-heidelberg.de or wink@uni-hd.de

The Canarian archipelago (Spain) consists of seven major islands in the eastern Atlantic Ocean (between 27°37' and 29°25' N, and 13°20' and 18°10' W), the distance to adjacent African mainland being between 110 km (Fuerteventura) and 460 km (La Palma). The islands are of volcanic origin and, according to general opinion, have never been connected to the African continent (Abdel-Monem et al. 1971, Kunkel 1976, Schmincke 1979, 2000). The age of the islands increases from east to west and ranges from less than 1 million to 20 million years (Fig. 1). Together with Madeira, the Azores and Cape Verde Islands, the Canary Islands form the Macronesian archipelago. Because of these characteristics the Canary Islands are a prime lo-

cation for investigations into the evolution and development of oceanic island biota. This is documented in an increasing number of publications with a focus on molecular phylogeny (e.g. Estoup et al. 1996, Gonzalez et al. 1996) and phylogeography (e.g. Thorpe et al. 1994, Brown & Pestano 1998, Emerson et al. 1999, Nogales et al. 1998) of different animal taxa. These papers highlight the differences in the colonisation pathways and histories of mainly flightless beetle species and reptiles (for review see Juan et al. 2000).

Due to their oceanic origin and volcanic history the Canarian flora and fauna contain a large proportion of endemic species, comparable to the Hawaiian and Galapagos Islands. The percentage of endemism in the



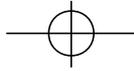
**Figure 1.** Location and age of the Canary Islands, Spain (after Juan et al. 2000). Ma = million years

native flora is approximately 30 % but can reach more than 90 % depending on the vegetational zone investigated (Schönfelder & Schönfelder 1997, Bergmann 2000). Animal taxa achieve similar values to plants, for example 70 % of carabid beetles, 42 % of aculeate hymenopterans (Bergmann 2000) and 100 % of reptiles (Bischoff 2000) are endemic. Amongst the 75 native breeding birds seven species (including two extinct) are endemic to the Canaries (13 %) and a further three are Macronesian endemics (Bannermann 1963, Martin & Lorenzo 2001). Most of the remaining species are represented by endemic subspecies ( $n = 26$ ; 35 %) distinct from their closest relatives on the European and African mainland (Baez 1992, Martin & Lorenzo 2001).

Our current knowledge of the taxonomy and systematic position of the Canarian avifauna is mainly based on morphological and bioacoustical studies (e.g. Vaurie 1959, 1965, Cramp 1988). So far, the systematics of only a few Canarian bird taxa have been investigated by using molecular tools, e.g. pipits *Anthus* spp. (Arctander et al. 1996), chaffinches *Fringilla* spp. (Marshall & Baker 1999), stonechats *Saxicola* spp. (Wittmann et al. 1995, Wink et al. 2002a, b), chiffchaffs *Phylloscopus* spp. (Helbig et al. 1996), and bustards *Chlamydotis* spp. (Gaucher et al. 1996, Broders et al. 2003). The use of molecular genetics for answering phylogenetic questions has become a valuable and widely applied tool,

especially if morphologically similar and closely related taxa are involved (e.g. Helbig et al. 1996, Wink et al. 1993, Heidrich & Wink 1994, Helbig & Seibold 1999).

The European robin *Erithacus rubecula* is distributed over large parts of the Western Palaearctic from western Siberia in the east to the Iberian Peninsula in the west (Cramp 1988). Several subspecies have been described (Vaurie 1955, 1959, Cramp 1988, Pätzold 1995) but the morphological differences are merely clinal and not very distinct. The nominate form *E. r. rubecula* inhabits large parts of Europe and northwest Africa and the western Canary Islands (La Gomera, El Hierro, La Palma), Madeira, and the Azores. The birds from these Atlantic islands have formerly been regarded as a separate subspecies *E. r. microrhynchos* (e.g. Hounscome 1993, Martin & Lorenzo 2001) but are usually included in *rubecula* (Lack 1946, 1951, Vaurie 1959, Cramp 1988, Clements 2000). The subspecies *E. r. melophilus* from the British Isles shows a slightly more intensive breast colouration and more olive upperparts. *E. r. witherby* from northern Africa is similar to *melophilus*. Several other subspecies occurring in eastern Europe, the Balkans and the Middle East are almost indistinguishable from the nominate form. The most obvious taxon, *E. r. superbus*, which inhabits the mountain forests of Tenerife and Gran Canaria, is easily separated from the nominate



form by its deep orange-red breastpatch, white eye ring, grey forehead and necksides, and white belly (Koenig 1890, Vaurie 1959, Cramp 1988). Recent morphological and acoustical research led to proposals for specific recognition of this taxon as *E. superbus*, the 'Tenerife robin' (e.g. Bergmann & Schottler 2001). Due to the lack of suitable habitat the two desert islands of Fuerteventura and Lanzarote are not inhabited by robins and the species there occurs in small numbers only during migration (Martin & Lorenzo 2001).

A project on the molecular phylogeography of several passerine bird species in the Macronesian Archipelago gave us the opportunity to investigate the systematics of *Erithacus rubecula* on the Canary Islands by using molecular tools. We used sequences of the mitochondrial cytochrome b-gene to study the phylogeographic differentiation, and test the phylogenetic relationships of the taxa involved, in particular the validity of the specific status of *E. superbus* as proposed by Bergmann & Schottler (2001). A further objective concerned the colonisation history of the robin in the Macronesian Archipelago.

## Material and methods

### Samples

The samples for this study were obtained from live birds on the Canary Islands in 2002 (Table 1). The birds were captured with mist-nets, measured, weighed and small blood samples obtained by puncturing the brachial vein. Afterwards the birds were released and the blood samples preserved in storage buffer containing 0.1 M Tris, pH 7.4, 10 % EDTA, 1 % NaF, 0.1 % thy-

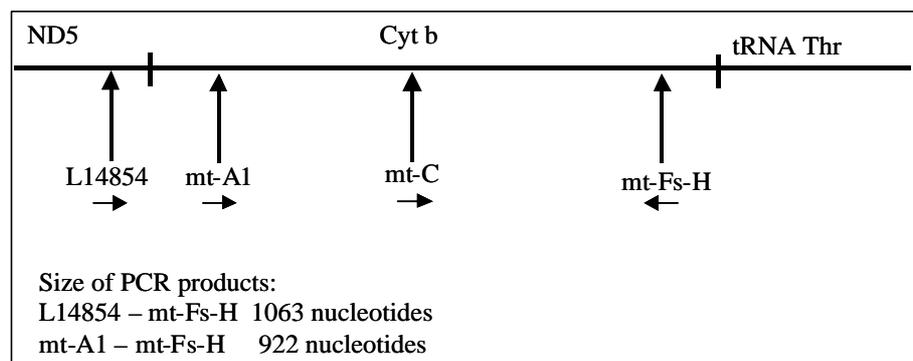
mol and frozen at  $-20^{\circ}\text{C}$  as soon as possible until further processing. Blood samples were collected with permission of the Consejería de Política Territorial y Medio Ambiente (permit No 249).

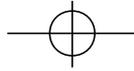
### Sequencing

Total genomic DNA was extracted from the stored blood samples by an overnight incubation at  $37^{\circ}\text{C}$  in lysis buffer (10 mM Tris [pH 7.5], 25 mM EDTA, 75 mM NaCl, 1 % SDS) including 1 mg Proteinase K (Boehringer Mannheim) followed by a standard phenol/chloroform protein extraction. DNA was precipitated from the supernatant with 0.8 volumes of cold isopropanol, centrifuged, washed, dried and resuspended in TE buffer.

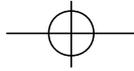
The mitochondrial cytochrome b-gene was amplified by PCR from the total genomic DNA using the specific primers L14854 (5'-GGK TCT TTC GCC CTM TC-3'), mt-A1 (L14995; 5'-GCC CCA TCC AAC ATC TCA GCA TGA TGA AAC TTC CG-3') with mt-Fs-H (H15917; 5'-TAG TTG GCC AAT GAT GAT GAA TGG GTG TTC TACTGG TT-3'; cf. Fig. 2). 'K' is coding for guanosine or thymidine, 'M' for adenosine or cytosine and 'Y' for thymidine or cytosine. The total reaction volume was 50  $\mu\text{l}$  containing 1.5 mM MgCl<sub>2</sub>, 10 mM Tris (pH = 8.5), 50 mM KCl, 100  $\mu\text{M}$  dNTPs, 0.8 units Taq polymerase (Pharmacia Biotech, Freiburg), 200 ng DNA and 5 pmoles of the above primers. The cycle protocol consisted of (1) an initial denaturation at  $94^{\circ}\text{C}$  for 10 min, (2) 30 cycles including denaturation at  $94^{\circ}\text{C}$  for 1 min, annealing at  $53^{\circ}\text{C}$  for 1 min and extension at  $72^{\circ}\text{C}$  for 2 min followed by (3) a final extension period at  $72^{\circ}\text{C}$  for 10 min. PCR products were stored at  $4^{\circ}\text{C}$  until further processing. Before

**Figure 2.** Position of primer sequences used for PCR and sequencing reactions in the mitochondrial genome of European robins and size of PCR products with different primer combinations. Small arrows indicate forward ( $\rightarrow$ ) and reverse ( $\leftarrow$ ) primers.



**Table 1.** Sampling locations for European robins *Erithacus rubecula* examined in this study.

No	Location	Latitude/Longitude	Island
R01	Maraditas	28° 42' N 17° 48' W	La Palma
R02	Laguna de Barlovento	28° 48' N 17° 48' W	La Palma
R03	Roque Nublo	27° 56' N 15° 36' W	Gran Canaria
R04	Roque Nublo	27° 56' N 15° 36' W	Gran Canaria
R05	Aguagarcia/Lomo de la Jara	28° 27' N 16° 22' W	Tenerife
R06	Aguagarcia/Lomo de la Jara	28° 27' N 16° 22' W	Tenerife
R07	Aguagarcia/Lomo de la Jara	28° 27' N 16° 22' W	Tenerife
R08	El Portillo	28° 18' N 16° 33' W	Tenerife
R10	Frielendorf	50° 58' N 09° 20' E	Germany
R11	Ladera de Tigaiga	28° 20' N 16° 31' W	Tenerife
R12	Ladera de Tigaiga	28° 20' N 16° 31' W	Tenerife
R15	Ladera de Tigaiga	28° 20' N 16° 31' W	Tenerife
R16	Ladera de Tigaiga	28° 20' N 16° 31' W	Tenerife
R17	Monte del Aguas	28° 19' N 16° 49' W	Tenerife
R18	Monte del Aguas	28° 19' N 16° 49' W	Tenerife
R19	Batán de Arriba	28° 31' N 16° 18' W	Tenerife
R20	Aguagarcia/Lomo de la Jara	28° 27' N 16° 22' W	Tenerife
R21	Aguagarcia/Lomo de la Jara	28° 27' N 16° 22' W	Tenerife
R22	Aguagarcia/Lomo de la Jara	28° 27' N 16° 22' W	Tenerife
R23	Aguagarcia/Lomo de la Jara	28° 27' N 16° 22' W	Tenerife
R24	Aguagarcia/Lomo de la Jara	28° 27' N 16° 22' W	Tenerife
R25	Barranco de Fernando	28° 49' N 17° 57' W	LaPalma
R26	Lomo de los Pajaros	28° 41' N 17° 47' W	LaPalma
R27	Juego de Bolas (Las Rosas)	28° 10' N 17° 12' W	La Gomera
R28	Lomo de la Mulata	28° 04' N 17° 15' W	La Gomera
R29	Lomo de la Mulata 2	28° 04' N 17° 15' W	La Gomera
R30	Hormiga	28° 09' N 17° 13' W	La Gomera
R31	Cruz de los Reyes	27° 42' N 18° 01' W	El Hierro
R32	Raya la Llania	27° 44' N 18° 00' W	El Hierro
R33	San Salvador	27° 43' N 18° 01' W	El Hierro
R34	La Mareta	27° 46' N 17° 59' W	El Hierro
R35	Reserva Natural de El Brezal	28° 07' N 15° 37' W	Gran Canaria
R36	Barranco de la Virgen	28° 03' N 15° 34' W	Gran Canaria
R37	Barranco del Laurel	28° 04' N 15° 35' W	Gran Canaria
R38	Barranco de la Virgen	28° 03' N 15° 34' W	Gran Canaria
R39	Barranco de la Torre	28° 19' N 13° 54' W	Fuerteventura
R40	Catalina Garcia	28° 16' N 14° 01' W	Fuerteventura
R41	Rio Samora	38° 59' N 08° 52' W	Portugal
R42	Taboaco	41° 06' N 07° 43' W	Portugal
R43	Rio Tedo	41° 06' N 07° 45' W	Portugal
R44	Rio Tedo	41° 06' N 07° 45' W	Portugal
R45	Cruz de los Reyes	27° 42' N 18° 01' W	El Hierro
R46	Cruz de los Reyes	27° 42' N 18° 01' W	El Hierro
R47	Cruz de los Reyes	27° 42' N 18° 01' W	El Hierro
R48	Cruz de los Reyes	27° 42' N 18° 01' W	El Hierro
R49	La Mareta	27° 46' N 17° 59' W	El Hierro
R50	La Mareta	27° 46' N 17° 59' W	El Hierro
R51	La Mareta	27° 46' N 17° 59' W	El Hierro
R52	El Brezal	27° 43' N 18° 00' W	El Hierro
R53	El Brezal	27° 43' N 18° 00' W	El Hierro
R54	Lomo de la Mulata	28° 04' N 17° 15' W	La Gomera
R55	Lomo de la Mulata 2	28° 04' N 17° 15' W	La Gomera



No	Location	Latitude/Longitude	Island
R56	Lomo de la Mulata 2	28° 04' N 17° 15' W	La Gomera
R57	Monte Garajonay	28° 04' N 17° 15' W	La Gomera
R58	Monte Garajonay	28° 04' N 17° 15' W	La Gomera
R59	Reserva Natural de El Brezal	28° 07' N 15° 37' W	Gran Canaria
R60	Barranco de la Virgen	28° 03' N 15° 34' W	Gran Canaria
R61	Barranco de la Virgen	28° 03' N 15° 34' W	Gran Canaria
R62	Barranco de la Virgen	28° 03' N 15° 34' W	Gran Canaria
R63	Barranco de la Virgen	28° 03' N 15° 34' W	Gran Canaria
R64	Barranco de la Virgen	28° 03' N 15° 34' W	Gran Canaria
R65	Barranco del Laurel	28° 04' N 15° 35' W	Gran Canaria
1.4338	Jan Festo	43° 20' N 05° 22' E	France
3.4340	Heidelberg	49° 24' N 08° 41' E	Germany
4.4341	Madeira	32° 44' N 16° 59' W	Portugal

sequencing PCR products (1 volume) were precipitated with 4 M NH<sub>4</sub>Ac (1 volume) and 6 volumes ethanol. After centrifugation for 15 min at 13 000 rpm, DNA pellets were washed in 70 % ethanol and diluted in 15  $\mu$ l of distilled water.

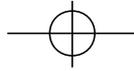
A cycle sequencing reaction (total volume of 10  $\mu$ l) contained 2  $\mu$ l of reaction mix (according to the BigDye Terminator Protocol: Applied Biosystems), 10 pmol primer L14854, mt-A1 or mt-C (L15320; 5'-TAY GTC CTA CCA TGA GGA CAA ATA TCA TTC TGA GG-3'), and 2–5  $\mu$ l of the template. The cycle sequencing protocol included 25 cycles of 10 s at 96 °C, 5 s at 52 °C and 4 min at 60 °C. Sequencing products were purified by precipitation: 1 volume of reaction mix, 1/10 volumes of 3 M NaAcetate (pH 4.6), 2.5 volumes of ethanol. After centrifugation for 15 min at 13 000 rpm, DNA pellets were washed in 70 % ethanol and diluted in 20  $\mu$ l of distilled water. The purified sample was diluted 1:5 in water and applied to a 16-column automatic capillary sequencer (ABI 3100) using 50-cm and 80-cm capillaries and POP6 as a polymer. Sequences of other turdid taxa used for comparison were obtained earlier using an ALFexpress II, as described previously (e.g. Wink et al. 2002a).

The sequences used in this analysis are deposited at GenBank under accession numbers AY286333–AY286400.

### Phylogenetic Analysis

By using different primer combinations, overlapping sequences with a combined length of 1125 nucleotides

were obtained. Sequences were carefully aligned and net pairwise genetic p-distances and corrected Kimura (1980) 2-parameter distances calculated with MEGA version 2.1 (Kumar et al. 2001). Phylogenetic trees were constructed employing PAUP\*4b10 (neighbour-joining and maximum parsimony; Swofford 2001) and MrBayes version 2.01 (maximum likelihood; Huelsenbeck & Ronquist 2001). Neighbour-joining analysis was performed using Kimura's (1980) two-parameter model and bootstrapped 1000 times. Results were similar to the maximum parsimony analysis, and only the latter is shown. For maximum parsimony analysis (heuristic search) all characters were unordered and of equal weight. Starting trees were obtained via stepwise addition with addition sequence as closest, and the branch-swapping algorithm was set to tree-bisection-reconnection (TBR). From the resulting 500 shortest trees a strict consensus and a 50 % majority rule consensus tree were estimated. For bootstrap analysis 500 replicates with branch-and-bound algorithm were run. To describe the trees obtained the following statistics were calculated as described by Swofford (2001): tree length, consistency index (CI), homoplasy index (HI), retention index (RI) and rescaled consistency index (RC). For maximum likelihood analysis the Bayesian inference of phylogeny was used (Huelsenbeck & Ronquist 2001). The calculations were based on the general time reversible (GTR) model (Tavaré 1986, Swofford et al. 1996) and performed with 500 000 Markov chains Monte Carlo from a random starting tree. The first 500 trees were ignored. Nucleotide frequencies for the starting tree were estimated (A = 0.27789, C = 0.35630, G = 0.13190, T = 0.23391).



The following population analyses were performed with Arlequin version 2.000 (Schneider et al. 2000). Gene flow between populations was estimated using F-statistics (Wright 1928) and Fst values were interpreted as suggested by Wright (1978). For investigations of population history, pairwise mismatch distributions were calculated after the 'infinite sites' model (Kimura 1971) and plotted against expected values following the 'model of sudden expansion' (Rogers & Harpending 1992). Genetic structure was evaluated using analysis of molecular variance (AMOVA). Two assumed genetic structures were tested with samples from Gran Canaria and Tenerife in one group opposed to the remaining samples in the second group, and with Gran Canaria, Tenerife and the remaining samples each forming separate groups.

### Morphometrics

All birds captured for sampling were measured and weighed. The following measurements were taken as described in Svensson (1992): maximum wing length, length of primaries (P) 1–9 and secondary (S) 1, length of tarsus, length of bill tip to distal end of nostril (NaLoSpi), bill width, bill height, bill length from tip to skull and length of footspan for outer, middle and inner toe. Measurements were exact to 0.5 mm (wing) and 0.1 mm (leg and bill) respectively; the weight of the birds was measured using a digital balance (Ohaus CS200) exact to 0.1 g.

All measurements were analysed for variance by MANOVA using SPSS version 5.0.2 (SPSS Inc. 1993). Significance levels were set at  $P \leq 0.05$  (\* significant) and  $P \leq 0.01$  (\*\* highly significant). To investigate possible morphological differentiation between popula-

tions the data were entered into a discriminant function analysis (Wilks's Lambda). Wingtip shape characteristics were calculated following Lockwood et al. (1998). Only adult birds not in moult were included.

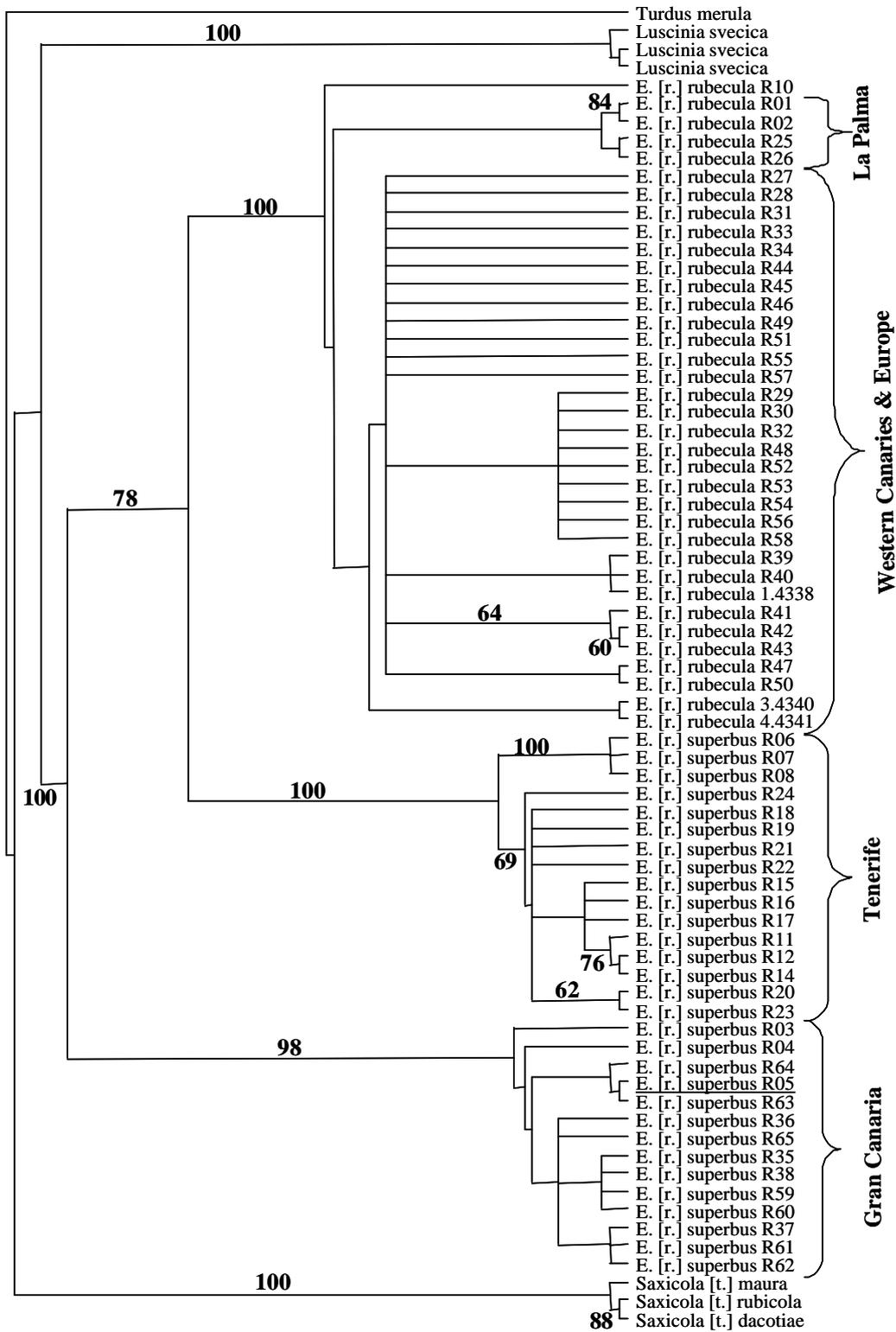
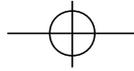
### Results

The cytochrome b-gene was sequenced from 66 robins and a further seven turdid species of the genera *Turdus* (outgroup), *Luscinia*, and *Saxicola*. The sequences obtained could be aligned without difficulty and no stop codons were encountered. The employment of different primers which produced overlapping sequences gave some additional proof that the sequences were correct and of mitochondrial origin.

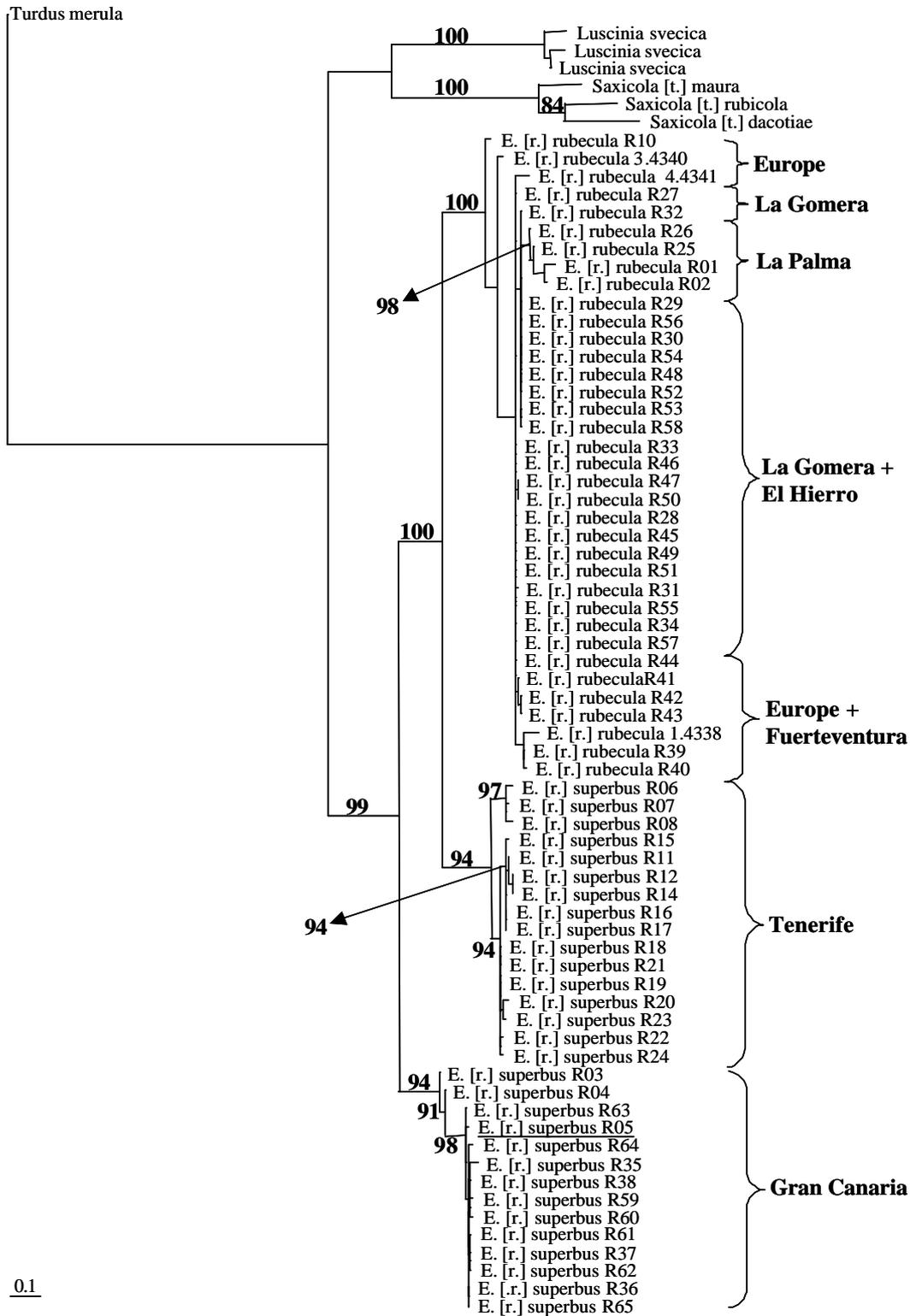
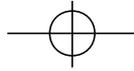
1125 nucleotides in the robin dataset showed 226 (20.1 %) variable sites of which 85 (7.5 %) were parsimony informative. The net pairwise genetic p-distances between and within the island populations are shown in Table 2. The distances between *E. r. rubecula* (*rubecula* hereafter) of the western Canary Islands and European mainland and *E. r. superbus* (*superbus* hereafter) varied between 2.7 and 5.1 % (mean 3.8 %). The most striking feature, however, is that *superbus* from Gran Canaria clearly differs from those of Tenerife by  $3.7 \pm 0.7$  %. The *superbus* from Tenerife differ from *rubecula* by 2.7–3.2 % (mean 2.9 %) while a genetic distance of 4.6–5.1 % (mean 4.8 %) was found between *superbus* from Gran Canaria and *rubecula*. In *rubecula* the divergence between different islands including mainland Europe did not exceed 1.1 % (0.11–1.1 %, mean 0.6 %). Within the island populations the genetic distances were small (mean 0.5 %), and the greatest within-group distance was found on Tenerife ( $1.1 \pm 0.2$  %).

**Table 2.** Uncorrected genetic p-distances (below diagonal) and Kimura-2-parameter distances (above diagonal) between populations of European robins *Erithacus rubecula* inferred from 1125 nucleotides of the mitochondrial cytochrome b-gene. In the diagonal (bold) are the within-group distances. Shown are the mean net distances [%]  $\pm$  s. e.

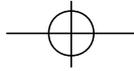
	[1]	[2]	[3]	[4]	[5]	[6]
[1] La Palma	<b>0.6 <math>\pm</math> 0.2</b>	0.3 $\pm$ 0.2	0.4 $\pm$ 0.2	3.4 $\pm$ 0.7	5.4 $\pm$ 1.0	0.5 $\pm$ 0.2
[2] La Gomera	0.3 $\pm$ 0.2	<b>0.1 <math>\pm</math> 0.1</b>	0.0 $\pm$ 0.0	2.9 $\pm$ 0.7	4.9 $\pm$ 1.0	0.1 $\pm$ 0.1
[3] El Hierro	0.4 $\pm$ 0.2	0.0 $\pm$ 0.0	<b>0.1 <math>\pm</math> 0.1</b>	2.8 $\pm$ 0.7	4.0 $\pm$ 1.0	0.1 $\pm$ 0.0
[4] Tenerife	3.2 $\pm$ 0.7	2.8 $\pm$ 0.6	2.8 $\pm$ 0.6	<b>1.1 <math>\pm</math> 0.2</b>	3.9 $\pm$ 0.7	2.8 $\pm$ 0.7
[5] Gran Canaria	5.1 $\pm$ 0.9	4.7 $\pm$ 0.8	4.7 $\pm$ 0.8	3.7 $\pm$ 0.7	<b>0.4 <math>\pm</math> 0.1</b>	4.9 $\pm$ 0.9
[6] Europe	0.5 $\pm$ 0.2	0.1 $\pm$ 0.1	0.1 $\pm$ 0.0	2.7 $\pm$ 0.6	4.6 $\pm$ 0.8	<b>0.6 <math>\pm</math> 0.2</b>



**Figure 3.** Maximum parsimony analysis (50% majority rule consensus tree) of robin taxa. Numbers refer to bootstrap values above 60% (500 replicates). Tree length 513, CI = 0.7271, HI = 0.2729, RI = 0.9176, RC = 0.6672. The underlined individual was caught on Tenerife.



**Figure 4.** Maximum likelihood analysis following Bayesian inference of phylogeny of robin taxa. Branch lengths correspond to genetic distances. The numbers indicate clade credibility values above 80. The underlined individual was caught on Tenerife.

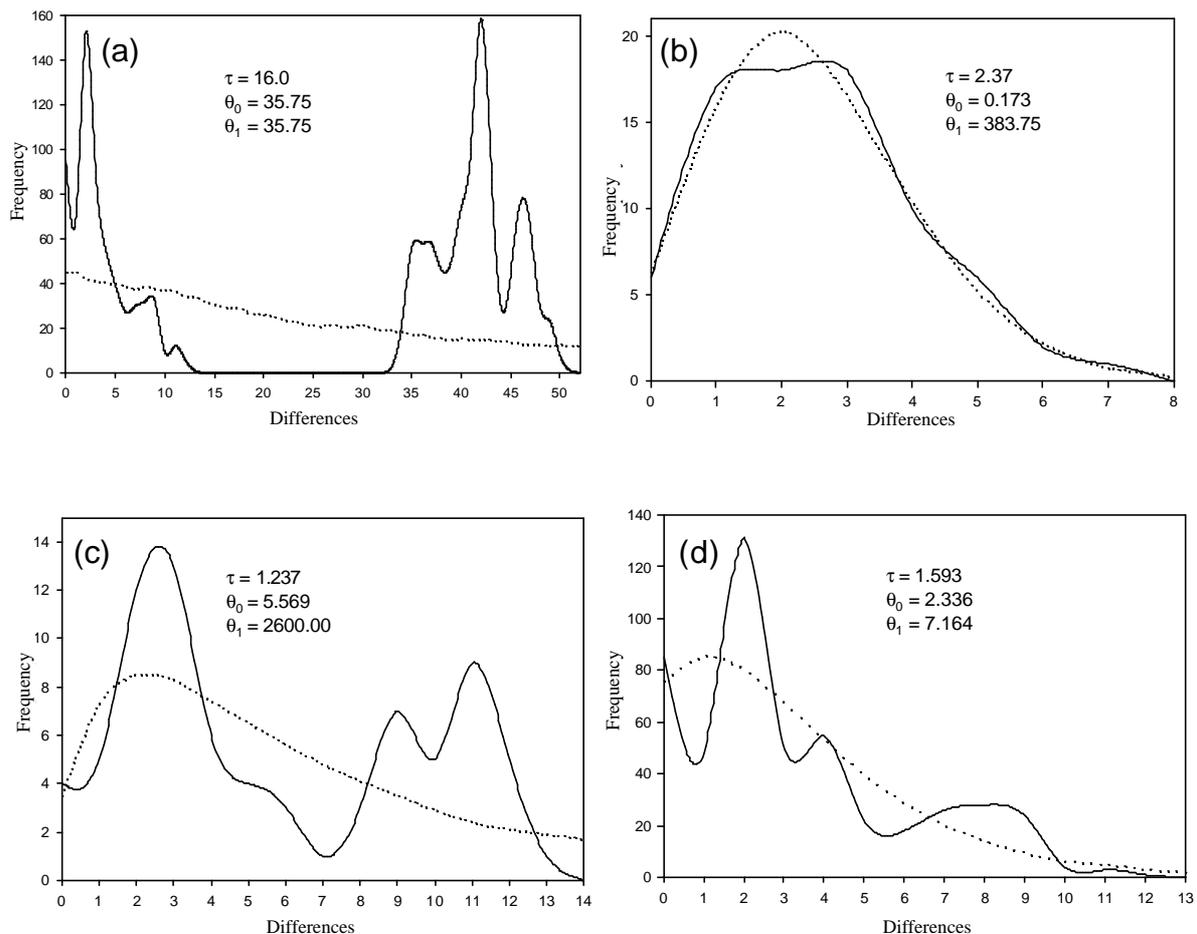


Most differences within the island populations were due to single nucleotide substitutions. Only on Tenerife could several distinct haplotypes be identified; one bird (sample R05) caught on Tenerife showed strong affinities to the haplotype found on Gran Canaria.

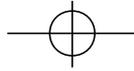
The phylogenetic analysis led to more or less identical tree topologies for all three tree building methods used (see Figs 3 and 4; neighbour joining results are not shown because they show a similar outcome to maximum parsimony and maximum likelihood). The genus *Erithacus* forms a monophyletic clade supported by high bootstrap values (99–100 %) in neighbour-joining and maximum parsimony analyses. Within *Erithacus* three distinct groupings can be recognised. The *superbus* from Gran Canaria take a more basal position and are opposed to a clade comprised of *superbus* from Te-

nerife and all *rubecula*. In this latter clade *superbus* is clearly separated from *rubecula*. All these groupings gain high bootstrap support (81–100 %). According to these results *E. r. superbus* is clearly paraphyletic. In the *rubecula*-clade no stable groupings could be detected with the exception of the birds from La Palma, which usually clustered together (61 % bootstrap support). Some of the Central European birds form a small well supported (82 % bootstrap) cluster within *rubecula*. Also the migrant birds caught on Fuerteventura are included in this cluster. The terminal positions within the groupings could not be resolved satisfactorily from the cytochrome-b sequences and bootstrap values are very low (2–56 %).

Fst values between robin populations from Gran Canaria, Tenerife and the western Canary Islands plus Eu-



**Figure 5.** Pairwise mismatch distributions among (a) all individuals of European robins *Erithacus rubecula*, (b) on Gran Canaria, (c) Tenerife and (d) nominate *E. r. rubecula*. Solid lines show the observed distribution and dotted lines the expected distribution after the 'sudden expansion' model (Rogers & Harpending 1992).



**Table 3.** Fst values for three populations of European robins *Erithacus rubecula* on the Canary Islands. Significant values are indicated by \*  $P < 0.05$ , \*\*  $P < 0.01$  and \*\*\*  $P < 0.001$ .

Populations compared	Fst
Gran Canaria v. Tenerife	0.9105***
Gran Canaria v. Western Canaries/Europe	0.9278***
Tenerife v. Western Canaries/Europe	0.8960***

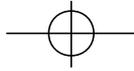
rope are all highly significant (Table 3) and indicate a very restricted gene flow between these populations (Wright 1978). But we note that one bird caught on Tenerife is genetically more closely related to the birds from Gran Canaria (cf. Figs 3 and 4). Results of the

AMOVA (not shown) gave much more support to the assumption of three groups (Tenerife, Gran Canaria and *rubecula*), which explains 89.79 % of the total variance, while the classical division into two groups (*superbus* and *rubecula*) could only explain 52.39 % of the total variance.

The pairwise mismatch distribution among all individuals of the genus *Erithacus* is clearly multimodal (Fig. 5a), indicating two classes of comparisons, within and between taxa. For the birds from Gran Canaria the pairwise mismatch distribution shows a relatively smooth and unimodal curve, as is typical for a recent range expansion (Fig. 5b; cf. Rogers 1995). The mismatch distribution for the birds from Tenerife is multimodal indicating geographic structure or population bottlenecks (Fig. 5c), but sample sizes from different

**Table 4.** Morphometric measurements of European robins *Erithacus rubecula* from the Canary Islands. Significance of variances (F) revealed by MANOVA are marked with n.s. (not significant), \* ( $P < 0.05$ ) or \*\* ( $P < 0.01$ ).

Character	La Palma			La Gomera			El Hierro			Tenerife			Gran Canaria			Fuerteventura			Sign. F
	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	
Weight [g]	15.7	0.3	3	15.7	1.1	9	15.9	0.9	13	15.2	2.7	16	15.3	0.9	11	14.8	0.1	2	**
Wing [mm]	72.5	1.5	3	71.9	2.7	9	71.1	2.6	13	68.9	4.8	16	67.5	2.2	11	71.3	0.4	2	**
P9 [mm]	45.3	1.0	3	44.8	1.5	9	45.5	2.0	12	43.3	0.4	2	41.2	1.7	10	44.3	1.1	2	**
P8 [mm]	54.5	0.5	3	53.6	2.1	9	53.8	2.1	12	52.3	0.4	2	49.5	1.5	10	54.0	1.4	2	**
P7 [mm]	57.7	0.3	3	56.9	2.1	9	57.0	1.9	12	56.0	1.4	2	53.2	1.6	10	57.3	0.4	2	**
P6 [mm]	59.3	0.6	3	58.7	2.5	9	58.0	2.1	12	58.3	2.5	2	55.0	2.0	10	58.3	0.4	2	**
P5 [mm]	59.2	0.8	3	59.2	2.2	9	58.0	1.8	12	58.8	1.8	2	55.7	2.1	10	58.3	1.1	2	*
P4 [mm]	55.2	0.3	3	55.4	1.7	9	54.7	1.9	12	57.5	1.5	2	53.3	1.9	10	54.3	1.8	2	*
P3 [mm]	53.2	0.8	3	53.7	1.6	9	52.6	1.6	12	55.0	1.4	2	51.9	1.8	10	52.8	1.1	2	n.s.
P2 [mm]	52.3	0.6	3	52.8	1.8	9	51.4	1.6	12	54.0	1.4	2	50.7	1.6	9	52.0	1.4	2	n.s.
P1 [mm]	52.3	1.0	3	52.2	1.9	9	50.9	1.7	12	53.5	0.7	2	50.1	1.5	10	51.8	1.8	2	n.s.
S1 [mm]	51.2	0.3	3	51.9	2.0	9	50.5	1.7	12	53.0	1.4	2	49.7	1.6	10	51.0	1.4	2	n.s.
Tarsus [mm]	24.4	0.8	3	24.1	0.8	9	24.4	0.9	12	24.0	0.1	2	25.3	1.0	10	24.6	0.8	2	n.s.
NaLoSpi [mm]	7.3	0.4	2	7.1	0.5	9	7.3	0.4	12	7.2	0.2	2	7.1	0.6	9	6.9	0.3	2	n.s.
Bill width [mm]	4.7	0.4	2	4.7	0.3	9	4.7	0.4	12	4.4	0.1	2	4.8	0.3	9	4.3	0.3	2	n.s.
Bill length [mm]	15.2	0.8	3	15.4	0.6	9	15.8	0.4	12	16.1	0.3	2	16.0	0.5	10	15.2	0.5	2	n.s.
Bill height [mm]	3.2	0.0	2	3.2	0.1	9	3.4	0.2	12	3.3	0.2	2	3.3	0.3	9	3.4	0.1	2	n.s.
Foot in [mm]	26.0	1.4	2	25.8	0.8	9	26.0	1.0	12	26.0	0.0	2	26.0	0.8	8	24.3	0.4	2	n.s.
Foot mid [mm]	32.5	2.1	2	32.6	1.0	9	33.0	1.3	12	33.0	1.4	2	32.3	1.3	8	30.5	0.7	2	n.s.
Foot out [mm]	27.0	1.4	2	26.4	0.9	9	27.1	0.8	12	27.0	0.0	2	26.9	0.6	8	25.5	1	n.s.	



**Table 5.** Results of the discriminant function analysis of measurements from European robins *Erithacus rubecula* on the Canary Islands. Canonical discriminant function coefficients (lines 1–3) are shown for the characters entered in the analysis (primaries (P) 4 + 8 and tarsus length).

	Function 1	Function 2	Function 3
P4	0.82071	1.19131	0.34852
P8	-1.56119	-0.49286	0.18676
Tarsus	0.82694	-0.35239	0.74861
Eigenvalues	2.3904	0.3584	0.0012
Percent variation	86.92 %	13.03 %	0.04 %
Cumulative percentage	86.92 %	99.96 %	100 %
Canonical correlation	0.8397	0.5136	0.0349

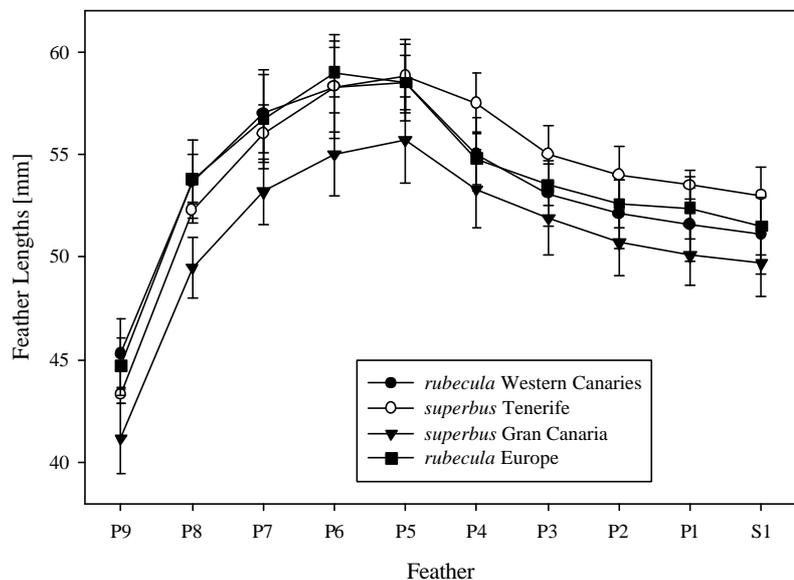
parts of the island are too small to distinguish between these options. The mismatch distribution for the nominate form is rather ragged (Fig. 5d) as is usually shown in populations in equilibrium (Zink 1997).

Statistical analysis of morphological measurements shows significant variance between populations, mainly due to differences in primary length and wingtip shape (Table 4). Average wing length increases obviously from Gran Canaria via Tenerife to the other islands but there is some overlap (Table 4). The mean length of P9 to P1 is shorter in birds on Gran Canaria than in those of Tenerife (Fig. 6). There is an obvious difference in the wing shape between birds from Gran Canaria and Tenerife as compared to those of the other islands. The former have a more rounded and convex

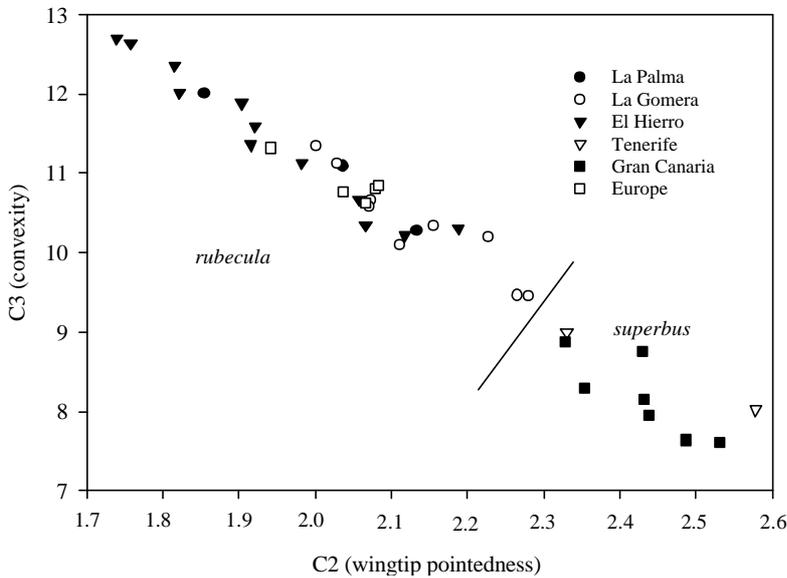
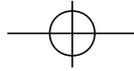
wing than the latter (Figs 6 and 7). The discriminant function analysis shows that the birds from the European mainland and the western Canary Islands are not separable but birds from Gran Canaria and Tenerife are different from each other and *rubecula*, respectively (Fig. 8). The analysis yielded three functions which explain 100 % of the variance between populations (Table 5).

## Discussion

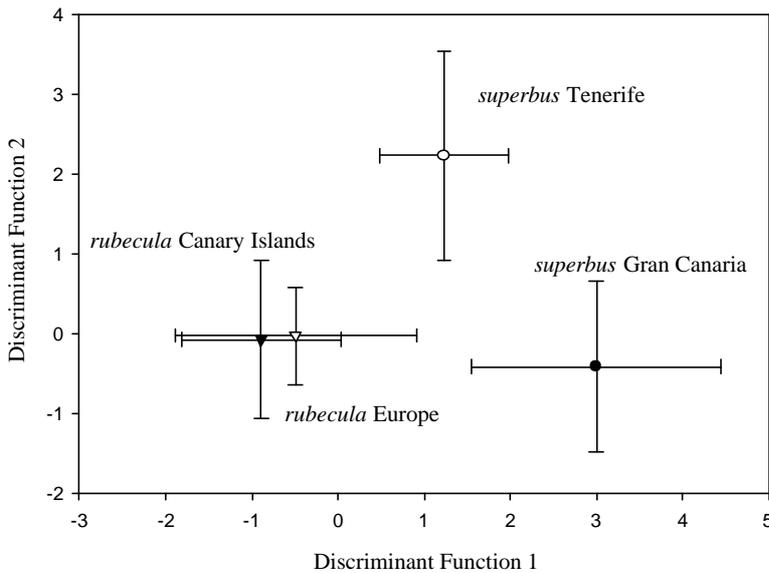
In the past, robins inhabiting the Canary Islands have been assigned to two subspecies. The birds on the westernmost islands (La Palma, El Hierro and La Gomera) were thought to belong to the nominate form *E. r. rube-*



**Figure 6.** Wing shape of European robins *Erithacus rubecula* on different Canary Islands and Europe (Portugal) based on measurements of primaries (P) 1–9 and secondary (S) 1.



**Figure 7.** Wingtip shape of European robins *Erithacus rubecula* in the Canary Islands. The two indices for characterisation of wing-shape were calculated following Lockwood et al. (1998). A decrease in C2 leads to an increase in pointedness while increasing C3 leads to an increase in convexity.

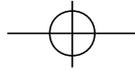


**Figure 8.** Plot of the first two of three discriminant functions for different populations of European robins *Erithacus rubecula* on the Canary Islands. The group centroids with standard deviations are shown.

*cula* (e.g. Cramp 1988) or to constitute another Macronesian subspecies together with birds from Madeira, *E. r. microrhynchus* (e.g. Hounscome 1993), while the birds from Gran Canaria and Tenerife were regarded as a subspecies of their own, *E. r. superbus* (Koenig 1890, Vaurie 1959, Cramp 1988). Recent analysis of song structure together with the distinct plumage differences led Bergmann & Schottler (2001) to propose species status for the latter taxon, the Tenerife robin, *E. superbus*.

From the genetic data it is evident that we have to distinguish between *superbus* from Gran Canaria and Te-

nerife. The former take a more basal position, while the robins from Tenerife are more closely related to *rubecula*. Robins from Gran Canaria and Tenerife show independent genetic histories in the maternally inherited mitochondrial genome and have clear morphometric differences. Assuming a molecular clock of 2% divergence for one million years (Shields & Wilson 1987) the populations on Gran Canaria and Tenerife have diverged independently from other island or European mainland populations 2.3 and 1.8 million years ago respectively. The degree of divergence between islands



increases with island age. From the genetic data it seems possible that Gran Canaria, the oldest island (15 Ma) of those inhabited by robins today, was colonised first by a common ancestor, followed by independent colonisation of Tenerife (12 Ma) by the common ancestor of the Tenerife robin and *rubecula*, while the western islands (1–10 Ma) were colonised fairly recently (c. 350 000 years ago), probably during Pleistocene glaciations. The strong similarities in colouration suggest that the common ancestor of today's robins was closer in appearance to *superbus*, and that the duller plumage of *rubecula* originated fairly late, after the colonisation of Tenerife and Gran Canaria. Another explanation, which has yet to be tested when samples from northern Africa are available, is whether the Canary Islands were colonised in two waves: the eastern islands of Tenerife and Gran Canaria from Africa and the western islands from Europe. Then Tenerife could form a contact zone between populations derived from Africa and Europe. This would also explain the higher degree of heterozygosity found on Tenerife as compared to the other islands.

Considering the results of the genetic comparisons, it is no longer tenable to regard the robins of Gran Canaria and Tenerife as one taxon (neither species nor subspecies). The pairwise genetic distances between *superbus* from Tenerife and Gran Canaria are as large as those between *rubecula* and *superbus* from either island (see Table 2). With regard to the genetic results (distance data, phylogenetic analysis) three distinct groups can be recognised: (1) *E. r. rubecula* from Europe and the western Canary Islands, (2) *E. r. superbus* from Tenerife, and

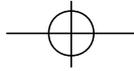
(3) *E. r. superbus* from Gran Canaria. All these groups show distinct mitochondrial cytochrome-b haplotypes and are separated by large genetic distances. Similar pairwise distances are found between good species of other closely related passerines (see Table 6). The between-group genetic distances exceed the range of 0.2–2.6 % usually assumed for subspecies and fall well within the range of good species with genetic distances of 0.5–3 % and more (Helbig et al. 1995). Although the geographical distances between the islands are small, no notable gene exchange (significant *F<sub>st</sub>* values, cf. Table 3) seems to occur between e.g. Tenerife and La Gomera. Only one bird caught on the northern slope of the Teide mountain, Tenerife, showed close affinities to the haplotype from Gran Canaria, indicating occasional migration between these islands. There are no indications for a substantial gene flow between the eastern islands. The open water between two islands works as a strong isolating barrier preventing exchange between populations.

The examination of the pairwise mismatch distributions (Fig. 5) with respect to the phylogenetic data provides evidence for a single colonisation of Gran Canaria followed by a range expansion on this island. Tenerife or its precursor islands was maybe colonised more than once, resulting in the observed multimodal distribution and the intermediate morphometric characteristics. More samples are needed to verify this hypothesis.

The results from our genetic study are in contrast to published morphological and bioacoustical analyses. In the recent literature there is no indication that *superbus* from Gran Canaria and Tenerife differ in plumage, mor-

**Table 6.** Pairwise genetic distances for closely related passerine taxa from published cytochrome-b sequence data.

Species-pair	Genetic distance [%]	Source
<i>Sitta krueperi/sedanti</i>	3.5	Pasquet (1998)
<i>Acrocephalus seychellensis/newtoni</i>	4.7	Leisler et al. (1997)
<i>Acrocephalus avicenniae/scirpaceus</i>	2.0	Leisler et al. (1997)
<i>Hippolais icterina/polyglotta</i>	6.5	Helbig & Seibold (1999)
<i>Luscinia luscinia/megarhynchos</i>	6.4	Wink et al. (2002a)
<i>Saxicola rubicola/maura</i>	4.3	Wink et al. (2002a)
<i>Phylloscopus collybita/brehmii</i>	4.2	Helbig et al. (1996)
<i>Phylloscopus collybita/canariensis</i>	3.7	Helbig et al. (1996)
<i>Phylloscopus nitidus/viridanus</i>	3.1	Helbig et al. (1995)
<i>Anthus correndera/antarcticus</i>	2.7	Voelker (1999)
<i>Anthus rubescens/japonicus</i>	3.3	Voelker (1999)
<i>Serinus citrinella/corsicana</i>	2.7	Pasquet & Thibault (1997), Sangster (2000)



phometrics or acoustics (e.g. Vaurie 1959, Cramp 1988, Martin & Lorenzo 2001, Bergmann & Schottler 2001). However, as far as we are aware, there has been no study concentrating on potential differentiation between robins of Gran Canaria and Tenerife, because all authors assumed these two populations to be conspecific. It seems possible that small differences could exist but have been overlooked due to the assumption that only one taxon is involved. However, statistical analysis of our measurements indicates morphological differences between *superbus* from Tenerife and Gran Canaria, as well as between *rubecula* and both populations of *superbus*. The *superbus* from Tenerife with relatively long primaries and rounded wings are again situated intermediately between *superbus* from Gran Canaria (short and rounded wings) and *rubecula* (long and pointed wings; cf. Figs 6–8). These characters are in line with the so called ‘island syndrome’ (e.g. shorter, more rounded wings, increased biometric variability, smaller size, wider niche occupation, change from migrant to resident populations; Hounscombe 1993) and are of little value for systematic analysis (Helbig et al. 2002). Due to small sample sizes for some island populations, we regard these results as preliminary and in need of further verification with larger sample sizes.

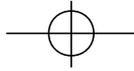
Hounscombe (1993) found a clear differentiation between *superbus* and *rubecula*. Furthermore he noted the robins from the western islands to be identical with those from Madeira and both differed from British robins. From these results he concluded the validity of *E. r. microrhynchus* as separate taxon and that Atlantic robins are different from *rubecula*. But since he did not include true *rubecula* in his analysis (British robins belong to *E. r. melophilus*) this conclusion is misleading. The Madeiran robin included here falls well into *rubecula* and there is no evidence for another taxon, i.e. *E. r. microrhynchus*, in the eastern Atlantic islands.

Our cytochrome-b sequence data, as well as the morphological information, give no indication for any obvious differentiation between *rubecula* from the western Canaries and Europe. Following this, we suggest keeping the Canary robins within nominate *rubecula* (cf. Clements 2000, Cramp 1988, Lack 1946). The data presented here indicate a relatively recent colonisation of the western islands which explains the lack of genetic and morphological differentiation. Low *F<sub>st</sub>* values (not shown) indicate some geneflow between these islands since the birds involved are probably still more

migratory than those on the eastern islands. It would be premature under any species concept to split *Erithacus* of the Canary Islands into three species as the genetic and part of the morphological data suggest. Following the Evolutionary Species Concept (ESC) we propose to treat the taxa involved as a superspecies (cf. Helbig et al. 2002). The taxa should then be named as (1) *E. [r.] rubecula* (Western Canaries, Europe and probably Azores and Madeira), (2) *E. [r.] superbus* (Tenerife) and (3) *E. [r.] ssp.* (Gran Canaria). This genetic structuring is supported by the analysis of molecular variance.

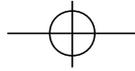
For conservationists our finding of two distinct taxa on Gran Canaria and Tenerife is quite important. Especially on the former island, the natural habitats are severely degraded and destroyed due to human activities, e.g. deforestation, lowering of groundwater table etc. This has resulted in the extinction of several taxa in the past (Johnson & Stattersfield 1990, Martin et al. 2000, Martin & Lorenzo 2001). On Gran Canaria the remaining forest cover is restricted to very few mountainous regions. The numbers and distribution of robins and other forest-dependent species (e.g. Blue chaffinch *Fringilla teydea polatzeki*) are declining (Martin & Lorenzo 2001). This endangered forest bird community certainly needs more attention from politicians and conservationists, especially on the densely populated island of Gran Canaria. This is particularly important when different evolutionary lineages are involved, as seems to be the case with the endemic robin.

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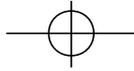


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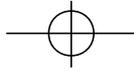
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## The ecology and evolution of crossbills *Loxia* spp: the need for a fresh look and an international research programme

Pim Edelaar<sup>1</sup>, Ron Summers<sup>2</sup> and Natalia Iovchenko<sup>3</sup>

In this paper we review how recent studies on crossbills *Loxia* spp. have dramatically changed our understanding of crossbill diversity in Europe. Instead of four separate species, each well-defined by ecology, morphology and distribution, we now can distinguish a larger number of populations that differ in vocalisations, but of which we know very little about their ecology, morphology, and (overlap in) distribution. Genetic differences between subspecies and even species are reported to be absent. We summarise the latest results as they were presented at a workshop at the 4<sup>th</sup> EOU Conference. Progress is being made to unravel some aspects of the ecology and evolution of crossbills, but new surprises keep arising. For instance, Mediterranean populations of the common crossbill are vocally more like Scottish and parrot crossbills than like common crossbills of northern Europe. We suggest and discuss avenues for further research by professionals and amateurs alike. Most importantly, the vocal identity of each individual or population should be taken into account when testing for geographical, ecological, morphological, physiological or genetic differentiation.

keywords: crossbill, calls, vocal type, cryptic biodiversity, speciation, specialisation.

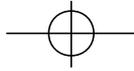
<sup>1</sup>Absveen 29, 2211 EX Noordwijkerhout, The Netherlands (graesc@sinectis.com.ar); <sup>2</sup>Royal Society for the Protection of Birds, Etive House, Beechwood Park, Inverness, IV2 3BW, UK (ron.summers@rspb.org.uk); <sup>3</sup>Biological Research Institute of St. Petersburg University, Oranienbaumskoe sh. 2, Stary Peterhoff, St. Petersburg, 198905, Russia (natalia@ni1339.spb.edu)

### From relative stability to full blown confusion

Crossbills *Loxia* spp. have always fascinated people, whether they are birdwatchers or not. With their special bill with crossed tips they can remove the seeds from closed cones of conifers as no other bird can. In some years, they appear in large numbers at locations where they normally are not found, such as treeless islands and coasts. Here they can be very tame, and many a person must have wondered what such funny birds were doing in their gardens or fields.

Their unusual feeding habits and irruptive migrations have stimulated many studies, which gradually painted a picture of specialised birds that lived by the rhythm of their food resource. When seeds became available in great numbers, they would breed, even if

this was in mid-winter with the forest under full snow cover. Even individuals in juvenile plumage would join the breeding population (Berthold & Gwinner 1972, Jardine 1994). In years that local cone crops failed, all the crossbills would leave the area in search of better feeding sites. If the crop failed over a large area, millions of crossbills would be on the move. Stragglers from the Russian boreal forest have been recorded as far as Greenland, Iceland and the Canary Islands (Cramp & Perrins 1994). The early bird taxonomists realised that three clearly different crossbills could be distinguished in Europe: the two-barred crossbill *Loxia leucoptera* with a rather small bill, the intermediate-billed common crossbill *L. curvirostra*, and the large-billed parrot crossbill *L. pytyopsittacus*. Observations of feeding birds and their general distribution indicated



that two-barred crossbills were specialised principally in feeding on the seeds of Siberian larch *Larix sibirica* which are protected by relatively weak cone scales, common crossbills attacked the cones of spruce *Picea* spp., which have fairly strong scales, and parrot crossbills fed mostly on the seeds of Scots pine *Pinus sylvestris*, which are well defended by strong scales (Lack 1944). The common crossbills in the south of Europe were an exception to this pattern, because they feed on pines, not spruce, and are also characterised by rather large bills (Cramp & Perrins 1994). Some isolated populations were recognised as separate subspecies, albeit sometimes by only slight differences in biometry and coloration (Griscom 1937).

This picture was stable for several decades, and most papers on crossbills would focus on different aspects of their biology (moult, migration, breeding etc.). A relatively recent change was the acceptance of the Scottish crossbill *L. scotica* as a fourth species, and therefore Great Britain's only endemic bird species, based on the co-occurrence of Scottish and common crossbills apparently without any hybridisation (Knox 1990).

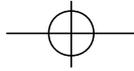
At present, however, these old 'truths' are quickly losing ground. The 'bad news' came from North America. Here a clear, stable classification of crossbill variability had not been attained until recently. Most authors agreed that several types could be distinguished (e.g. Griscom 1937), but they disagreed about their number and distribution. In fact, locations that were visited by different collectors in different years would sometimes yield crossbills that could hardly be more different in biometry. A breakthrough was achieved when the focus shifted from studying the biometry of collected birds towards the vocalisations of live birds. It was realised that eight distinct groups of crossbills could be recognised that differed in their calls (Groth 1993a). Their status as distinct groups was justified by the fact that both the flight calls and the excitement calls clustered together. On top of that, the variation in biometry was highly restricted within these so-called vocal types: some vocal types are composed of only large individuals, other types only of small ones. In addition, many vocal types were found to have widely overlapping distributions, which explained why differently sized individuals had been collected at the same localities in the past.

Such sympatric distributions and size differences among the groups suggested that the vocal types could

not be regarded as mere geographic dialects, but should be regarded as full biological species (Groth 1993a). Their specific status is supported by reports on assortative mating between the vocal types in sympatry (although hardly any quantitative data is published yet (Benkman 1993, Groth 1993a,b)).

This focus on vocalisations in America was followed up in some European studies, with surprising results. Crossbills in the Pyrenees and the Alps were found to have distinct local vocalisations, despite both being traditionally classified as belonging to the nominate subspecies of the common crossbill *L. c. curvirostra* (Clouet & Joachim 1996). In The Netherlands, the rare parrot crossbill is sometimes difficult to distinguish from some large common crossbills by sight, so an attempt was made to distinguish them on recorded calls. Besides finding a few parrot crossbills, six different vocal types of common crossbills were encountered and described (Robb 2000). In Scotland, the endemic Scottish crossbill was receiving much attention due to its status as a Globally Endangered bird (though it was recognised that data were deficient in this classification) in the IUCN Red List. In one study to determine habitat use by Scottish crossbills, crossbills were caught, measured and colour banded (Marquiss & Rae 2002). In another (initiated by the Royal Society for the Protection of Birds) crossbills were caught, measured and recorded upon release (Summers et al. 2002). Surprisingly, instead of being rare vagrants, parrot crossbills turned out to be locally common breeders. Even more surprising, three different vocal types of common crossbill were identified and described. These independent studies were in accordance with each other in that at least some of the identified vocal types were the same (see table 1). In the Dutch study, several breeding pairs were found and in each case, both members of the pair were of the same vocal type. Samples sizes were not large enough to draw firm conclusions, but this pattern was suggestive of a species status for the vocal types. If this were true, they would represent the first truly new bird species for science (not raised from lower taxonomic ranks to species) discovered in Europe for almost a century! In this respect, it would mirror the discovery of different species of bats based on their call frequencies.

The Scottish studies provided yet another surprise. An attempt to identify Scottish crossbills by genetic markers not only failed to do that, but also found that



**Table 1.** Agreement between three studies on the existence and classification of common crossbill vocal types in western Europe. Names for each type differ between the studies and types are distinguished by different criteria, but characteristic sonograms are (virtually) identical (see original papers).

Clouet & Joachim 1996 (location)	Robb 2000 (flight call)	Summers et al. 2002	
		(flight call)	(excitement call)
-	A	2	B
-	B	-	-
French Alps	C	4	E
-	D	-	-
-	E	1	A
-	F	-	-

there was no genetic differentiation between parrot and common crossbills (Piertney et al. 2001). This was despite using rapidly evolving neutral genetic markers (nuclear microsatellites and the mitochondrial control region) that normally have the power to detect such differences (and did show the two-barred crossbill to be highly distinct). Another study, including several European and North American populations of the common crossbill, found a clear genetic difference between North American and European crossbills but that there was neither genetic difference among the North American vocal types nor among the European subspecies of the common crossbill (Questiau et al. 1999).

Thus, the comfortable stability in crossbill systematics has been severely disturbed. Instead of four clear species in Europe, we now have several co-occurring 'populations' of common crossbills that do not seem to interbreed. Yet, three of the four formerly recognised crossbill species are genetically indistinguishable, suggesting high levels of hybridisation. Therefore, this situation seems to be similar to that in North American crossbills (Groth 1993a) as well as the ground finches *Geospiza* spp. of the Galapagos (Petren et al. 1999). Resolving this paradox is clearly interesting from an ecological and evolutionary point of view, and is highly relevant for the conservation of the Scottish crossbill and for other crossbill populations that were formerly not recognised as distinctive, but might be threatened. What is going on?

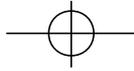
Below, we outline the main results of the workshop organised at the 4<sup>th</sup> EOU Conference by briefly discussing the presentations given (full abstracts, author affiliations, co-authors and addresses are in Die Vogelwarte

42 (2003): 113–118) and by describing the avenues for future research that were identified in the discussions.

## Results

### Old problems potentially resolved but new surprises abound

Ian Newton revisited his earlier analysis of recoveries of crossbills ringed in western Europe. Some authors regard the massive invasions of crossbills from Russia and Fennoscandia to western Europe as largely suicidal. Others suggested, based on numbers and directions of migrating crossbills, that birds arriving in western Europe in summer do return but do so within a few months. Ian Newton showed that all recoveries of crossbills within the same year are within western Europe, although sometimes quite far from the place of ringing. In stark contrast, 11 recoveries in subsequent years during the breeding season (January–April) were all in north-western Russia and there was an additional recovery even from southern Russia. This not only shows that (at least some of) the birds of invasions return to Russia to breed, but also that birds wait until the next crop is produced in that region. Indeed, if invasions are triggered by food shortage when the cone crop fails, it makes little sense to return to the same area in the same year since the food situation will not change until the next cohort of cones has been produced. Instead, crossbills flee the scene, and wait somewhere else. If they happen to arrive in western Europe at a site with a good cone production, they will stay and even breed. How-



ever, the core distribution of crossbills that occur in western Europe during large invasions seems to be in Russia, west of the Ural Mountains.

Natalia Iovchenko presented results on the annual cycle of the common crossbill. Experimental and field studies show that post-breeding movements are an inherent seasonal event. They generally start in May and function to find sites available for wintering and future breeding. Field observations, captures and some recaptures show that in years with a good new crop, a breeding population is formed by autumn, before the main phase of moult. In years with a poor new cone crop, post-breeding movements are extended in time and acquire the character of invasions. This variation in movements reflects on the moult. Few passerines have such a confusing moult as crossbills, with sometimes up to three generations of feathers present, or feathers of different colours (Noskov & Smirnov 1990a, Jenni & Winkler 1994). The first (spring) stage of post-breeding moult (started in experiments about 4 months after photostimulation and in nature generally in late April–May) is inhibited or interrupted by increasing day-length. The extent and rate of the main phase (August–November) are under photoperiodic control (Noskov & Smirnov 1990a), but can be complicated by the effects of local food availability and the possibility to breed or the need to move. This has the effect that large variation among individuals and among years can be found in moult patterns.

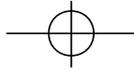
Natalia Iovchenko also demonstrated an example of population variation in moult in the common crossbill. In the subspecies *L. c. tianshanica* from the Tian Shan Mountains in Central Asia, breeding occurs in late summer when the seeds of Schrenk spruce *Picea schrenkiana* ripen (Kovshar 1976). Since this is also the usual time of moult, this creates a dilemma. Examination of study skins showed that many breeding females and males with large testes were in active or suspended primary moult. Others might moult directly after the young fledge and before the onset of winter. Many juveniles did not show a post-fledging moult until the next autumn, and can thus commonly be found to breed in juvenile plumage. These results suggest that, despite a clear flexibility in adjusting features of the annual cycle, ecological specialisation might result in characteristic moult patterns that could be used to distinguish between ecologically differentiated populations occurring in other areas.

Bob Dawson showed the results of a time-lapse video system able to record both day and night at a parrot crossbill nest. It provided unprecedented detailed data on the breeding biology of crossbills, e.g. that feeding visits by parents become increasingly spaced in time, that the female stops incubating the chicks at night at the end of the nestling phase, and that night disturbances by (potential) predators can be a cause for desertion.

Ron Summers presented data on the timing of breeding in a Scottish forest that consists only of Scots pine. This pine species keeps its seeds in closed cones until spring. Parrot and Scottish crossbills with their big bills can already access these seeds early in the year, and can be found to breed in February and March. Common crossbills, with their smaller bills, cannot access the seeds until later in spring, when the sun heats the cones and the scales start to separate, making the seeds readily available. Thus, common crossbills only breed in Scots pine forest in April and May. Differences in bill size thus create ecological differentiation, but it might also create pre-zygotic reproductive isolation between crossbill taxa by causing them to separate their reproduction not in space (allopatry) but in time (allochrony).

Daniel Alonso showed the results of a large comparative study of biometric differences between crossbills from the north, east and south of Spain and the Balearic Islands. The latter site has a distinct race *L. c. balearica*. Significant differences were observed between several populations in a number of traits. Birds from the east of Spain resembled birds of the Balearic Islands, even though taxonomically all crossbills from mainland Spain belong to the nominate subspecies. Since Balearic and eastern birds eat seeds of Aleppo pine *P. halepensis* whereas those in the north use other pines, these biometric differences might well reflect ecological differences between the populations involved.

Paul-Christophe Schroder showed that the Balearic birds seem to be genetically differentiated from mainland birds in microsatellite variants and frequencies. This is in agreement with the subspecific status of the Balearic birds, but contrasts with the earlier genetic studies that did not detect genetic differences even at the species level. It is clear that more studies with sufficiently large sample sizes are needed to clarify the genetic relationships among crossbill populations and species.



Pim Edelaar presented results bearing on some of the unknowns of the vocal types recorded in western Europe. Large numbers of crossbills were caught by two different amateur bird ringers at two different locations. Both observers caught individuals of four vocal types (including two types not described before!), and their measures show significant differences in bill depth between the types. These differences are real, since the patterns were almost identical in males and females, and for both observers. This shows that small bill size differences do exist between the vocal types, which indicates that they could be ecologically different too (i.e. utilise seeds of different conifers). However, it is also clear that these average differences are small (about 0.2 mm) whereas the measurement difference between observers is greater! Comparing crossbill biometry between studies conducted by different observers is therefore highly problematic when dealing with such small differences between crossbill populations.

Pim Edelaar also showed that the anecdotal evidence for assortative mating between the vocal types was firmly upheld in a larger study. Within the same small geographical area, 25 breeding pairs of crossbills were found. Despite clear geographic overlap in the breeding of the four vocal types, no mixed pairs were observed. While not all alternative explanations can be refuted at this stage, this pattern is highly similar to the North American situation where several ecologically differentiated vocal types can be found breeding sympatrically without much interbreeding, and which seem to represent incipient species if not full species.

David Jardine presented evidence that while the difference in biometry between crossbill populations and vocal types presented by Alonso and Edelaar suggests ecological specialisation, the importance of ecological specialisation might also be gleaned from the comparison of vocalisations. Currently, the Mediterranean populations and subspecies are classified as common crossbills. One would therefore expect that these populations would have vocalisations that are similar to common crossbills of northern Europe, or perhaps have unique vocalisations if isolation has been strong enough (especially for the subspecies living on islands). In fact, vocalisations of crossbills from North Africa, the Balearic Islands, Cyprus and the Pyrenees were found to be rather similar to the vocalisations of the supposedly less related parrot and Scottish crossbills from northern Europe! Since these two species and the Mediterranean

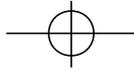
crossbill populations share their utilisation of pine (not spruce such as the northern common crossbills), two explanations are possible. Either feeding on pine selects for bigger bills, and this morphology influences the vocalisations, or the pine crossbills of northern and southern Europe are in fact more closely related to each other than to the northern common crossbill. This scenario has been published before based on crossbill fossil evidence and the palaeobiogeography of conifers (Tyrberg 1991), but would call for a remarkable change in crossbill taxonomy. There would also be a need to find the new geographical delineation of the common crossbill (if such a border – or even a single species of common crossbill – indeed exists).

Bob Dawson closed the presentations by showing how one can make sonograms of recordings. Using a crested tit recorded the day before, he showed how a tape recording can be transformed into a picture of the call with a few mouse clicks. All the necessary software can be downloaded free from the Internet, and relatively simple and cheap recording equipment suffices to obtain recordings that can be used for a serious study. When it comes down to crossbills, there is no more need for binoculars or a telescope, just a recorder and a computer.

## Discussion

### Suggestions for future research by professionals and amateurs in Europe

The results presented at the workshop support the earlier studies reporting previously unrecognised crossbill diversity, and suggested ways of resolving and understanding the ecology and evolution of this diversity. For instance, is the parrot crossbill really a separate species, or is there more hybridisation going on than previously realised? Or, was this taxon perhaps justifiably recognised and described, and are there many more crossbill populations that deserve the same specific status? Given that studies in North America show a strong ecological specialisation of the vocal types (Benkman 1993, 2003), the ecological requirements of the European vocal types clearly also need investigation. This is especially pertinent if the vocal types are found to be widely sympatric yet reproductively isolated, as data suggest they are.



This ecological differentiation might be gleaned from biometric differences between populations, as even tiny differences in bill depth have been shown to have dramatic effects on feeding efficiency and survival (Benkman 2003). However, identical measurement of e.g. bill depth by several observers or by the same observer between years or areas might not be easy. This problem is not specific to the study of crossbills but, given the small degree of differentiation (sometimes less than 2%), additional sources of variation become acutely important. These sources might not even be just observer effects, but could be changes in the bills themselves by growth and wear, or differential development. A number of experiments could be performed in order to test if, for example, use of a conifer with weak or strong cone scales results in different development or wear of the bill, and which bill measures are most affected by this. These should include breeding experiments that determine the extent of the heritable component of the total variation that we see in the wild.

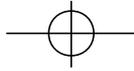
Some suggestions to cope with the problem of observer bias were brought forward at the workshop: reduction of the number of people that measure plus calibration between observers, calibration of different measuring sessions by a single observer using a number of practise study skins, or photographing bills in a standard way for simultaneous measurement of all bills later. It would be worthwhile to conduct a study where each of these methods is tested simultaneously on the same set of birds, in order to determine whether they yield good results in dealing with the observer effect.

Instead of deriving ecological differentiation from biometric differences between populations, ecological differentiation can be studied directly in the field by observing in which conifer species birds are feeding, as done previously for the four crossbill species in Europe (Lack 1944, Marquiss & Rae 2002). Virtually no data on ecological differentiation between the European vocal types exists, but one member of the audience mentioned that in the same general area he found one vocal type mostly in Scots pine while another used mostly Norway spruce. Even though this does not mean that these two vocal types are specialised on these two resources, it does indicate that while both resources were equally available at the same time to these birds, they chose to use them differentially.

Recording ecological specialisation by noting which trees are utilised is confounded by the fact that cross-

bills will prefer trees that have good seed availability. Thus, both parrot and two-barred crossbills might be found feeding on larch if it has a high density of opening cones. When seed availability drops, all crossbills might shift from one conifer species to the next. However, we might observe at least some degree of differentiation of the species/vocal types if they shift at different times or to different conifer species. Such studies could be performed everywhere where crossbills and several conifer species with a cone crop are present at the same time. If the bills differ enough between the crossbills present to have an ecological effect, we should at least sometimes see such different timing of shift or most commonly used conifer species.

It will be more difficult to identify if and to which ecological circumstances the populations have adapted over evolutionary time. This most likely has to be performed in the natural habitat (although specifically designed feeding trials in the laboratory with suspected key resources may also be able to resolve this). Paradoxically, far fewer conifer species are known from the range of the common crossbill than the number of recognised vocal types. Several explanations are possible. Perhaps the vocal types are not specialised at all, but represent cultural differences in vocalisations that arose for reasons unrelated to ecological circumstances, e.g. in stable family groups (the calls are reportedly not genetically inherited but learned from adults, as in many other passerines; e.g. Beecher 1996). Another possibility is that these populations are not specialised on a particular conifer species, but on geographic variants. This has been observed in North America, where two types of crossbill are specialised on local varieties of lodgepole pine *Pinus contorta* that differ in cone structure due to the presence/absence of red squirrels *Tamiasciurus hudsonicus* (Benkman et al. 2001). Perhaps Norway spruce and Scots pine differ enough in relevant cone and seed traits over the range of the common crossbill to favour the evolution of specialised populations. This would predict that the distribution of the different vocal types and species would similarly differ geographically, except in situations of crop failure. Yet another alternative is that each population is not specialised to a particular species or variety of conifer, but to a mix of conifers. This hypothesis is even more difficult to test, although a quantitative description of habitat and resource use over a longer time period would be one way to approach this. A final, perhaps even more spe-



culative but highly intriguing hypothesis is that the vocal types are specialising on the many introduced species of conifer, such as Douglas fir *Pseudotsuga menziesii*, Sitka spruce *Picea sitchensis* and lodgepole pine. This hypothesis has been forwarded to explain the smaller bill of Scottish crossbills relative to parrot crossbills (Marquiss & Rae 2002), but might be applicable in a more general sense. Since these conifers are known to support specialised crossbill populations in North America, it is not inconceivable that large-scale planting of these new resources in Europe will be followed by colonisation and specialisation by European crossbills as well.

Crossbills are highly dispersive (at least in the boreal range) and occur naturally in forests not visited often by ornithologists. So perhaps the application of other techniques such as stable isotopes might be able to show that birds of different vocal type in the same invasion come from different areas or have used different resources. Other clues that would support such a different geographical/ecological background would be a difference in aspects of the yearly cycle, such as moult patterns, temporal patterns of fat storage, migration and breeding, proportions of juveniles, etc. (for examples see Noskov & Smirnov 1990a,b, Marquiss & Rae 2002).

In studying the biometric, ecological and geographic differences of crossbill species and populations, it is highly relevant to give a primary role to vocalisations. While it is not completely clear if and how all the different populations can be identified using vocalisations, it is increasingly clear that ignoring the different kinds of crossbills that can be recognised at a single location could seriously mix up vital data (similar to counting roosting waders or migrating passerines but not differentiate between the many species involved). Differences in biometry or ecology between sites or years might then reflect different proportions of the composite populations. Currently extensive recording of calls happens far too little, but there simply is no alternative.

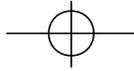
However, a lot of additional work is needed to determine if and how we can recognise discrete populations of crossbills by distinct vocalisations without (much) overlap. Studying sonograms may seem less enjoyable than studying the behaviour or plumage of birds through binoculars, but the rewards will be great with every step of clarification. It probably takes a profes-

sional, computerised, statistical approach to test objectively for discrete classes in crossbill vocalisations, but amateurs could contribute significantly by collecting vocalisations from all the corners of the continent and making them accessible (e.g. through the web). It would also be interesting to find very old (published or unpublished) recordings, in order to test how much these vocalisations have changed over the years.

How exactly these differences in vocalisations have evolved is a complex subject, but existing data sets might shed some light on this. If size differences between and within species and vocal types are correlated to features of the vocalisations (such as mean or maximum frequency), then vocal differentiation might be a by-product of (naturally selected) size differentiation. However, if such a correlation is absent, there might have been direct (sexual) selection on the vocalisations that has led to their differentiation.

One assumption of using the vocalisations as a grouping criterion is that they are stable within an individual's lifetime. Since the calls are presumably not genetically determined but learned from other individuals (Groth 1993a), this might not be true. This assumption of call stability is supported by the finding that there are biometric differences between the vocal types and anecdotal evidence from captive birds and re-recorded colour-ringed birds, but better tests would be welcome. Anybody keeping captive crossbills could test for call stability over the years, e.g. when housed with other crossbill types or when only individuals of a different vocal type or species are available as a breeding partner.

Genetic relationships between populations and even species are badly resolved, and much work needs to be done here. It is clear that, in some cases, no large differences are present, but especially for populations that are more resident it might be possible to achieve a better resolution, especially if sample sizes are sufficiently large. There might also be scope for different markers such as AFLPs, which have given good results in some formerly unresolved species-complexes. Again, it will be necessary not to lump all individuals from a particular location, but to know the vocalisations of each and every individual included in the genetic analyses. Bird ringers are in a good position to collect such data on biometry, moult, breeding and migratory physiology, vocalisations and genetics (blood or feather sample) as well as working on ring recoveries that shed light on movements of the different populations.



Such genetic differences would be expected if the vocal types/species are evolutionarily independent, and interbreeding is rare. So far, this seems supported by the data on assortative mating with respect to vocal type, but many more data on assortative mating (also between other vocal types) are needed for better estimates of interbreeding. Recording both male and female of a pair of crossbills seen mate guarding, courtship feeding, or at a nest, would yield a valuable contributing data point. After fledging, however, unrelated adult crossbills might join feeding families, so a pair bond cannot be reliably assumed between a male and a female in that situation.

Despite the need to resolve the genetic relationships between crossbill populations, genetic differentiation could turn out to be negligible or absent even when hybridisation no longer occurs. Population differentiation of neutral genetic markers depends on mutations and changes in marker frequencies by chance. This process takes a long time, and is slowed down if populations are large and internally well mixed. Crossbill populations are probably large and well mixed, and above all some discrete populations might have evolved rather recently (in the last 15,000 years or less, perhaps even in the last 200 years). Therefore, such differentiation might be most useful in older, smaller and more resident populations.

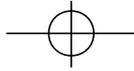
The Mediterranean crossbills are a clear example where an integrated approach combining ecology, vocalisations and genetics is both needed and expected to be successful. Here, crossbills have been found to be fairly resident. Up to four different conifer species occur in the area that are all known to be able to support a resident crossbill population (mountain pine *P. uncinata/mugo*, Scots pine, black pine *P. nigra/laricio* and Aleppo pine). Yet, most research so far has lumped all crossbills from particular geographic localities followed by subsequent comparison of biometry between localities, and this has yielded little insight. Instead, we propose that crossbills are caught and measured in different habitats and their vocalisations recorded upon release. Genetic, biometric and vocal comparison between locations and taking habitat into account, might reveal that several crossbill populations are specialising on these very different resources at any one location. Genetic and vocal population structure could indicate if these populations evolved locally, or if they have large geographic distributions suggesting an allopatric ori-

gin. Vocal and biometric differences are already reported for crossbills in different habitats in Spain, and we look forward to seeing the next results.

Despite decades of study, recent findings are uncovering new dimensions in crossbill biology that were unforeseen a few years ago. Any enthusiastic person or group of people can contribute significantly to answering the many questions that remain unanswered. Some of these will be hard to tackle and might be left for professionals with more time and resources available. But several simple projects are possible for the dedicated amateur. Currently, very little is known about crossbills in south-eastern Europe, but it is clear that even in countries such as The Netherlands and Great Britain (perhaps the best studied countries in the world ornithologically) big surprises and achievements lie ahead.

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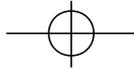
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Revision accepted: 2003



## S.2: Wesolowski: I=polnisches I (mit Querstrich)

# Minutes of the EOU General Meeting 2003

## Wolfgang Fiedler (EOU Secretary)

About 80 members attended the General Meeting, which was held during the 4<sup>th</sup> EOU conference on 18 August 2003, 11:30–12:40 hrs in Chemnitz, Germany.

### 1. Minutes of the last General Meeting

The minutes of the last General Meeting, held 2001 in Groningen during the 3<sup>rd</sup> EOU Conference, are accessible on the EOU website and were accepted by the assembly.

### 2. Report of the President

The President of the EOU, Jacques Blondel, gave an overview of the situation of the EOU and current problems with budget and memberships. These problems mainly arise from a lack of interest among European ornithologists (except Swiss and German ornithologists) in joining the EOU as members. As a consequence the anticipated and much-needed income from membership fees has not yet been reached (for details see the report of the Treasurer). The present number of countries with EOU members is 42 (31 European and 11 non-European), but only 12 of them include more than 10 members.

Jacques Blondel gave cordial thanks to the Ala (Schweizerische Gesellschaft für Vogelkunde und Vogelschutz) and the Swiss Ornithological Institute (Vogelwarte Sempach) for their financial support in maintaining the journal 'Avian Science' and the EOU Membership Bureau. The President also thanked the organisers of the 4<sup>th</sup> EOU Conference in Chemnitz and everybody who contributed to the conference and to the EOU in general.

### 3. Report of the Secretary

Wolfgang Fiedler, Secretary of the EOU, had had his main task in organising the conference and gave a brief report about it. Preparations for the 4<sup>th</sup> EOU Confer-

ence were carried out together with the local organising team from the Society of Saxonian Ornithologists (VSO), headed by Hartmut Meyer, and in close cooperation with the Scientific Programme Committee, chaired by Liz Pasztor. Altogether 317 contributions were scheduled (6 plenary talks, 15 symposia with 117 oral contributions, 5 workshops and round table discussions, 25 orally contributed papers, 114 posters and 5 films). The number of delegates was around 320.

### 4. Report of the Editor

The report of the Editor of 'Avian Science' was presented by the Acting Editor Beat Naef-Daenzer on behalf of Peter Jones, who was not able to join the assembly due to fieldwork in Africa. The written report of the Editor is accessible on the EOU homepage.

### 5. Report of the Treasurer

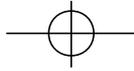
Lukas Jenni gave his report as Treasurer. This report is also available on the EOU homepage.

### 6. Report of the Auditors

The auditors Reinhard Mache and Helmut Sternberg had checked the financial accounting and found it to be balanced and well kept. The financial report was accepted by the meeting with no votes against and 1 abstention.

### 7. Programme and budget of the EOU

Lukas Jenni reported on the programme and budget for the EOU for the coming years. The main problem still is a membership rate that is far too low to maintain the



budget (see also topic 9 and Treasurer's report). The full version of this report is available at the EOU homepage.

## 8. Elections to the Council

In accordance with the statutes, Jacques Blondel stepped down after 4 years of presidency and Liz Pasztor, Hungary, advanced from President-Elect to the office of the EOU President. Jeremy Greenwood (UK) was elected unanimously (1 abstention) to be the new Vice President (at the same time President-Elect) of the EOU.

In accordance with the statutes half of the ordinary members of the Council also stepped down. These were Casimir Bolshakov (Russia), Anton Krištin (Slovakia), Erik Matthysen (Belgium), Eulalia Moreno (Spain) and Arie van Noordwijk (The Netherlands).

The following new members of the Council were elected unanimously: Indrikis Krams (Latvia), Anvar B. Kerimov (Russia), Kate Lessells (The Netherlands), Karel Weidinger (Czech Republic), Emilio Barba (Spain) and Bruno Faivre (France). The composition of the EOU Council for the period 2003–2005, including contact addresses, can be accessed at the EOU homepage.

## 9. The future of the EOU and 'Avian Science'

A crisis plan for the EOU was proposed by Council and discussed in the General Meeting. The main points were:

A steering committee of active and former Editorial Board and Council members will contact publishing houses immediately to see if they are interested in publishing 'Avian Science'. It appears that purely commercial publishers have problems in getting good referees and good submissions for average level journals. Journals from societies seem to do better here. Therefore, publishers might be interested in acquiring society-based journals and sell them as part of their packages, particularly to libraries. In any negotiations, a change of the general style of the journal to cover more 'Trends in Ornithology' will be taken into account.

If these negotiations with publishing houses fail, or if important decisions have to be made before contracting with any publisher, an electronic poll by e-mail will be organised.

A level of 800 members would be enough to maintain

the journal, but this aim seems unrealistic to be reached in the near future after all experiences so far. Therefore, if no other solutions can be found soon, 'Avian Science' may be stopped after one last issue that will contain mainly the proceedings from the Chemnitz conference.

The delegates voted for this strategy unanimously (3 abstentions).

A Newsletter will be edited by council members and other volunteers and distributed electronically. All EOU members are strongly encouraged to contribute to this.

## 10. EOU Conference in 2005

The next EOU conference will be held in August 2005 in France, most probably in Strasbourg. The invitation is jointly issued by the French Ornithological Society, the 'Ligue pour la Protection des Oiseaux' and the 'Office National de la Chasse et de la Faune Sauvage'.

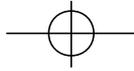
## 11. Any other business

a) Liz Pasztor organized a poll among participants of the EOU conference. In response to the question 'Are you a member of the EOU?' 23 people said Yes and 11 said No (with 2 of the latter saying they would join). Main reasons nominated for joining the EOU were the 'European idea' (11), the conferences (7) and the journal (4). Those who are not EOU members justified this with 'only first contact with EOU at this conference' (4), membership in other societies (2), avoidance of getting another journal (2) and costs (1).

b) The audience unanimously adopted a resolution concerning the preservation of the Bialowieza Primeval Forest in Poland. The initiative for the resolution came from Tomasz Wesolowski who also gave a short introduction into the problem. The text of the resolution is attached to these minutes.

### Resolution of European Ornithologists' Union concerning the preservation of the Bialowieza Primeval Forest (Poland)

The Bialowieza Primeval Forest in Poland is the last relic of a pristine European lowland forest. It provides a window to the past and remains a peerless template for forest restoration in Europe. Scientific research conducted in the forest has yielded nearly 4,000 scientific



publications and demonstrates the value of the Bialowieza Forest as a unique reference point.

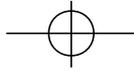
In the Bialowieza Primeval Forest, different forest types and high structural diversity result in an exceptional species richness. More than 5,500 plant species have been recorded. By the end of 2001, the corresponding count of animals was 11,564 species. The list of mammals includes wolf, lynx and the European bison (Wisent). The forests bird communities are characterized by rare species of woodpeckers, owls and hole-nesting songbirds that depend on old growth and standing dead trees.

Protection of the Bialowieza Forest dates back to the sixteenth century. In 1921 the Polish Forest Service established a preserve that subsequently became the Bialowieski National Park. This park was included in the list of World Biosphere Reserves in 1977 and became a UNESCO World Heritage site in 1979. In 1996 the area of the National Park was doubled to its current size of 10,500 ha. This comprises only about 18 % of the total Bialowieza Forest area in Poland, leaving 82 % still open to forestry activities.

The European Ornithologists' Union urges the Polish government to halt further logging of old growth and

conversion of relict stands to commercial plantations in the Bialowieza Forest. A strong decline in species that are dependent on old growth and standing dead wood has already been documented. There is no plausible justification for sacrificing this invaluable wilderness for narrow interests of one human generation. The remaining primeval forest warrants strict protection. Suitable means for protection include expanding the National Park and listing the forest as a 'Natura 2000' reserve.

The European Ornithologists' Union urges the EU Commission and national governments to express their desire for protection of the Bialowieza Forest as a unique component of European cultural heritage and an irreplaceable biological treasure. Both the EU and European governments are challenged to help provide the means for the Bialowieza Forest to become a model for the successful implementation of nature conservation and the development of local communities. This will require a shift of economic activities from the current timber-dependent industry to a diverse economy, one compatible with the maintenance of vital ecological processes, levels of biological diversity, continued existence of endemic and threatened species, and a sustainable standard of living for human communities.



## Birds in urban landscapes

Jeremy Greenwood<sup>1</sup> and Dan Chamberlain<sup>2</sup>

A review is presented of the 13 presentations given in the symposium on Birds and Urban Landscapes at the Chemnitz meeting. These covered general principles, habitat relationships, the importance of gardens for farmland species in winter, predation, a quantitative population study, a declining house sparrow *Passer domesticus* population, wildfowl, and differences in migration between urban and forest blackbirds *Turdus merula*.

Key words: Urban birds, gardens, farmland birds, migration, landscape, habitat.

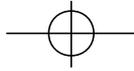
<sup>1</sup>British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK; <sup>2</sup>BTO Scotland, School of Biological & Environmental Sciences, Cottrell Building, University of Stirling, Stirling FK9 4LA, UK. Corresponding author: jeremy.greenwood@bto.org

Naturalists have a long-standing prejudice against studying the ecology of those landscapes most obviously affected by man, preferring to work in those that appear more natural. Even the realisation that few, if any, places on the earth's surface (or even under the sea) are truly pristine and the acceptance that ecological principles apply equally to human-dominated ecosystems have done little to change this bias. Recently, however, ornithologists and others have begun to turn their attention to urban ecology (Marzluff et al. 2001). It is important that they do so, for the extent of urban areas is increasing in all parts of the world, at the expense of natural and semi-natural habitats, and the main contact that many citizens have with wildlife is in built-up areas (Cannon 1999). This contact may provide much enjoyment, judging from the fact that UK citizens spend £120–130 million p.a. on providing food and other resources for birds in their gardens. The symposium on Birds and Urban Landscapes, held during the 2003 EOU Conference, brought together a number of those currently working on urban birds.

The six oral presentations and seven associated posters covered a wide variety of topics and it will require much further work for many general principles to be established. However, Ludwig Tomialoc (Wrocław, PL) began the symposium by considering general ideas about the establishment of urban bird populations seen as a 'natural experiment'. He suggested that it is useful to think of two phases in such establishment: colonisa-

tion and 'synurbisation', the latter being the phase when the birds are actually adapting to city life rather than merely managing to live in cities. Such adaptations apply to individual birds, to populations and to communities. He pointed out that the colonisation phase could involve two different sorts of event: some species, especially smaller ones, may persist as relict populations in pockets of effectively rural habitat remaining in cities; others may invade the city from other habitats (some species may do both).

Tomialojc pointed out that, whatever the general principles, the details will differ according to a wide variety of factors. This was exemplified clearly in the poster of Klaus Witt (Berlin (DE), with Alexander Mitschke and Maciej Luniak), which contrasted the avifaunas of Hamburg, Berlin and Warsaw. These three cities are comparable in area, human population and extent of their heavily built-up areas; they differ in the extent of more natural habitats and in climate. They also differ greatly in their bird communities: species breeding in bushes or trees are more abundant in Hamburg, those breeding on buildings being more abundant in Warsaw, with Berlin being intermediate in most cases. For example, blackbirds *Turdus merula* were 20 times more abundant in Hamburg than Warsaw, but jackdaws *Corvus monedula* were 45 times more abundant in Warsaw than Hamburg. It is not clear whether this is because of the climatic or of the habitat differences.



The importance of habitat on bird communities was taken up by Christopher Lepczyk (Wisconsin, USA), with Volker Radeloff, Curtis Flather and Jiango Liu. Using data for 12 species in the Midwest USA, they found that species diversity declined monotonically with human housing density, in contrast to studies in Europe (Araújo 2003) and Africa (Chown et al. 2003), though the correlation was weak. They found a much stronger negative correlation of species diversity with human-influenced land-cover, though their definition of such cover included farmland, so the result may not be directly relevant to urbanisation. Not surprisingly, the different species reacted differently to these human influences, though, contrary to expectation, the differences did not appear to depend on either foraging or nesting guild.

In contrast to these broad-scale studies, Andrew Cannon (Sheffield, UK) presented results from an intensive investigation of a single area of high-density housing, where the birds are generally dependent on small gardens. The density of birds in this area was, not surprisingly, at the lower end of the spectrum recorded in other studies of urban birds, with over a quarter of the biomass (and one-third of the energy flux) of breeding adults dependent on just one species, the blackbird. There were no obvious patterns in bird distribution in relation to broad-scale habitat variables such as vegetation cover or garden size. As in most areas in Britain, the human inhabitants tend to feed the birds in the gardens well: there are as many people actively providing food as there are birds in the study area. On the debit side, cats outnumber breeding birds in the area by about 50 %.

Green spaces of various sorts can be important for city birds. Danka Némethová (Bratislava, SK), with L'udovit Kocien, Dana Melicherová and Adriana Matušková, assessed the breeding bird communities in three cemeteries (of 6, 16 and 18 ha) in Bratislava, finding total densities of 3–15 breeding pairs/ha. Their poster showed clearly that the abundance of individual species depended on the habitats available in each area.

As bird populations have declined in the farmland that makes up the major part of the landscape in western Europe (Donald et al. 2001), and the extent to which people feed birds in their gardens has grown, bird-watchers have been wondering how important gardens may be as refuges for farmland birds. This question was addressed by Dan Chamberlain (British Trust for Ornithology, UK), with Juliet Vickery and David Glue,

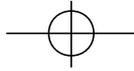
using counts made over 30 years in about 200 gardens per year. They focused on granivorous species, which have fared particularly badly on British farmland. It is clear from the data that many of these species have increased their use of gardens, often coming into gardens earlier in the winter than they did in the past, but this was the case for several non-granivorous species as well. However, there were some intriguing patterns shown by yellowhammers *Emberiza citrinella* and reed buntings *E. schoeniclus*, where initial increases in gardens closely matched decreases in population size in the wider countryside.

Several contributors took a narrower focus than the community-based approaches described above. The poster of Darius Wysocki (Szczecin, PL) described the effects of predation by red squirrels *Sciurus vulgaris* on the breeding success of urban blackbirds in two city parks. In years when one park had no squirrels, blackbirds produced four times as many fledged young per pair than in the park that had squirrels; and after a squirrel arrived in the formerly squirrel-free park, breeding success was significantly lower in the parts over which the squirrel ranged than in the rest of the park.

A behavioural focus was provided by Jesko Partecke (Andechs, DE) and Eberhard Gwinner, who have investigated differences in migratory disposition of urban and forest blackbirds. Urban birds were already known to have a lesser migration tendency than forest birds. Using hand-reared birds, Partecke and Gwinner found that the heritability of migratory fattening in the first year of life was high. However, such heritability was not apparent in the second year and the heritability of migrating activity was low even in the first year, suggesting that the differences between rural and urban birds depend on environmental factors as well as genetic differences. As a further complication, some of the differences were sex-specific.

The focus of Kate Vincent (Leicester, UK), with Will Peach and Jim Fowler, was on a single species, the house sparrow *Passer domesticus*, particularly into the causes of its decline in Britain. She had worked on an urban-suburban-rural gradient and found that foraging sites were different along this. She suggested that breeding productivity in suburban areas may be limited by the availability of key invertebrate food, finding evidence of starvation of chicks in the nests in late summer.

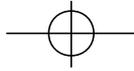
Wildfowl tend to be neglected by students of urban birds. However, they were covered in four linked pos-



ters by Ksenia Avilova (Moscow, RU), with Anastasia Popovkina and Grigori Eremkin. Over 5 years in the Moscow region (1000 km<sup>2</sup>), 11 species (6–9 of them breeding) occurred in summer and 19 in winter. Mallards *Anas platyrhynchos* have increased as the expanding urban areas have included appropriate seminatural habitats, as have introduced populations of ruddy shelduck *Tadorna ferruginea* and goldeneye *Bucephala clangula*, though teal *Anas crecca* have decreased. The ruddy shelduck population is some 800 km northwest of the species' natural range in Russia and, although the birds disperse around the city to breed, they return in winter to the zoo, the site of their original introduction 55 years ago.

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## Fuelling rates of garganey *Anas querquedula* staging in the Camargue, southern France, during spring migration

Matthieu Guillemain<sup>1</sup>, Hervé Fritz<sup>2</sup>, Marcel Klaassen<sup>3</sup>,  
Alan R. Johnson<sup>4</sup> and Heinz Hafner<sup>4</sup>

Most species of long-distance migratory birds put on energy stores to fuel their travels. However, recent studies have highlighted the potential costs associated with carrying too much fuel, either through increased predation risk or decreased flight efficiency. Consequently, it is now widely accepted that migratory birds should carry optimal rather than maximum fuel loads. Information from 372 garganey *Anas querquedula* ringed and recaptured at least once during the same spring in the Camargue, southern France, was used to document fuelling rates of individual ducks in relation to environmental variation and individual variation in condition. On average, garganey added very little fuel stores in the Camargue (mean gain per day = 0.33 g, less than 2 % of mean body-mass over an average stay of 5 days). Fuelling rates were negatively correlated with body mass at capture, but it cannot be excluded that this pattern was a statistical artefact. Given their body-mass at ringing, garganey could potentially still fly long distances when they stop in the Camargue. It is therefore likely that the aim of their stay in southern France is more for resting than refuelling, which may be implications for the proper management of stop-over sites.

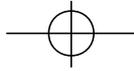
Key-words: Migration, fuelling rates, body condition, garganey, *Anas querquedula*, Camargue.

<sup>1</sup>Office National de la Chasse et de la Faune Sauvage, CNERA Avifaune Migratrice, La Tour du Valat, Le Sambuc, 13200 Arles, France; <sup>2</sup>Centre d'Etudes Biologiques de Chizé, CNRS-UPR 1934, 79360 Beauvoir sur Niort, France; <sup>3</sup>Netherlands Institute of Ecology, Centre for Limnology, Rijksstraatweg 6, 3631 AC Nieuwersluis, The Netherlands; <sup>4</sup>Station Biologique de la Tour du Valat, Le Sambuc, 13200 Arles, France. Corresponding author: m.guillemain@oncfs.gouv.fr

It is well established that energy stores of adult breeding birds are correlated with their breeding success. For example, females may produce more offspring if they accumulate larger stores reserves starting reproduction (e.g. Ebbinge & Spaans 1995), because they will be able to produce more eggs of better quality (Ankney et al. 1991, Esler & Grand 1994) and/or because they will be able to reduce the time spent feeding and hence maximise time allocation to territory establishment or nest attendance (Afton 1980, Gloutney & Clark 1991, Sandberg & Moore 1996). For males, an increase in body stores may be enable them to allocate more time

to social display possibly resulting in a higher dominance status and mating success (Wishart 1983, Holmberg et al. 1989, Sandberg & Moore 1996). In addition, heavier males may devote more time to mate guarding and provide more protection against predators, thus increasing the pair's breeding success (Sandberg & Moore 1996).

Storing large amounts of fat also has its drawbacks, as reviewed by Witter & Cuthill (1993): higher body-mass may hamper locomotion, especially for flight as the mechanical power requirement of flight is an accelerating function of body-mass (e.g. Pennycuik 1975,



Kvist et al. 2001). Heavier birds are also less manoeuvrable and have more difficulty in taking off (e.g. Witter et al. 1994) which, together with the fact that maintenance of higher body-mass requires longer feeding times (hence longer periods exposed), should increase predation risk (e.g. Lima 1986). As a consequence of the above trade-off, many studies, both theoretical (Lima 1986, McNamara & Houston 1990, Witter & Cuthill 1993) and empirical (e.g. Freed 1981, Rogers 1987, Witter et al. 1995, Gosler 1996, Schaub & Jenni 2000), have shown that birds aim at reaching an optimal body mass during migration stop-overs. This means that birds do not necessarily use stop-over sites as fattening places if they still have enough fuel for migration.

In the context of this trade-off between the costs and benefits of carrying extra fat stores, the fuelling rate on the staging areas may be a key determinant of the migration strategy. Fuelling rate affects the speed of migration and consequently the date of arrival at the breeding grounds, potentially a main determinant of breeding success (e.g. Duncan 1987, Alerstam & Lindström 1990, Lindström & Alerstam 1992, Klaassen & Lindström 1996, Blums et al. 1997). In addition, for large birds like ducks, body condition upon arrival at the breeding grounds may not only depend on the environmental conditions there, but may also on their ability to build-up stores at wintering and migratory stop-over sites (e.g. McLandress & Raveling 1981, Tamisier et al. 1995, Klaassen et al. 2001, Klaassen 2002).

To date, fuelling rates of migrants have been mainly documented in passerines, waders, and a few geese (review in Lindström 1991, 2002). With the exception of mallards *Anas platyrhynchos* (LaGrange & Dinsmore 1988), fuelling rates of dabbling ducks are unknown. This is unfortunate, since they face high levels of disturbance and massive reductions in habitats. Dabbling ducks are hunted in many countries and make use of wetlands as stop-over sites which, compared to most other habitats, are highly spatially segregated and heterogeneously distributed between their wintering and breeding area. Over the past century, and at an ever-increasing rate, the quality of these sites has decreased, leading to an increase in migratory distances for the residing waterfowl. Management of these wetlands and their inhabitants requires sound ecological knowledge of the species' annual cycle and knowledge of the course, extent and requirements of migratory fuelling (Bairlein 1998).

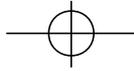
Garganey *Anas querquedula* are declining over most of their breeding range (Tomialojc et al. 1995), thus requiring special attention to the constraints affecting the species in spring and summer. Fuelling rates in (Western Palearctic) migrating dabbling ducks are generally difficult to ascertain because their breeding ranges are huge and the breeding, wintering and staging areas of different populations overlap greatly. Fortunately, this problem does not exist with garganey, which is a long-distance migrant: birds from the European/West African population winter almost exclusively between 10° and 20° N, while they breed mainly in Russia, Ukraine and Byelorussia (Scott & Rose 1996, Schricke 2001). Many birds cross Western Europe through Spain, France and Italy in spring, but these countries serve mainly as staging areas since they host only a tiny fraction of the breeding population (under 1000 pairs [Schricke 2001] whereas total population size is estimated at 2 million individuals [Scott & Rose 1996]). In the Camargue, southern France, garganey traditionally stop during spring and autumn migration, but only exceptionally do the birds winter or breed: a female with five young in 1990 was the first proof of reproduction in the area since 1966, and only twice was the species (one individual each time) recorded in the Camargue in November and January between 1990 and 1994 (Thibault et al. 1997).

In this paper, we use information from garganey ringed and recaptured within the same season over 13 years in the Camargue to document fuelling rates of individuals during spring migration. We analyse males and females separately, and study the environmental and individual factors that may affect these rates.

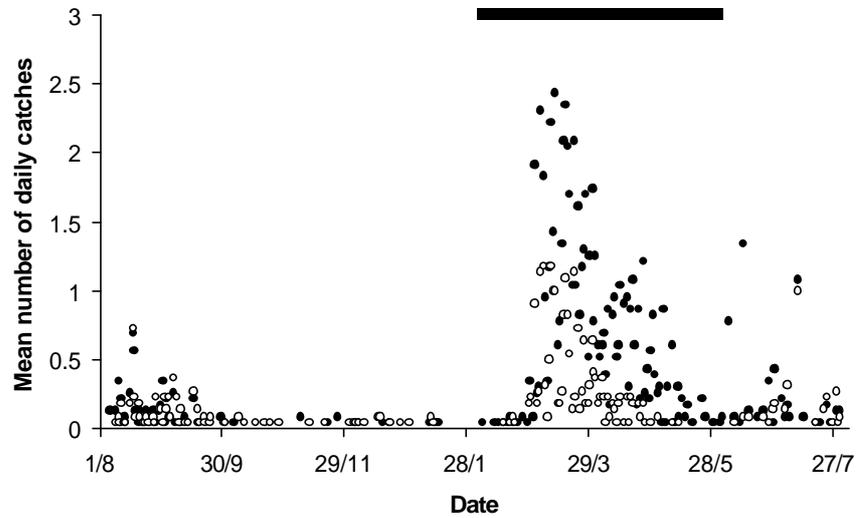
## Methods

### Study site

Garganeys in the Camargue were caught at the Domaine de la Tour du Valat (43° 30' N, 4° 40' E) between March 1952 and May 1974 using standard dabbling duck automatic traps hidden in the vegetation (details of the Camargue technique in Bub 1991). Traps were baited with rice, which may lead to a slight over-estimation of bird weight at capture. However, this should not affect the results since the goal of the study was to calculate the rate at which individuals gain body mass



**Figure 1.** Mean number of garganey (black dots: males, white circles: females) ringed per calendar date (average of all years of ringing) at the Tour du Valat, 1952–1974. The horizontal bar at the top of the graph shows the limits of the season considered in the analyses, i.e. first catches between 1 February and 31 May.



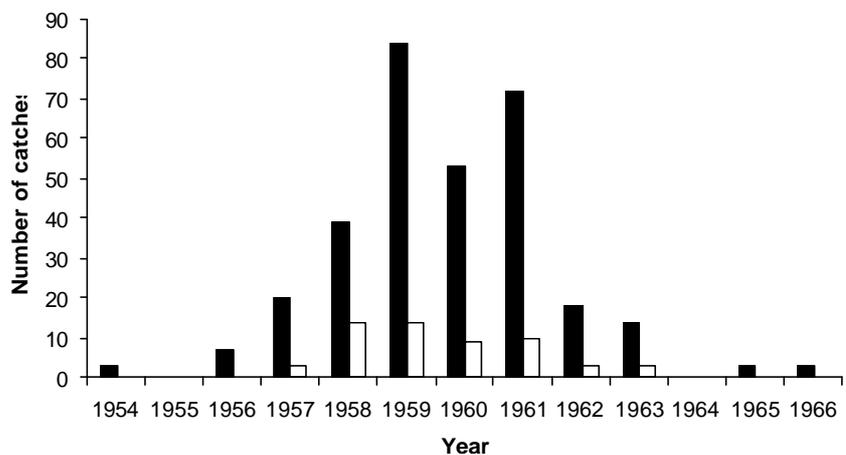
rather than describing average body mass in the population. Using baited traps may also bias sampling towards food-stressed individuals (Dufour et al. 1993). However, in this case one would predict that the body mass of birds recaptured at least once would be lower than that of birds never caught again after initial ringing, which was not the case (see below).

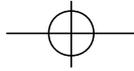
**Bird measurements**

Ducks were sexed using plumage criteria and examination of the cloaca and bursa of Fabricius. Because garganey can be sexually mature at one year of age, the age of individuals often could not be ascertained in spring, and ages were consequently not distinguished in the

analyses. A total of 2447 individuals were ringed at the Tour du Valat between March 1952 and May 1974. The analysis was restricted to birds ringed during the period 1 February–31 May each year, assumed to encompass the whole period of spring migration (Fig. 1). During this period, 1,978 birds were caught of which 383 were recaptured at least once during the same spring. Data from the years when there was only one individual of a given sex (i.e. 1953 for males and 1954, 1956 and 1971 for females) were discarded from the analyses. In addition, body mass was not measured in three males at ringing and four males at last recapture. The dataset therefore consisted of 316 males caught between 1954 and 1966, and 56 females caught between 1957 and 1963 (Fig. 2). Most of these birds were re-

**Figure 2.** Annual total number of garganey (black columns: males, white columns: females) caught and recaptured at least once at the Tour du Valat during the same spring.



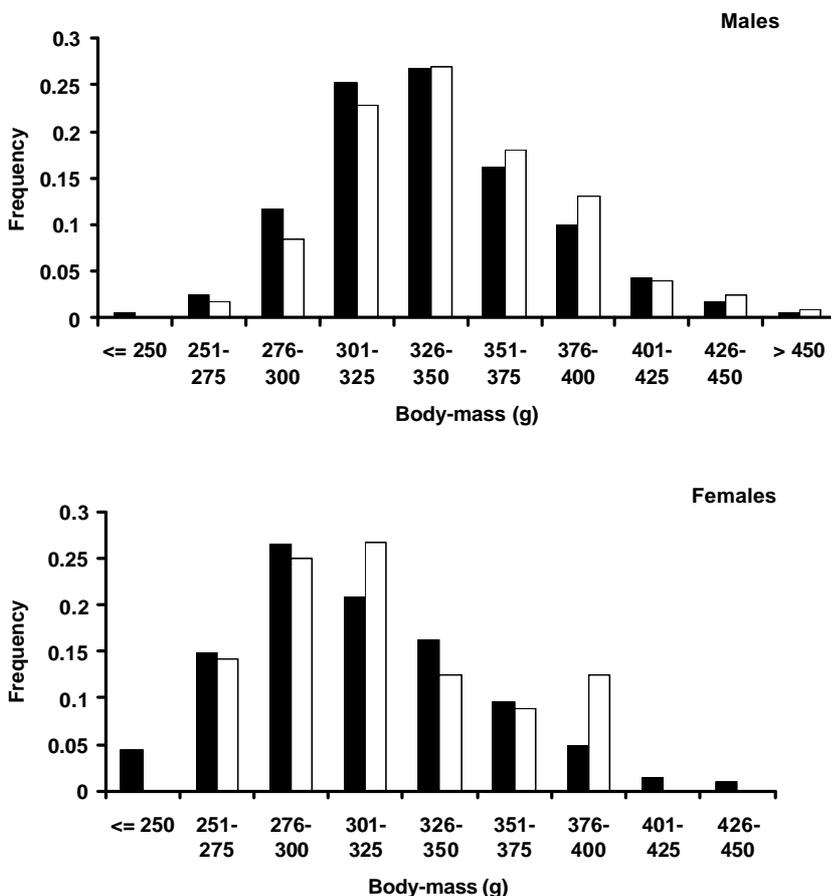


captured only once or twice; 90 % of the birds were caught less than five times during the same spring. The number of days between first catch and last recapture varied between 1 and 67 days (median: 7 days). Average time between successive captures was 5.2 days ( $\pm 5.3$  s.d., range: 1–38,  $n = 372$  individuals).

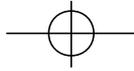
The fuelling rate of an individual might vary depending on whether it is 'early' or 'late' within the migration season. Also the onset and end of the migratory season is likely to change from one year to another depending on environmental conditions. Therefore, we included in the analyses for each individual the number of days elapsed since the first arrival of migrants that year, rather than the calendar date. The first arrival of migrants was arbitrarily assumed to be the first day of a year when at least two garganeys were caught simultaneously (which was always followed by more captures on the following days). This date of first arrival of migrants varied from 19 February (1960) to 18 March (1966),

with no significant trend over years (Spearman rank correlation,  $r_s = -0.55$ ,  $P > 0.06$ ).

Birds caught were weighed to the nearest gram in both sexes. The frequency distributions of body masses did not differ between females caught only once and females subsequently recaptured during the same spring (Kolmogorov-Smirnov tests: females:  $P > 0.10$ ; Fig. 3). In males, the  $P$ -value was just equal to the significance threshold ( $P = 0.05$ ). Also average body mass did not differ significantly between females caught only once and females subsequently recaptured ( $311.7 \text{ g} \pm 39.8$  s.d.,  $n = 410$  and  $316.1 \text{ g} \pm 37.2$  s.d.,  $n = 56$ ;  $t = -0.78$ ,  $P > 0.40$ ). Although in males this difference was statistically significant and birds subsequently recaptured were heavier on average than birds that were ringed and never recaptured, this difference was only 6 g, or less than 2 % of average body mass ( $345.1 \text{ g} \pm 38.7$  s.d.,  $n = 316$  and  $339.3 \text{ g} \pm 39.0$  s.d.,  $n = 1180$ , respectively;  $t = -2.39$ ,  $P = 0.0171$ ). It could therefore not be con-



**Figure 3.** Frequency distributions of body masses of female (top) and male (bottom) garganey ringed and recaptured (white columns) or ringed and not recaptured (black columns) at the Tour du Valat. For each sex and category (either ringed and recaptured or ringed and not recaptured), frequencies refer to the number of individuals in a given body-mass class as a proportion of the total number of individuals. See text for statistics.



**Table 1.** Correlation\* matrices between the independent variables entered in the GLM model to explain variations of body mass change in male ( $n = 316$  individuals) and female ( $n = 56$ ) garganey. Significant correlations at  $P < 0.05$  are indicated by an asterisk. Abbreviations are: DAY = number of days since arrival of first migrants; NBDAYS = number of days between ringing and last recapture; IBM = initial body mass at ringing; TEMP = average temperature at the Tour du Valat between capture and last recapture.

	DAY	NBDAYS	IBM
<i>Males</i>			
DAY			
NBDAYS	-0.06		
IBM	0.25	-0.08	
TEMP	0.77*	0.28*	0.04
<i>Females</i>			
DAY			
NBDAYS	0.09		
IBM	0.25	-0.08	
TEMP	0.76*	0.43*	0.07

\* all correlations are Pearson coefficients. Note that due to missing values, sample size in correlations including temperature is 219 for males, and 32 for females.

cluded that the body mass of birds recaptured at least once was lower than that of birds never caught again, nor that use of baited traps biased the sample towards food-stressed individuals.

The flattened wing length at ringing was measured to the nearest 1 mm. Only 9 out of the 372 birds were still moulting when first caught. Moulting feathers in this case were small body feathers, not remiges. These birds were retained in the sample. Initially, we aimed to correct body mass for structural size to obtain a body condition index. However, in males there was only a weakly significant positive relationship between body mass and wing length ( $r = 0.18$ ,  $P < 0.05$ ). In females, the relationship was non-significant ( $r = 0.12$ ,  $P = 0.37$ ). Even when considering a potential effect of the year of capture and of the number of days elapsed since arrival of first migrants in addition to wing length (to take into account potential time effects on the mass v. size relationship), models only explained 11 % and 29 % of variation in body mass of males and females, respectively. Because of these poor relationships, we considered it inappropriate to derive a body condition index from the residuals of the reduced major axis linear regression of

body mass on wing length (Green 2001). Instead, body mass at ringing was considered to reflect body condition. Because of sexual size dimorphism (Fig. 3), analyses were carried out separately for males and females.

## Data analyses

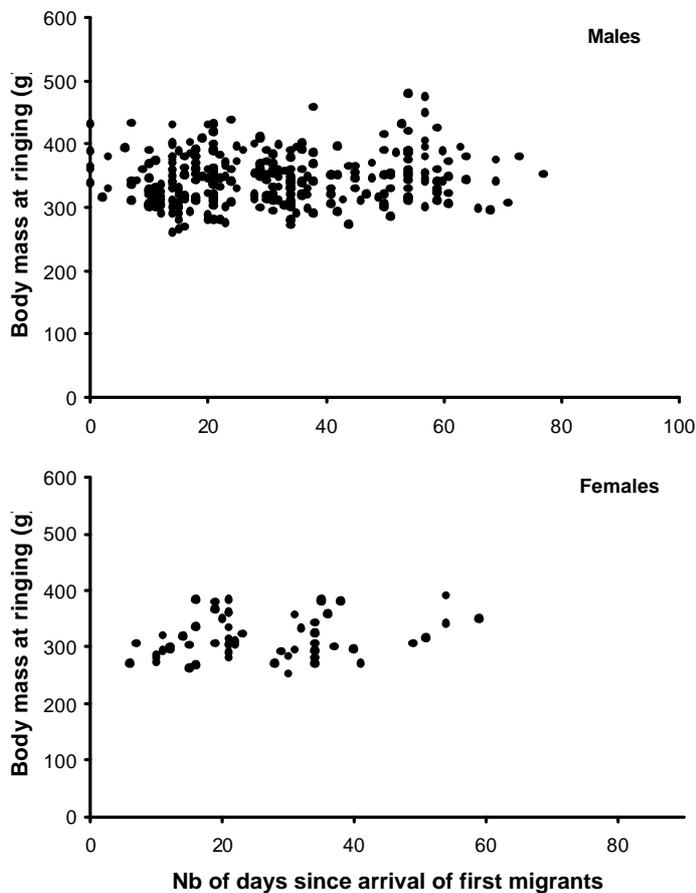
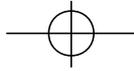
We first tested whether body mass differed between sexes and, for each sex, if body masses differed between years or showed a significant trend with time within the migration season, i.e. if body mass was significantly correlated with the number of days between the first arrival of migrants and ringing date. Body mass gain (in grams per day) between first and last capture was then computed for each individual. We tested if there was a significant difference in body mass gain between years, to analyse the potential effects of annual differences in the environment. Then for each individual the effects of day of capture (since first arrival of migrants), number of days between ringing and last recapture, initial body mass, and average temperature at the Tour du Valat between capture and last recapture were assessed through a backwards stepwise general linear model (threshold  $P$ -value 0.05). All analyses were run separately for the two sexes. Correlation matrices for the independent variables in the male and female GLM models are shown in Table 1. Temperature data were only available from 1 January 1959 onwards, except for March 1960, and hence for only 219 out of the 316 males, and 32 of the 56 females. All analyses were run with Statistica (Statsoft 2002).

## Results

### Body mass

Males were heavier than females at ringing ( $345.2 \text{ g} \pm 38.7 \text{ s.d.}$ ,  $n = 316$  and  $316.1 \text{ g} \pm 37.2 \text{ s.d.}$ ,  $n = 56$ , respectively;  $t = 5.22$ ,  $P < 0.0001$ ; Fig. 2).

The body mass of males at ringing did not show any significant trend with increasing number of days since arrival of first migrants ( $r^2 = 0.01$ ,  $df = 314$ ,  $P = 0.068$ ; Fig. 4). A significant difference was observed between years of capture (ANOVA:  $F_{10,305} = 2.14$ ,  $P = 0.021$ ). However, year only explained 6.6 % of male body mass variation and Bonferroni-adjusted  $t$ -tests showed that only the average values from two years differed signi-



**Figure 4.** Initial body mass of male (top) and female (bottom) garganey in relation to the number of days between their capture date and the date at which the first migrants arrived that year. Neither of the two regressions was significant (see text).

ificantly from one another ( $P < 0.05$ ): 1960 ( $356.2 \text{ g} \pm 45.8 \text{ s.d.}$ ,  $n = 53$ ) and 1963 ( $313.1 \text{ g} \pm 35.3 \text{ s.d.}$ ,  $n = 14$ ).

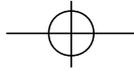
In females, body mass did not show a significant trend with increasing number of days since arrival of first migrants ( $r^2 = 0.07$ ,  $df = 54$ ,  $P = 0.060$ ; Fig. 4), and did not differ significantly between years (ANOVA:  $F_{6,49} = 0.61$ ,  $P = 0.720$ ).

#### Fuelling rates

In males, fuelling rates differed significantly between years (ANOVA:  $F_{10,305} = 2.85$ ,  $P = 0.0021$ ). However, Bonferroni-adjusted t-tests showed that this was only due to a significant difference ( $P < 0.05$ ) between average values from two years: 1960 ( $-4.0 \text{ g.day}^{-1} \pm 9.5 \text{ s.d.}$ ,  $n = 53$ ) and 1961 ( $2.7 \text{ g.day}^{-1} \pm 8.9 \text{ s.d.}$ ,  $n = 72$ ). When only the 219 males for which temperature data were available were considered, and temperature was included in the first step of the GLM to explain variations in body mass gain, the final model at the end of the

backwards stepwise procedure retained only the initial body mass and number of days since arrival of first migrants (final model:  $F_{2,216} = 28.65$ ,  $P < 0.0001$ ,  $r^2 = 0.21$ ). The analysis was therefore re-run without including temperature, and considering all 316 males. The result of the backwards stepwise procedure was similar, as only the initial body mass and the number of days since arrival of first migrants were eventually retained (Table 2). This model explained 19.4 % of the variance in body mass gain, of which 74 % was explained by initial body mass alone. Males gained body mass when their initial condition at ringing was low, and lost body mass when their initial condition at capture was high (Fig. 5).

In females, no significant differences in fuelling rates were detected between years (ANOVA:  $F_{6,49} = 0.77$ ,  $P = 0.601$ ). When only the 32 females for which temperature data were available were considered, and temperature was included in the first step of the GLM to explain variations in body mass gain, the final model at



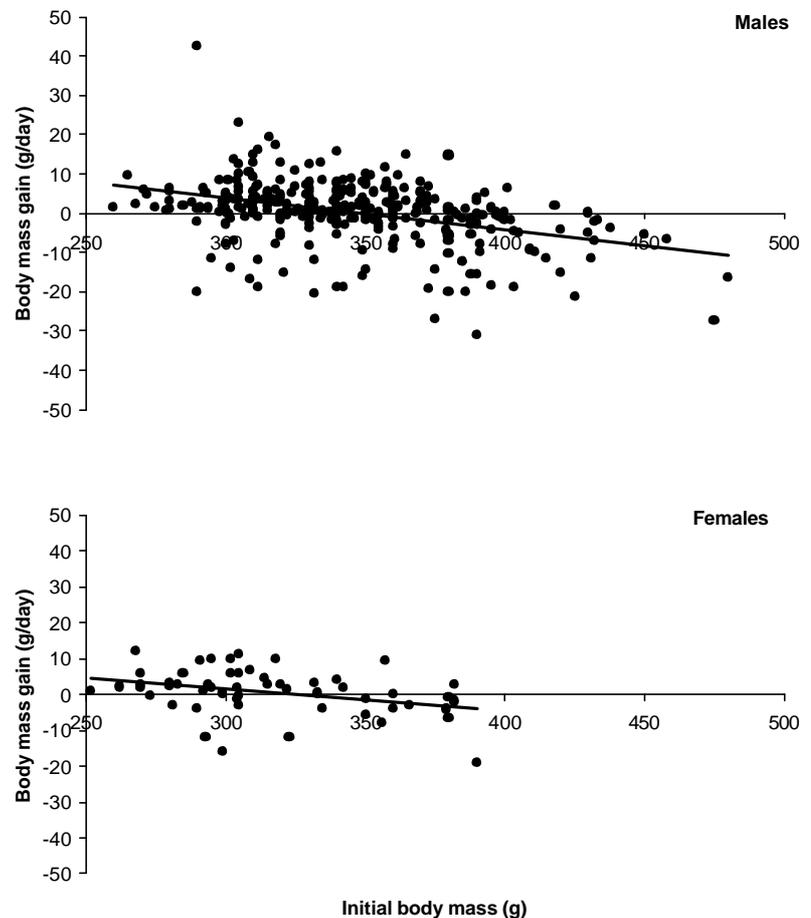
**Table 2.** Best fitting models of variation in individual body-mass gain ( $\text{g}\cdot\text{day}^{-1}$ ). Only final models of backwards stepwise general linear models are presented (see Methods for complete list of dependent factors and variables used). Sample size was 316 males and 56 females.

	Estimate $\pm$ s.d.	F	df	P
<i>Males</i>				
Model		37.78	2	< 0.0001
No. days since arrival of first migrants	$-0.10 \pm 0.02$	17.66	1	< 0.0001
Body mass at ringing	$-0.08 \pm 0.01$	50.92	1	< 0.0001
<i>Females</i>				
Model (Body mass at ringing)	$-0.06 \pm 0.02$	8.32	1	0.0056

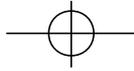
the end of the backwards stepwise procedure retained only the initial body mass (final model:  $F_{1,30} = 5.25$ ,  $P = 0.0291$ ,  $r^2 = 0.15$ ). The analysis was therefore re-run without including temperature, and considering all 56 females. The result of the backwards stepwise procedure was similar, as only the initial body mass was

eventually retained (Table 2). This model explained 13.4% of the variance in body mass gain, with the same pattern of decrease in body-mass gain with increasing initial body condition at capture (Fig. 5).

Mean body-mass gain was close to nil in both sexes:  $0.27 \text{ g}\cdot\text{day}^{-1} \pm 8.22$  s.d. ( $n = 316$ ) in males and  $0.68$



**Figure 5.** Fuelling rates of male (top) and female (bottom) garganey in relation to their initial body mass at capture. Regressions were significant in both cases ( $r^2 = 0.15$ ,  $df = 314$ ,  $P < 0.0001$  and  $r^2 = 0.13$ ,  $df = 54$ ,  $P < 0.01$ , respectively).



$\text{g.day}^{-1} \pm 6.29$  s.d. ( $n = 56$ ) in females and did not differ significantly between sexes (t-test:  $t = -0.34$ ,  $P = 0.737$ ). On average, the body mass of garganeys during their stay in the Camargue hardly changed.

## Discussion

### Average body-mass changes

On average garganey did not accumulate significant reserves in the Camargue: less than 1g per day and therefore less than 5 g for an average stay of approximately 5 days, i.e. less than 2 % of average body mass. It remains possible that garganey do not put on weight in the Camargue because foraging conditions are poor. However, the fact that birds could have found food in the trap and that foraging is a minor activity for this species in the area in spring (J-Y. Pirot, unpubl. data) does not support this hypothesis. Potential predation pressure was not measured, so it can-not be excluded that predation risk prevented birds from engaging in foraging activities. Further studies on available food stocks and behaviour of spring-staging dabbling ducks are currently being undertaken (C. Arzel, pers. comm.).

Stress linked to capture and manipulation has been found to affect fuelling rates of migratory birds, leading in some cases to body mass loss (e.g. Ens et al. 1990). There was no significant difference in average body-mass change between birds recaptured once, twice, three times, four times or five or more times (ANOVA:  $F_{4,311} = 1.66$ ,  $P = 0.159$ ). It is therefore unlikely that the lack of fattening observed in the birds resulted from the handling during capture. Another hypothesis could be that birds do not put on weight because they devote most of their time to non-foraging activities. In spring, social displays to acquire a mate or mate guarding by males would be good candidates for such activities. However, this is most unlikely since pair-bonds are very strong in this species, rape attempts are very rare and most (i.e. 97 %) females are already paired at the end of winter (Cramp & Simmons 1977 and references therein). Behavioural observations in the Camargue in March (J-Y. Pirot, unpubl. data) have shown that 100 % of females were paired, and that courtship was very infrequent.

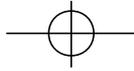
Of course, because garganeys do not put on weight at the Camargue stop-over, the question arises as to why

this site is not by-passed during spring migration altogether. Although some garganey may have passed through Spain before arriving in the Camargue, most had probably just crossed the Mediterranean Sea. Only three garganey ringed in the Camargue and one of 61 recovered garganey ringed in Britain were recovered in Spain between December and May (Owen et al. 1986). Furthermore, garganey are only occasionally observed in the Maghreb, and this species is consequently thought to migrate directly to southern Europe from sub-Saharan regions (Moreau 1967). Analysis of spring ringing recoveries ( $n = 189$ ) shows that the next stop-over sites after the Camargue are either other areas in France (28 recoveries) or Northern Italy (100 recoveries), which in both cases is an easy flight over land from the Camargue (600 km between the Camargue and northern Italy). Assuming that the leaner birds captured in the Camargue were close to the starvation body mass of garganey (i.e. 220 g in females and 230 g in males), males and females with the average body mass recorded in this study still had 96 g and 115 g of body stores left at first capture, respectively. Assuming the energy content of these body stores was  $30 \text{ kJ.g}^{-1}$  (Jenni & Jenni-Eiermann 1998), the flight speed of these birds is  $14.1 \text{ m.s}^{-1}$  (Bruderer & Boldt 2001) and using Norberg (1996) to predict power requirements for flight, males and females arriving in the Camargue would on average still be capable of covering 2005 and 1797 km, respectively.

The stop in the Camargue therefore does not appear to be used for fattening purposes by migrating garganey. Because of the very long flight from the sub-Saharan region before arriving in southern France and the short length of their stay there, it is possible that resting is the main purpose of the Camargue stop. In addition, it is also possible that garganey try to optimise their migration overall, and do not skip the Camargue because the timing may be too early for flying directly to subsequent stop-overs (in terms of food availability or climatic conditions there), therefore making it more profitable to wait in southern France.

### Inter-individual variation

When first caught in the Camargue, the body mass of garganey showed considerable variation, some birds being much heavier than others. Because the direct



journey from south of the Sahara to southern France must require considerable amounts of energy, birds probably store large fuel stores before departure in order to buffer potential adverse effects of bad conditions encountered en route. We hypothesise that some individuals in fact had an easier journey than expected (because adverse desert winds are potentially a major threat, but their frequency is such that some birds may pass through without encountering any), and consequently arrived in the Camargue with still a large share of their initial stores.

Body-mass at ringing was the main factor explaining subsequent variation in fuelling rates, while annual variation in the environment or temperature experienced by the birds had no significant effect. Garganey arriving lean in the Camargue gained body mass, while initially fat birds lost mass. Several studies have shown that the fuelling rate at a migration stop-over decreases with individual body-mass (e.g. Klaassen & Lindström 1996, Fransson 1998, Schaub & Jenni 2000), for which extra resting metabolic and transport costs associated with an increase in fuel load may be held responsible (Klaassen & Lindström 1996). It would be premature in our case, however, to conclude that this indicates that the fattest garganey deliberately lost mass to reduce the costs associated with carrying too much load (e.g. because this hampers flight ability and/or increases predation risk), because this pattern is likely to reflect only a mathematical artefact: because fuelling rate is derived from initial body mass at ringing, a correlation between the two is likely to arise automatically for statistical reasons (part-whole correlation, Sokal & Rohlf 1995, see the application to mass loss in relation to initial mass in Gebhardt-Henrich 2000). Only if the result of the major axis regression between mass loss and initial body mass differs significantly from 1 can one be sure that the relationship is due to biological effects in addition to statistical effects. In Camargue garganey, the slopes of the reduced major axis regressions were 1.04 and 1.09 in males and females, respectively. In males, the standard error of the slope was computed with software RMA (Bohonak, 2002), and was equal to 0.05, therefore encompassing the value of one. In females, the standard error could not be computed due to too small a sample size. However, for females the value of the slope was very close to one, and therefore it cannot be concluded that the observed pattern has a biological explanation.

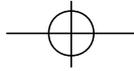
From a management point of view, it is often argued

that the main value of stop-over sites for migrating birds is the ability to find the necessary food resources to re-fuel after a previous flight, and to prepare for the next. This study does not provide any insight into the foraging value of the Camargue for migrating garganey, but suggests that the main reason for this stop could be for resting after a long and hazardous journey. It is important to realise that management providing quietness and safety at stop-overs may be at least as important for this species as feeding opportunities.

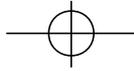
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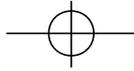
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## Hybridisation between great reed warblers *Acrocephalus arundinaceus* and clamorous reed warblers *A. stentoreus*: morphological and molecular evidence

Bengt Hansson<sup>1</sup>, Edward Gavrilov<sup>2</sup> and Andrey Gavrilov<sup>2</sup>

We present morphological and molecular evidence of the occurrence of hybrids between great reed warblers *Acrocephalus arundinaceus* and clamorous reed warblers *A. stentoreus* in Kazakhstan where both species breed. Three males and one female of 249 examined individuals had wing characteristics that were intermediate between the parental species. Molecular analyses of a nuclear microsatellite locus and a mitochondrial gene confirmed that these four individuals were hybrids: genetic material came from both parental species. Three hybrids carried clamorous reed warbler mitochondria and one carried great reed warbler mitochondria. Our finding does not support hypotheses suggesting that hybridisation occurs as a last resort when conspecific mates are rare, because both species were common in the area. Instead, we suggest that hybridisation might have resulted from mistakes in mate recognition in general and/or that the highly variable song of male great reed warblers might have acted as supernormal mate choice stimuli for female clamorous reed warblers.

Key words: Hybridisation, mate choice, microsatellite, mtDNA, *Acrocephalus*.

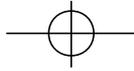
<sup>1</sup>Department of Animal Ecology, Lund University, Ecology Building, SE-22362 Lund, Sweden; <sup>2</sup>Animal Marking Centre, Institute of Zoology, Akademgorodok, Al-Farabi Ave. 93, Almaty, 480032, Kazakhstan; corresponding author: [bengt.hansson@zoekol.lu.se](mailto:bengt.hansson@zoekol.lu.se)

Avian hybridisation may occur when two related species meet and one of them is rare (Grant & Grant 1992, Wirtz 1999). In such situations, individuals that remain unpaired might choose heterospecific mates. Alternative hypotheses postulate that hybridising females are attracted to heterospecific males when these are larger in size than the conspecific males, or that heterospecific song and plumage characteristics sometimes act as supernormal mate choice stimuli (Randler 2002). Hybridisation might also result from general mistakes in mate recognition (Randler 2002).

The great reed warbler and the clamorous reed warbler, *Acrocephalus arundinaceus* and *A. stentoreus*, are closely related passerines, similar in morphology and behaviour, with partly overlapping breeding ranges in Israel, the Middle East and southern Central Asia (Cramp 1992). The great reed warbler is a long-dis-

tance migrant throughout its range, whereas clamorous reed warblers are either sedentary or perform a short-distant migration. In the hand, the species are distinguished most easily on differences in wing characters (Cramp 1992). In the field, males of the two species are distinguished easily by their song: the great reed warbler has a variable and high-pitched song, whereas the clamorous reed warbler has a monotone song of low frequency (Cramp 1992, B. Hansson et al., pers. obs.). Hybridisation has been suspected to occur between these species in Israel (Glutz & Bauer 1991), but so far there are no indications of hybridisation elsewhere (Kovshar 1972, Levin & Belyalov 1988).

In May 2001, we ringed and examined great reed warblers and clamorous reed warblers in southern Central Kazakhstan where the species co-occur (Cramp 1992, Lopatin et al. 1993). During the field work, we



encountered a few birds with intermediate morphology whose species identity was impossible to categorise, and one of these birds was also observed to sing a song that contained elements of the normal song of both species. Here, we present morphological and molecular evidence that viable hybrids between the two species occurred in the population, and discuss this in relation to proposed hypotheses regarding avian hybridisation.

## Materials and methods

### Study species and field work

Great reed warblers breed in lakes and marshes throughout the western and central Palaearctic and spend the winter in Africa south of the Sahara (Cramp 1992). Currently, two subspecies are recognised, *A. a. arundinaceus* in the western part of the range, and *A. a. zarudnyi* in the eastern part. The species is facultatively socially polygynous (Cramp 1992, Hasselquist 1998). Song is important for mate choice and males with large repertoires frequently become polygynous (Catchpole 1986, Hasselquist 1998).

Habitat requirements of the clamorous reed warbler are similar to those of the great reed warbler, although it is also found in less vegetated wetlands. Four subspecies are distinguished of which *A. s. brunnescens* occurs in southern Central Asia. This subspecies performs a short-distance migration mainly to the Indian

sub-continent, whereas other subspecies are sedentary (Cramp 1992, Ali & Ripley 1997).

In southern Central Kazakhstan, great reed warblers *A. a. zarudnyi* are at their south-eastern range limit, whereas clamorous reed warblers *A. s. brunnescens* are at their northern range limit (Cramp 1992, Lopatin et al. 1993). In this region, the clamorous reed warbler has expanded its range northwards during the last two decades, with increasing numbers in the newly colonised areas (Table 1). Currently, the breeding ranges of the two species overlap over a zone 500 × 1400 km wide (E. Gavrilov et al., unpubl., cf. Lopatin et al. 1993). The birds arrive in this region between mid April and early May, with clamorous reed warblers about a week ahead of the first great reed warblers (Kovshar 1972).

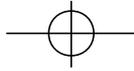
We studied these species at Stone Lake, southern Central Kazakhstan (42° 49' N, 70° 56' E), where they co-occur with a total population size of approximately 500 territorial males (E. Gavrilov et al., unpubl.). During four days in the period 14–19 May 2001, we captured, ringed and measured as many birds as possible. Most individuals were captured in stationary mist nets, and only a few birds (six great reed warblers and one hybrid) were captured close to their territories using song play back. At this locality, we examined 30 great reed warblers, 192 clamorous reed warblers and four putative hybrids. We also captured 23 clamorous reed warblers nearby at Kremenevskiy pond (42° 35' N, 70° 39' E), during 12–13 May 2001. Thus, in total, 249 individuals were examined. We recorded songs of a few individuals of each species at Stone Lake.

**Table 1.** Percentages of great reed warbler, clamorous reed warbler and their hybrids ringed at different localities in Kazakhstan between 1975 and 2001 (data from Levin & Belyalov 1988, Lopatin et al. 1993, E. Gavrilov et al., unpubl.). Data are given as percent of the total number of ringed birds at each locality.

Place	Coordinate	Years	Great reed warbler	Clamorous reed warbler	Hybrids	Total no. of birds
Turgay Hollow <sup>1</sup>	48° 44' N, 62° 02' E	1975–1977	100.0	0.0	0.0	274
Sorbulak Lake <sup>2</sup>	43° 46' N, 76° 05' E	1979–1981	98.8	1.2	0.0	81
Sarysu Lower	45° 01' N, 66° 47' E	1985–1986	92.5	7.5	0.0	106
Alakol Lake	46° 16' N, 81° 36' E	1986–1993	100.0	0.0	0.0	3960
Chushkakol Lake	42° 59' N, 68° 25' E	1988–1990	61.3	38.7	0.0	287
Stone Lake and nearby	42° 49' N, 70° 56' E	2001	12.1	86.3	1.6	249

<sup>1</sup>First clamorous reed warbler appeared in 1983

<sup>2</sup>First clamorous reed warbler appeared in 1981



Great reed warblers and clamorous reed warblers differ in the length and structure of the wings and there are also measurable differences in bill-head size and tail length (Cramp 1992, B. Hansson et al., pers. obs.). Some plumage differences occur. For example, the great reed warbler is greyish brown on the mantle, whereas the clamorous reed warbler is buffish brown. Measurements were taken by one of us (BH) according to Svensson (1995). We used a stopped ruler and a calipers. The length of the left wing (max method, Svensson 1995, p. 20) and tail (Svensson 1995, p. 24), and the distance between the tip of the first secondary and the tip of longest primary (Svensson 1995, p. 17), were measured to the nearest 0.5 mm. Bill-head length was measured to the nearest 0.1 mm. The number of primaries with emargination was noted as well as the length of the second outer primary (which is the outermost large primary) relative to other primaries (Svensson 1995, p. 18). These data were collected for the 56 birds from which we collected DNA (including the four putative hybrids; see below), whereas only some of these measurements were collected for the remaining 193 examined birds. In the analyses, we used the 56 birds from which all data (and DNA) were collected (with one exception – the wing shape analyses). Wing shape of males, i.e., wing sharpness (in degrees), wingtip pointness (in degrees) and surface area of one wing (in mm<sup>2</sup>), were based on measurements of all primaries (measured by AG) and calculated according to Gavrilov (1999). The wing shape dataset included most males from which DNA was collected and also a few other males (which explains the differences in sample size in Table 2).

### Molecular analyses

At examination, a small amount of blood (< 25 µl) was taken from the brachial vein of 56 birds (29 great reed warblers, 23 clamorous reed warblers and the four putative hybrids). Blood samples were stored in SET buffer. In the laboratory, DNA was extracted using standard phenol/chloroform extraction (Hansson et al. 2000).

In a study of the breeding ecology of a great reed warbler population in Sweden, breeding birds have been scored routinely for allelic variation at 21 microsatellite loci (Hansson et al. 2000, 2001, B. Hansson et al., unpubl.). From knowledge of the allelic variation in

this population, we chose eight microsatellites that varied relatively little in great reed warblers. By doing so, we maximised the chances of finding microsatellite loci with no overlap in allele lengths between great reed warblers and clamorous reed warblers. The sources of the eight loci were: Aar1, Aar2, Aar8 (Hansson et al. 2000), Ase15, Ase18, Ase44, Ase50 (Richardson et al. 2000; D. S. Richardson et al. unpubl.) and Hru5 (Primmer et al. 1996). Microsatellites were amplified using the PCR-technique as described in Hansson et al. (2000), and Richardson et al. (2000).

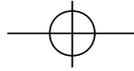
In addition, to determine species identity of the mothers of the hybrids, we sequenced a short fragment of the mitochondria that included the 3'-end of the control region, the tRNA<sup>Phe</sup> gene and the 5'-end of the 12S RNA gene, by using the primers BCML4 and 12SH1 (Mundy et al. 1996). The BCML4-primer was used in the sequence reaction. The sequences were checked against published sequences of the great reed warbler (121 bp) and clamorous reed warbler (123 bp) (Bensch & Hasselquist 1999). In this part of the mitochondria, the two species differ at six bp-positions (Bensch & Hasselquist 1999).

Finally, all birds from which we took DNA were sexed by using a molecular method that detects the female-specific W-chromosome (Fridolfsson & Ellegren 1999). There was a perfect match between the molecular sexing and the sex we had suggested in the field (based on wing length and the shape of the cloacae). The molecular analysis showed that one bird that we were not able to sex in the field was a female.

## Results

### Morphology

In both species, we found differences between sexes for all the measured characters. Therefore, we present data separately for males and females (Table 2). Three of the four putative hybrids were males. There was some overlap between the species in all measurements, except for the distance between the tip of the first secondary and the tip of the longest primary, where all great reed warblers scored higher values than the clamorous reed warblers (Table 2). On average, great reed warblers had a longer, sharper, more pointed and larger wing, but a shorter tail and bill-head length, than clamorous reed



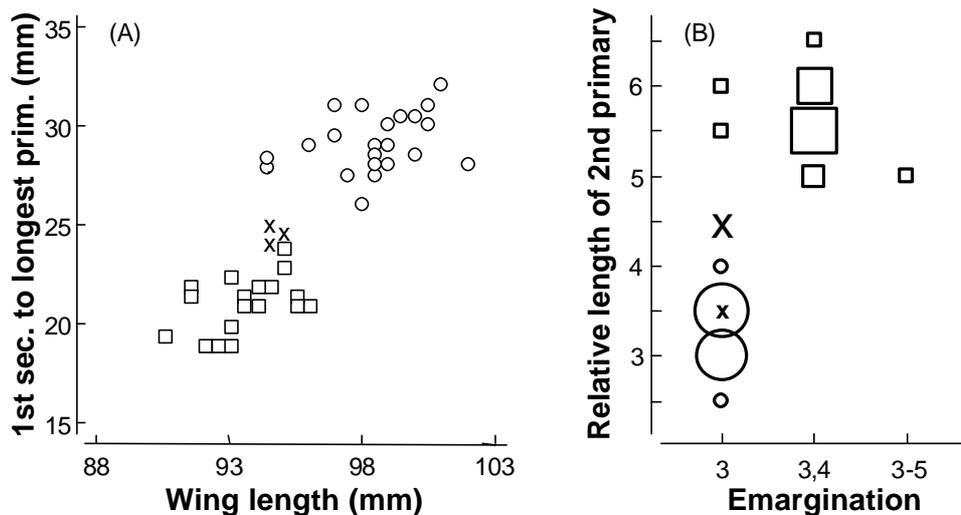
**Table 2.** Morphological data of great reed warblers, clamorous reed warblers and their hybrids at Stone Lake and Kremnevskiy pond, southern Central Kazakhstan, in May 2001. Data are given as mean  $\pm$  s.e. (n).

	Great reed warbler	Clamorous reed warbler	Hybrids
<i>Males</i>			
Wing length (mm)	98.5 $\pm$ 0.41 (22)	93.5 $\pm$ 0.37 (18)	94.7 $\pm$ 0.17 (3)
Distance between tips of 1st S and longest P (mm)	29.1 $\pm$ 0.31 (22)	21.1 $\pm$ 0.33 (18)	24.5 $\pm$ 0.29 (3)
Tail length (mm)	78.1 $\pm$ 0.56 (22)	83.7 $\pm$ 0.70 (18)	78.0 $\pm$ 0.58 (3)
Bill-head length (mm)	44.3 $\pm$ 0.13 (22)	46.3 $\pm$ 0.16 (18)	46.4 $\pm$ 0.42 (3)
Wing sharpness (degrees)	47.6 $\pm$ 0.16 (17)	43.6 $\pm$ 0.27 (35)	44.9 $\pm$ 1.13 (2)
Wing pointness (degrees)	44.4 $\pm$ 0.28 (17)	48.3 $\pm$ 0.15 (35)	45.5 $\pm$ 0.63 (2)
Surface area of one wing (mm <sup>2</sup> )	5538 $\pm$ 53.2 (17)	5368 $\pm$ 33.7 (35)	5465 $\pm$ 45.7 (2)
<i>Females</i>			
Wing length (mm)	94.2 $\pm$ 0.54 (7)	87.8 $\pm$ 0.37 (5)	93 (1)
Distance between tips of 1st S and longest P (mm)	28.4 $\pm$ 0.53 (7)	20.7 $\pm$ 0.37 (5)	26 (1)
Tail length (mm)	75.4 $\pm$ 1.04 (7)	76.2 $\pm$ 0.74 (5)	(0)
Bill-head length (mm)	43.3 $\pm$ 0.29 (7)	45.6 $\pm$ 0.41 (5)	45.2 (1)

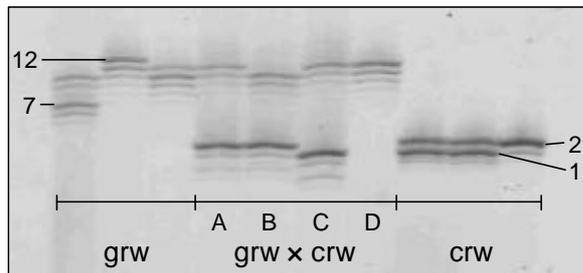
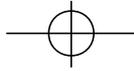
warblers (Table 2). Hybrids were intermediate in wing measurements. Interestingly, however, they exhibited as short a tail as great reed warblers and as large a bill-head length as clamorous reed warblers (Table 2). In Figure 1a, we have plotted wing length against distance between the tip of the first secondary and the tip of the

longest primary for males (22 great reed warblers, 18 clamorous reed warblers and the three hybrids) to illustrate the interspecific differences.

All great reed warblers (both males and females) had emargination of the third primary, whereas most clamorous reed warblers had emargination at both the third



**Figure 1.** Wing length plotted against the distance between the tip of the first secondary and the tip of the longest primary in males (A). Primaries with emargination plotted against length of the second primary relative to other primaries in males and females (B). Circles are for great reed warbler, squares for clamorous reed warblers, and x for hybrids. In B, the size of the symbols is proportional to sample size.



**Figure 2.** Alleles at the microsatellite locus Ase50 in great reed warblers (grw), hybrids (grw × crw) and clamorous reed warblers (crw). The locus is located on the Z-chromosome, which means that males (ZZ) have two alleles and females (ZW) one allele (see text). The figure shows that the three male hybrids (A–C) had alleles from both parental species and that the female hybrid (D) had a single allele inherited from a great reed warbler father.

and the fourth primaries (Fig. 1b). The second primary of all great reed warblers was as long as, or longer than, the fourth primary (Fig. 1b). In contrast, the second primary of all clamorous reed warblers was as short as, or shorter than, the fifth primary (Fig. 1b). The four hybrids had emargination at the third primary only (as all the great reed warblers and two of the 23 clamorous reed warblers), and the relative length of the second primary of three of them was intermediate between the two parental species (Fig. 1b).

#### Molecular data

Great reed warblers and clamorous reed warblers had non-overlapping allele frequencies at only one of the microsatellites, the Ase50 locus. At this locus, the great reed warblers from Kazakhstan had longer alleles (alleles 7–12) than clamorous reed warblers (alleles 1–2; Fig. 2). This locus is located on one of the sex chromosomes, the Z-chromosome (B. Hansson, unpubl. data), of which females have one and males two in birds. Hence, we expect females to have one allele only at this locus – an allele that is inherited from the father. As shown in Figure 2, all three male hybrids (A–C) had both short and long alleles at Ase50: male A had alleles 2 and 11, male B alleles 2 and 10, and male C alleles 1 and 11. This shows that the three males were hybrids. The female hybrid (D) had a single long allele (allele 11) inherited from a great reed warbler father (Fig. 2).

In a larger sample of great reed warblers from Sweden ( $n = 347$ ) genotyped at Ase50, the detected alleles were within the same range as the sample from Kazakhstan (alleles 7–12) and there was no indication of any potential problems with non-amplifying alleles (B. Hansson, unpubl. data).

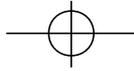
The mtDNA data also confirmed that the female (D in Fig. 2) was a hybrid because she carried a clamorous reed warbler sequence (inherited from a clamorous reed warbler mother). Two of the male hybrids carried a clamorous reed warbler mitochondrial sequence, whereas one carried a great reed warbler sequence. Thus, three of four hybrids had resulted from matings between clamorous reed warbler females and great reed warbler males.

#### Discussion

Our data show that great reed warblers and clamorous reed warblers do hybridise and that viable hybrids are present in populations in southern Central Kazakhstan: four of the examined individuals had intermediate wing characteristics and carried genetic material from both parental species. We do not know, however, whether the hybrids are fertile and if backcrossing occurs (cf. Bensch et al. 2002). Occasionally, heterospecific matings and/or viable hybrids have also been documented between other *Acrocephalus* species (Glutz & Bauer 1985, Cramp 1992): for example, between reed warblers *A. scirpaceus* and marsh warblers *A. palustris* (Lemaire 1977), and between reed warblers and great reed warblers (Beier et al. 1997).

Interestingly, three of four hybrids carried clamorous reed warbler mitochondria, and, hence, had clamorous reed warbler mothers. In the study area, there were about eight times as many clamorous reed warblers than there were great reed warblers, but still both species were common. There was no indication of any difference in sex-ratio between species (E. Gavrilov et al., unpubl.). Therefore, our data neither support the hypothesis suggesting that females of the rarer sex should be engaged in hybrid matings, nor the hypothesis proposing that hybridisation happens when either species is rare (Grant & Grant 1992, Wirtz 1999).

Why would some clamorous reed warbler females mate with great reed warblers despite the abundance of conspecific males? We do not believe that such a choice will give females benefits that are related to ter-



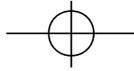
ritory quality. Male great reed warblers arrive at the breeding grounds in Kazakhstan shortly after clamorous reed warblers (Kovshar 1972), and are therefore likely to settle in territories that are, if anything, of poorer quality than the territories of the clamorous reed warblers. Moreover, the two species are of similar size, which suggests that male great reed warblers have no obvious size advantage in inter-specific competition over already occupied territories. In contrast, ideas suggesting that supernormal mate choice stimuli might cause females to choose heterospecific mates may be relevant for our findings (Randler 2002). Great reed warblers have a more variable song than clamorous reed warblers (Cramp 1992, B. Hansson et al., pers. obs.). Female great reed warblers prefer to mate with (conspecific) males having large song repertoires (Catchpole 1986, Hasselquist 1998), and song complexity is important also in other species of the same genus (Catchpole 1980, Buchanan & Catchpole 1997). It is not known, however, whether female clamorous reed warblers respond to song cues in the same way. But if they do, they may have been attracted to the variable song of the great reed warblers, with hybridisation as a result. An additional, non-mutually exclusive explanation is that hybridisation resulted from general mistakes in mate recognition (Randler 2002). Such mistakes may have been facilitated by the majority of territories of the two species being very small and tightly packed into the area (B. Hansson et al., pers. obs.).

Finally, our finding of viable hybrids between great reed warblers and clamorous reed warblers may throw light on the first discovery of an over-wintering great reed warbler in India, which is well outside the species' normal wintering grounds in central Africa (Cramp 1992). In May 1989, an adult bird was ringed at Chushkakol Lake where both great reed warblers and clamorous reed warblers breed (Table 1). The bird was identified as a great reed warbler by its wing characteristics (E. Gavrilov et al., unpubl.). In December 1990, this bird was re-captured and identified as a great reed warbler close to Calcutta, India (22° 15' N, 88° 12' E; Ali & Ripley 1997). It is well known that the migratory programme is under strong genetic control in passerine birds (Berthold & Querner 1981, Helbig 1991). Thus, it is possible that this specimen was a hybrid having some genes leading it to the typical winter quarters of the clamorous reed warbler, and some genes coding for an external morphology typical of a great reed warbler.

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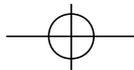
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## Ornithology and the genesis of the Synthetic Theory of Evolution

Thomas Junker

During the 1930s and 1940s many of the controversies that had shaped discussions about evolution for more than a century came to an end. This unification of evolutionary biology was achieved on a Darwinian basis. Together with selection, which was regarded as the only causal factor leading to adaptation, further evolutionary factors were integrated (mutation, recombination, drift, geographic isolation). This Synthetic Theory of Evolution or Synthetic Darwinism has dominated evolutionary biology since the early 1950s. In contrast to the situation during the nineteenth century, when leading ornithologists opposed Darwinian evolution, ornithologists played a central part in the formulation of the new model. Both Bernhard Rensch and Ernst Mayr based much of their evolutionary theorising on ornithological data. The British zoologist Julian Huxley did intense research on the ecology of birds. On the other hand the leading ornithologist Erwin Stresemann, teacher of both Rensch and Mayr, never really accepted Synthetic Darwinism. By comparing the theoretical views of Stresemann, Rensch, and Mayr, I will discuss in which respect ornithologists were especially prepared to appreciate the new genetical theory of evolution.

Key words: History of ornithology, history of evolution, Erwin Stresemann, Bernhard Rensch, Ernst Mayr.

Zum Laurenburger Hof 12, D-60594 Frankfurt am Main, Germany; email: Thomas.Junker@uni-tuebingen.de

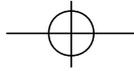
'I took much pleasure in watching the habits of birds, and even made notes on the subject. In my simplicity I remember wondering why every gentleman did not become an ornithologist'. With these words Charles Darwin remembered one of his favourite childhood hobbies (Darwin 1958: 45). The enthusiasm of the founder of the modern theory of evolution for birds, however, was not matched by most ornithologists of his time and it was only in the 1930s that ornithologists actively participated in the development of the theory of evolution.

What was the relationship between ornithology and the theory of evolution? Did the majority or the leading ornithologists of the time accept evolution, did they actively support it, or can we observe strong opposition? From the viewpoint of the evolutionists on the other hand, we might ask if they were interested in ornithological data to verify their ideas, or did both fields exist

in isolation? The answers to these questions, of course, vary with time and place. Not only ornithology has experienced fundamental change, but the theory of evolution itself was greatly modified during the nearly two hundred years since it was first formulated by Lamarck, and later Darwin.

### Ornithology and evolution in the nineteenth century

In the nineteenth century not one of the major evolutionists can be regarded as an ornithologist. Jean-Baptiste de Lamarck, the author of the first comprehensive theory of evolution (*Philosophie zoologique*, 1809), mainly worked with molluscs. Darwin did most of his original research on barnacles (Cirripedia) and later on botany. Birds, however, became very important for Darwin in several respects.



First there is the famous case of the Galapagos birds. In March 1837 the ornithologists John Gould informed Darwin that the mockingbirds he had collected on three different islands in the Galapagos should be regarded as different species, and not as varieties as Darwin had originally suspected. Species and varieties it seemed were only quantitatively differing stages in a continuous process. As he remembered in *Origin of Species*: 'Many years ago, when comparing, and seeing others compare, the birds from the separate islands of the Galapagos Archipelago, both one with another, and with those from the American mainland, I was much struck how entirely vague and arbitrary is the distinction between species and varieties' (Darwin 1859: 48). The Galapagos finches were particularly remarkable, because gradual stages could be observed: 'a nearly perfect gradation of the structure in this one group can be traced in the form of the beak, from one exceeding in dimensions that of the largest gros-beak, to another differing but little from that of a warbler' (Darwin 1839: 462).

Another bird species became equally important for Darwin – his famous pigeons. Pigeons were his favourite model organism to demonstrate the power of selection. They supplied him with a test-case for rapid evolution under artificial selection: 'when I first kept pigeons and watched the several kinds, knowing well how true they bred, I felt fully as much difficulty in believing that they could ever have descended from a common parent, as any naturalist could in coming to a similar conclusion in regard to the many species of finches, or other large groups of birds, in nature' (Darwin 1859: 28). Although the breeding of pigeons is only a narrow aspect of ornithology it gives an impression of the immense diversity and lavishness of forms that can be observed under natural conditions.

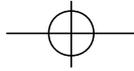
And finally birds provided Darwin with beautiful examples of traits acquired by sexual selection: 'Secondary sexual characters are more diversified and conspicuous in birds [...] than in any other class of animals. On the whole, birds appear to be the most aesthetic of all animals, excepting of course man, and they have nearly the same taste for the beautiful as we have' (Darwin 1871, 2: 38).

Although birds were very important for Darwin and the emergence of his theories of evolution and selection, he had no special interest in ornithology as such. A very similar picture arises when we look at Darwin's supporters. The most important proponents of the the-

ory of evolution came from other biological disciplines (Mayr 1982, Junker 1998, Junker & Hoßfeld 2001). Ernst Haeckel and Thomas Henry Huxley were morphologists working originally with marine invertebrates, Joseph Dalton Hooker and Asa Gray were botanists, August Weismann worked with butterflies and crustaceans, to mention just a few of Darwin's influential followers. Like Darwin, however, they were interested in the evolution of birds and their traits from different perspectives: Haeckel, for example, published a first provisional phylogeny of birds as early as 1866, tracing them back to the archaeopteryx and reptiles.

On the other hand leading ornithologists of the time were among the most outspoken critics of Darwin's theories. In Germany a significant number of them were not only opponents of the theory of selection, but even of evolution as such. As Erwin Stresemann has remarked in his history of ornithology, 'among the leading ornithologists in Germany the opponents of Darwinism still [in the early 1870s] were in the majority: J[ean] Cabanis, H[ermann] Schlegel, Th[eodor] von Heuglin, E[ugen] F[erdinand] von Homeyer, B[ernard] Altum, W[ilhelm] von Nathusius formed a mixed-coloured coalition that attempted to prevent the advance of the 'world-shaking' doctrine' (Stresemann 1951: 237). According to Stresemann this opposition can be explained in part by the fear that the acceptance of evolution would destroy the species concept and, as a consequence, be detrimental for taxonomy in general. Even those ornithologists who accepted evolution, such as Joel Asaph Allen, Henry Seebohm, and Ernst Hartert, rejected selection as the major causal factor and endorsed Lamarckian or orthogenetic explanations.

Although a similar picture emerges when we look at other biological disciplines, such as botany, anthropology or paleontology, the leading ornithologists seem to have been particularly hostile to Darwin's theories. Nineteenth century evolutionists, on the other hand, used ornithological data to support their theory, but they had no special interest in ornithology. This situation changed fundamentally during the first decades of the twentieth century. The anti-Darwinian tradition in ornithology that had prevailed in the nineteenth century still had its adherents. The creationist Otto Kleinschmidt, for example, was one its most extreme representatives. But, and this was the great difference, a school of evolutionists within ornithology had emerged. Before I discuss these new developments with special reference to



Stresemann and his pupils Bernhard Rensch and Ernst Mayr, it is necessary to look at the fundamental changes the theory of evolution encountered during the first decades of the twentieth century.

### Twentieth century: The origin of Synthetic Darwinism

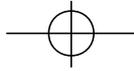
In *Origin of Species* and other publications Darwin had presented his theory as a unified concept and spoke of it in the singular. Very soon, however, single elements were isolated, criticised and accepted independently. For example many biologists of the nineteenth century accepted the idea of evolution, i.e. the gradual change of species over time, but rejected Darwin's mechanism, natural selection. Ernst Mayr has identified five major theories in Darwin's work: '(1) evolution as such, (2) common descent, (3) gradualism, (4) multiplication of species, and (5) natural selection' (Mayr 1985: 757). A sixth theory has to be added: Darwin's understanding of the origin of hereditary variation. Variation is an absolutely crucial prerequisite for the theory of selection – without variation there can be no selection. Darwin, who was well aware of this problem, devoted three chapters of *Origin of Species* to the origin of variation: The first two chapters deal with 'Variation under Domestication' and 'Variation under Nature', and in chapter 5 'Laws of Variation' are analysed. In addition he published a two volume book *The Variation of Animals and Plants under Domestication* (1868) comprising nearly 900 pages.

There is probably no other problem to which Darwin devoted more energy and at the same time was as unsuccessful as to the origin of variation. The reason for this disappointing result is that before 1900 the laws of inheritance were largely unknown and Darwin, like most of his contemporaries, accepted the inheritance of acquired characteristics (Lamarckism). According to this original Darwinism of the 1860s and 70s selection is the most important factor in evolution and explains the origin of most adaptations. At the same time Lamarckian effects were acknowledged for a number of cases. In 1883 August Weismann rejected the inheritance of acquired characteristics. His theory, based on a purely selectionist mechanism was called neo-Darwinism. As the major source of variation he identified recombination in sexual reproduction. Weismann, however, had no clear understanding of the laws of inher-

itance and no mechanism for the production of new heritable traits.

When modern genetics originated during the first decades of the twentieth century its main representatives – Hugo de Vries, William Bateson, Wilhelm Johannsen – believed that genetics would not only provide a correct understanding of the laws of inheritance, but of evolution as well. They assumed that evolution was driven by rare and large mutations. Genetics and Darwinism were considered incompatible. This seeming contradiction was overcome in the 1920s when several authors showed how the findings of genetics can be combined with selection. It could be empirically demonstrated that mutations are much more frequent and less conspicuous than the early geneticists had assumed, i.e. mutations together with recombination are a source of abundant hereditary variation. The new mutation-selection-theory of evolution was based on Darwin's ideas of evolution, common descent and selection. At the same time Darwin's erroneous Lamarckian theory of inheritance was replaced by the genetical theory of hard, particulate inheritance. The most important protagonists of the new model were Sergej S. Chetverikov, Erwin Baur, Ronald A. Fisher and J. B. S. Haldane among others and they considered themselves Darwinians (Provine 1971). Some historians and biologists equated this 'Mendelised 'neo-Darwinism' (Gayon 1998: 320) with the modern 'Synthetic theory of evolution'. The philosopher John Beatty, for example, wrote: 'According to the simplest such characterization of the [evolutionary] synthesis, Mendelian genetic theory and Darwinian evolutionary theory – once considered irreconcilable – were eventually reconciled in the theory of population genetics, which is the core of the synthetic theory' (Beatty 1986: 125).

If this characterisation is correct, the role of ornithology and other naturalists' disciplines was purely receptive. They had to accept the new theory and apply it to their field. This actually happened, but it is not the whole story. As long as evolution is understood as a process taking place within a single interbreeding population, genetics, population genetics and selection explain most of the observable changes. This, however, is only one aspect of evolution and one of the most conspicuous phenomena of organic nature is ignored: the origin of diversity. Species do not only evolve in time, but they also multiply. On the other hand, a population does not have to produce new species in or-



der to stay adapted, i.e., a theory about the mechanisms that sustain adaptedness does not automatically entail an explanation about the multiplication of species.

Darwin also had a theory about the multiplication of species. In *Origin of Species* and his later works he assumed that selection would favour the splitting of species, because the struggle for existence between the most divergent variants is less severe (principle of divergence). The 'more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers' (Darwin 1859: 112).

This mechanism was criticised by the geographer Moritz Wagner in 1868. He argued that isolation between two groups of individuals was necessary for the splitting of species. The situation is the same if we look at the breeding of animals or at evolution under natural conditions: free crossing has to be prevented, because it destroys the emergence of new races. Wagner, however, could not convince his contemporaries. One of the reasons for his failure was that he presented isolation as an alternative to selection. It took more than half a century until Wagner was vindicated and geographic isolation was integrated into the modern theory of evolution. The elaboration of a sophisticated theory of the multiplication of species was probably the most important contribution of ornithology to modern Synthetic Darwinism. The way was prepared by Stresemann and systematically elaborated by Rensch and especially Mayr in the 1930s and 40s.

The modern theory of evolution is Darwinian in the sense that it is based on evolution, common descent and selection. Two of Darwin's notions have been replaced by new concepts: his Lamarckian theory of inheritance was replaced by the genetical understanding of inheritance and mutations, and divergence as the mechanism of species splitting was replaced by geographic isolation. Despite these changes twentieth century Darwinism is very close to Darwin's original ideas. Theodosius Dobzhansky, for example, had not only given his 1937 book, which is considered the most influential document of the emerging theory, the title *Genetics and the Origin of Species* but this is also more than a superficial allusion, because Dobzhansky directly reproduced the structure of Darwin's argument in *Origin of Species*.

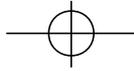
In the United States the theory is usually called 'synthetic theory of evolution', in England biologist prefer to speak of 'Darwinism' or 'Neo-Darwinism' and on the European continent both names are common. The theory is called synthetic, because it originated through a synthesis of theories, methods and data from various biological disciplines, in particular genetics, systematics, and palaeontology. The name 'Darwinian' derives from the fact that its evolutionary mechanism is built around Darwin's theory of selection (Mayr & Provine 1980, Junker 2003).

To sum up: Synthetic Darwinism as it was formulated in the 1930s and 40s does not only claim to stand in the Darwinian tradition, but its argument is actually structured in the same way as Darwin's. Together with selection, which is regarded as the only causal factor leading to adaptation, further evolutionary factors are integrated. Mutation and recombination were identified as the sources of genetic variability. The important effects of population size were stressed, in particular for small populations, where chance effects limit the power of selection. Geographic isolation was seen as an important requirement for the splitting of a species into two separate species. This modern theory of evolution evolved not only through the collaboration of biologists from a variety of disciplines, but also through the synthesis of different national traditions. It was a joint venture of Soviet, German, American and British biologists (Junker 2003, Junker & Hoßfeld 2002; see Table 1).

Next to entomologists, who constitute the majority of the naturalists among the architects of the synthetic theory of evolution, we find a number of botanists and ornithologists. Both Rensch and Mayr based much of their evolutionary theorising on ornithological data. The British zoologist Julian Huxley did intense research on the ecology of birds.

#### Ornithology and the genetical theory of selection: Stresemann, Rensch and Mayr

The role of ornithology in the origin of modern synthetic Darwinism can only be properly understood when we distinguish between two consecutive periods: the years 1924 to 1930, when a synthesis between genetics and Darwinism was achieved, and a second period from 1930 to 1947. While the first dealt with evolution within populations, i.e. anagenesis, the second also included cladogenesis, the multiplication of species. What is the



**Table 1.** The national origin of the major architects of modern Darwinism, the year of their early publications and their main fields of research. Italics indicate which authors contributed to the predominately genetical in contrast to the synthetic phase of the emergence of modern Darwinism.

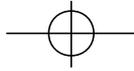
Nationality	Author of Darwinism	Year	Fields of research
Soviet Union	<i>Chetverikov</i>	1926	<i>entomology, genetics</i>
	Dobzhansky	1937	entomology, genetics
	Timoféeff-Ressovsky	1939	entomology, genetics
Germany	<i>Erwin Baur</i>	1924	<i>botany, genetics</i>
	Zimmermann	1930, 1938	botany, systematics
	Rensch	1943, 1947	zoology, systematics
	Heberer, ed.	1943	
	Mayr	1942	ornithology, systematics
England	<i>Fisher</i>	1930	<i>mathematical population genetics</i>
	<i>Haldane</i>	1932	<i>mathematical population genetics</i>
	Huxley	1942	zoology
United States	<i>Wright</i>	1931	<i>mathematical population genetics</i>
	Simpson	1944	paleontology
	Stebbins	1950	botany

reason for the strong position of ornithologists in the second synthesis, was it more or less accidental, or was ornithology especially suited to fill in a gap in this synthesis? When I asked Ernst Mayr this question his answer was 'yes and no'. He continued: 'In the 1930s–40s no other group of organisms was better known taxonomically than the birds. Therefore the understanding of geogr[aphical] speciation was documented better than for any other higher taxon. However, the work of Karl Jordan and Ed[ward Bagnall] Poulton on selected groups of insects led to the same results. So it is not completely restricted to birds' (Ernst Mayr to the author, 2 August 2003).

The sophisticated status of ornithological systematics as such, however, did not necessarily lead to the acceptance of the mutation-selection theory. Even though systematics in the hands of Stresemann and Rensch had become a branch of evolutionary biology this did not mean it could only be combined with a Darwinian theory of evolution. A comparison of the evolutionary ideas of Stresemann, Rensch and Mayr will show the possible connections between evolution and the new systematics (Junker 2003).

#### *Erwin Stresemann*

Erwin Stresemann (1889–1972) was one of the most influential ornithologists of the first half of the twentieth century (Haffer et al. 2000). From 1921 to 1924 he was assistant curator of ornithology, from 1924–1961 curator of ornithology at the Zoological Museum in Berlin. From 1922 until 1944 he was the General Secretary of the *Deutsche Ornithologische Gesellschaft*, from 1949 to 1967 president of the *Deutsche Ornithologen-Gesellschaft*. During four decades, from 1922 to 1961, he edited the *Journal für Ornithologie*. Stresemann emphasised a populational approach to systematics and he was an early advocate of the biological species concept as well as of geographic speciation. For example as early as 1921 Stresemann asserted that mutations alone will usually not produce a new species, but that geographic isolation is required: 'I am not inclined to believe that 'sports', mutations, will establish good species, if they arise in the midst of normally coloured individuals. [...] Only a very long and complete geographical separation of the descendants from the same ancestors may have caused the rise of such important differences [...] – or perhaps, in some rare cases, a certain physiological mutation accompanied or not accompanied by mutation of external characters' (Draft of a



**Figure 1.** Erwin Stresemann and Ernst Mayr, 1954.

letter by Stresemann to R. Meinertzhagen, December 1921; from Haffer 1997: 927–28). These concepts were central tenets of the new systematics. Species were seen as groups of populations which vary geographically and are isolated from other species genetically.

Recently Mayr has emphasised that it ‘is important to realize the great influence of Stresemann in these developments [i.e. origin of Synthetic Darwinism], for Stresemann was the teacher both of Rensch and of Mayr. Virtually everything in Mayr’s 1942 book was somewhat based on Stresemann’s earlier publications’ (Mayr 1999: 23). On the other hand Stresemann was never really convinced that the Darwinian mechanism was sufficient to explain evolution. Instead he sympathised with a variety of other models – Lamarckism, mutation pressure and orthogenesis. So Mayr came to the conclusion: ‘As progressive as Stresemann was in practicing population systematics and in his concepts of species and speciation, he was rather backward in his understanding of the mechanisms of evolution. He probably would have called himself an orthodox Darwinian, but he felt quite strongly that there were severe limits to the power of natural selection’ (Mayr 1980: 415).

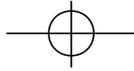
#### *Bernhard Rensch*

Bernhard Rensch (1900–1990) was a zoologist with very broad interests (Dücker 2000). In the summer of

1922 he worked as a volunteer for Stresemann at the Zoological Museum in Berlin. In 1925 he joined the Zoological Museum as an assistant and later became curator at the department of molluscs with close contacts to Stresemann’s department of ornithology. In his 21 books and more than 200 papers Rensch discussed a variety of topics, ranging from evolution, animal psychology, biophilosophy, sensory and brain physiology, to biogeography, ecology and systematics. Roughly 20 % of this publications dealt specifically with birds. He was especially interested in the geographical variation of songbirds and attempted to find borderline cases between races and species to support the notion that species originate from isolated geographic races.

As early as 1929 Rensch had maintained that geographic isolation precedes physiological isolating mechanisms in the process of speciation. Later he established various ecological rules that demonstrated the adaptive nature of geographic variation (Rensch 1933). However, until the middle of the 1930s Rensch combined both the geographic model of speciation and the ecological rules with a Lamarckian mechanism and explicitly rejected a purely selectionist theory. Under the influence of the Berlin geneticist N. W. Timoféeff-Ressovsky Rensch was slowly convinced that the mutation-selection-theory was valid. Interestingly, this change did not require major changes of his systematic theory, which was equally adaptable to a Lamarckian and a selectionist model.

As we have seen, in the late 1920s systematists already had an explanation for the gradual origin of species through geographic isolation, i.e. for the origin of biological diversity. They assumed that species split when populations are mechanically separated from each other and during this geographic isolation become reproductively isolated. This can either be caused by sterility barriers or through behavioral incompatibilities. Races were seen as incipient species. These ideas about speciation were ignored by the majority of evolutionary geneticists who attempted to explain speciation through special mutations. Many naturalists, on the other hand, had strong sympathies with Lamarckian or other non-Darwinian mechanisms. The two authors who did more than anyone else to bring the question of biological diversity into synthetic Darwinism were Dobzhansky and Mayr. Dobzhansky, in his *Genetics and the Origin of Species* (1937), discussed genetics, selection and evolution, but had not included a detailed



analysis of speciation. Mayr's *Systematics and the Origin of Species* (1942) filled this gap.

#### Ernst Mayr

In 1926 Ernst Mayr (b. 1904) was invited by Stresemann to come as an assistant to the Zoological Museum in Berlin. After his expedition to New Guinea and the Solomon Islands (1928–1930) Mayr accepted an assignment at the American Museum of Natural History in New York. In 1932 he became associate curator, and in 1944 curator at the Whitney-Rothschild Collection of the American Museum. Originally he worked on bird collections of the Whitney South Sea Expedition. When the Rothschild bird collection of 280,000 specimens was bought by the American Museum in 1932, Mayr was in charge of ordering, cataloguing and integrating it with the Whitney collections and other material of the American Museum. Until 1953, when Mayr became Alexander Agassiz Professor of Zoology at Harvard University, he was first of all an ornithologist.

In *Systematics and the Origin of Species* Mayr integrated the progressive ideas of European systematics on populations and speciation with the mutation-selection theory. In the tradition of the new systematics Mayr showed that the origin of distinct species can be explained as the result of a gradual, continuous process: 'A new species develops if a population which has become geographically isolated from its parental species acquires during this period of isolation characters which promote or guarantee reproductive isolation when the external barriers break down' (Mayr 1942: 155). Like Stresemann and Rensch he demonstrated the potential of systematics for the study of evolution, but unlike Stresemann and the early Rensch (until 1935) he based his inferences on the mutation-selection theory, developed by Dobzhansky and his predecessors. He convinced the evolutionists that discontinuities could gradually arise and can be explained by studying geographic variation. The vertical dimension of evolution was thus supplemented by the horizontal dimension.

#### Conclusion

Birds played a very important role in the history of the theory of evolution. They provided Darwin with two important test cases: the Galapagos birds convinced him of the continuous transition from varieties to spe-

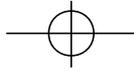
cies, the breeding of pigeons demonstrated the power of selection. Nineteenth century ornithologists, however, were overwhelmingly reluctant to accept the new dynamic theory.

This changed in the second third of the twentieth century. Museum ornithologists were among the most progressive systematists of their time. Important proponents like Stresemann and Rensch were also very much interested in basing systematics on evolution. They did not, however, accept the new mutation-selection-theory of the geneticists, but preferred other evolutionary mechanisms.

Two phases in the development of the modern Darwinian theory of evolution have to be distinguished: the synthesis of the genetical theory of inheritance and selection (anagenesis) during the 1920s and the integration of a theory explaining the splitting of species through geographic isolation (cladogenesis) in the 1930s and 40s. Mayr and Rensch (after 1938) demonstrated that systematics could play a central role in Synthetic Darwinism by providing a theory for the horizontal component of evolution, i.e. cladogenesis.

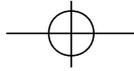


**Figure 2.** Ernst Mayr at a meeting of the Saxony Ornithologists' Association (about 1925).



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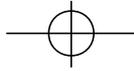
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## Migrating swans profit from favourable changes in wind conditions at low altitude

Marcel Klaassen<sup>1</sup>, Jan H. Beekman<sup>1,2</sup>, Jari Kontiokorpi<sup>3</sup>,  
Roef J. W. Mulder<sup>1,2</sup> and Bart A. Nolet<sup>1</sup>

Because energy reserves limit flight range, wind assistance may be of crucial importance for migratory birds. We tracked 8 Bewick's swans *Cygnus columbianus bewickii*, using 95 g satellite transmitters with altimeters and activity sensors, during their spring migration from Denmark to northern Russia in 1996. During the 82 occasions where a swan's location was recorded in flight, average flight altitude was 165 m a.s.l. with a maximum of 759 m a.s.l., despite winds often being more favourable at higher altitudes. We also counted Bewick's swans departing from the Gulf of Finland and subsequently passing an observatory in the next major stop-over area 800 km further north in the White Sea, northern Russia, during the springs of 1994, 1995 and 1996. A comparison of these counts with wind data provided evidence for Bewick's swans using favourable changes in wind conditions to embark on migration. Changes in the numbers of birds arriving in the White Sea correlated best with favourable changes in winds in the Gulf of Finland one day earlier. Again, migratory volume showed a correlation with winds at low altitudes only, despite wind conditions for the swans being more favourable at high altitudes. We conclude that the relatively large Bewick's swan tends to gear its migration to wind conditions at low altitude only. We argue that Bewick's swans do not climb to high altitudes because of mechanical and physiological limitations with respect to the generation of power for flight and to avoid rapid dehydration.

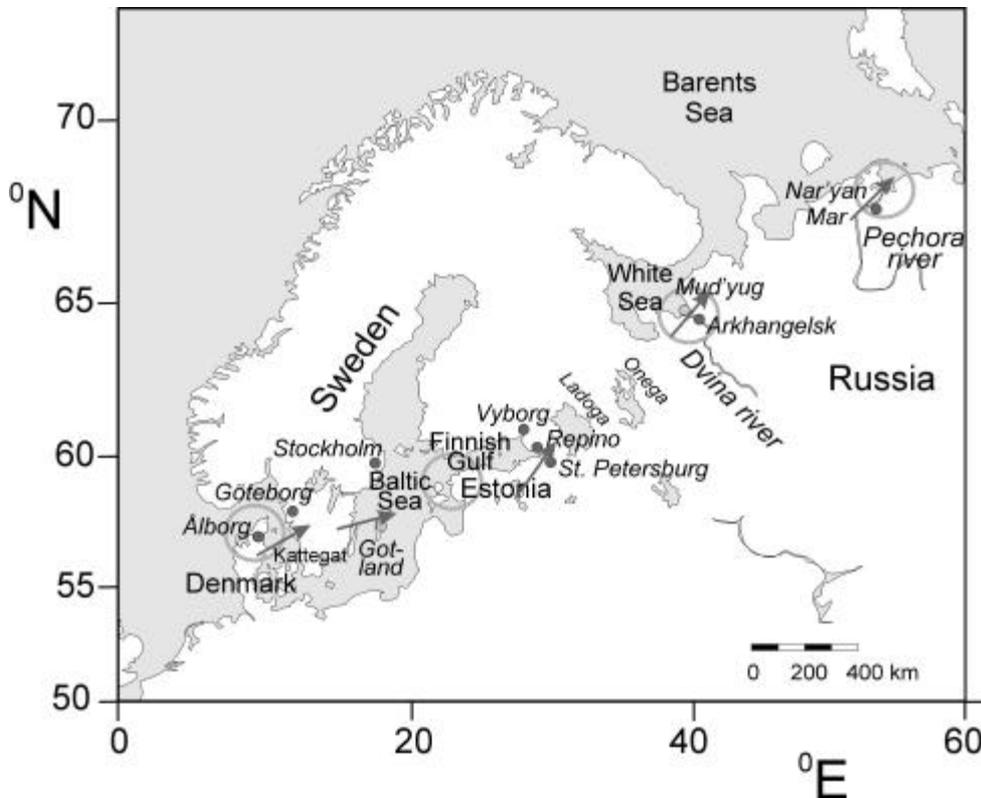
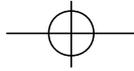
Keywords: Bewick's swan, *Cygnus columbianus bewickii*, migration, flight altitude, tailwind vector, satellite transmitters.

<sup>1</sup>Netherlands Institute of Ecology, Centre for Limnology, P.O. Box 1299, 3600 BG Maarssen, The Netherlands; <sup>2</sup>Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands; <sup>3</sup>Reinikaisenkatu 5 E 21, FIN-56800 Simpele, Finland; <sup>1</sup>corresponding author: m.klaassen@nioo.knaw.nl

Migratory birds may save energy by flying with tailwinds. In various species of birds a strong correlation has been observed between the number of birds passing ('migratory volume') and the degree of wind assistance (e.g. Alerstam & Bauer 1973, Alerstam 1978, Bergman 1978, Blokpoel & Richardson 1978, Richardson 1978). For some species of birds it is even claimed that these are unable to complete the migratory journey successfully without substantial wind assistance (Piersma & Jukema 1990).

Wind conditions change with altitude. While wind force tends to increase with altitude, wind direction

may change by as much as 180 degrees under special conditions. Based on these meteorological phenomena it has been argued that migratory birds may virtually always enjoy wind assistance by selecting the right flight altitude (e.g. Piersma & Jukema 1990, Piersma & Van de Sant 1992). That large birds may indeed fly at altitudes exceeding 6 km has been substantiated by various visual and radar observations (e.g. Manville 1963, Swan 1970, Elkins 1979). However, these might be extreme cases, since many radar studies on flight altitudes show that most birds do not fly at altitudes above c. 2000 m a.s.l. (Alerstam 1990). Especially



**Figure 1.** Spring migratory flyway of Bewick's swans from Denmark to the Pechora Delta in northern Russia. The major stop-over sites are indicated with circles. Arrows indicate migratory directions assumed in the calculations of tailwind vectors. All geographic names appearing in the text are indicated.

large birds, such as geese and swans, may be limited in their capacity to climb to and fly at high altitude, because of their slow rate of ascent (Hedenström & Ålerstam 1992) and their already high power requirement and water loss during flight, both of which are predicted to increase with an increase in altitude (Pennycuik 1989, Klaassen et al. 1999).

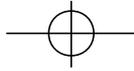
To investigate how wind conditions may govern migration in large birds, we studied the timing of migration and flight altitude in Bewick's swans *Cygnus columbianus bewickii* (4.5 to 7.5 kg) in relation to wind conditions at a range of altitudes. Ten birds were equipped with satellite transmitters with pressure, temperature and activity sensors providing regular information on location and altitude of flight during their spring migration from Denmark to northern Russia. In addition, we correlated migratory volumes of Bewick's swans flying from the Gulf of Finland to the next major staging site in the Russian White Sea with temporal changes in wind conditions at ground level, 1.5 km and 3 km altitude. The results indicate that Bewick's swans tend to tune their departure to favourable changes in

wind conditions. However, apparently only winds at low altitude are used, despite more favourable wind conditions at high altitude. We argue that high altitude migration may become increasingly problematic for migratory birds with an increase in size as a result of physiological and mechanical limitations.

## Methods

### Satellite tracking

Ten male Bewick's swans were caught by cannon netting near Ålborg, Denmark (57° 11' N, 09° 52' E; Fig. 1) between 26 March and 1 April 1996. The birds were equipped with 95 g PTT (Platform Transmitter Terminal) transmitters (Microwave Telemetry Inc.), attached by a neoprene flexible harness to (for methods see Pennycuik et al. 1996) and glued onto the back feathers. The birds were kept in captivity overnight after which they were released and subsequently tracked by the ARGOS satellite system. The satellite transmitters were



programmed to relay a message every minute. When located by one of the ARGOS satellites (8 to 20 times per 24h), the satellite could estimate the transmitter's longitude and latitude using the Doppler shift in frequency. The transmitters were also equipped with sensors providing data on external air temperature, barometric pressure and the bird's activity (by a mercury switch). Transmitted data from the barometric pressure sensor allowed for the calculation of the altitude of the swan with an accuracy of  $\pm 35$  m after correction for barometric pressure at ground level. Local weather data at ground level were taken from the 'European Meteorological Bulletin' (Deutscher Wetterdienst, Offenbach, Germany). To determine whether the bird was located in flight or on the ground we used the telemetric measurements on activity, and the measurements on external air temperature and barometric pressure in combination with the ground level local weather data. One of the transmitter-equipped Bewick's swans was killed by a red fox *Vulpes vulpes* close to the catching site 5 days after release. One transmitter had a technical failure. The bird wearing this transmitter was identified by its neck collar in southern Sweden 16 days after release, and was thus considered as migrating according to normal timing. For the remaining eight swans, battery lifetime of their satellite transmitters ranged between 33 and 66 days. These swans were tracked over varying distances along their migratory flyway, ranging between 518 and 2,800 km. One PTT ceased transmission early on the island of Gotland. One of the swans died en route after covering 723 km. Of the remaining six swans, five were about two weeks behind schedule with respect to most swans in that year, when data transmission ceased in the Gulf of Finland. We were able to track only one swan to the centre of the Bewick's swans' breeding distribution. It arrived near the Pechora river delta on 5 June, which was one day after ice break-up at this location (J. H. Beekman, pers. obs.). At least five individuals were resighted on the wintering grounds the next season.

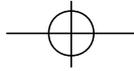
For comparing flight altitude with wind conditions aloft for individual swans equipped with satellite transmitters, daily wind speed and direction for 15 March 1996 until 7 June 1996 over Kattegat (meteorological stations Ålborg and Göteborg), NW Baltic (Stockholm), Gulf of Finland (St. Petersburg), White Sea (Arkhangelsk) and the Pechora Delta (Nar'yan Mar) were taken from synoptic weather maps in the 'Euro-

pean Meteorological Bulletin' (Deutscher Wetterdienst, Offenbach, Germany). Data were taken from surface level maps (i.e. 10 m above ground level [a.g.l.] measured at 00 UTC), and from maps of pressure levels of 850 hPa (c. 1500 m a.s.l.) and 700 hPa (c. 3000 m a.s.l.; both at 12 UTC). These wind data were used in the calculation of the potential tailwind vector ( $V_{tw}$ ,  $m.s^{-1}$ ), which was calculated for each day and altitude according to Piersma & Jukema (1990) and assuming that Bewick's swans fly at an airspeed of  $20 m.s^{-1}$  (pers. obs., T. Alerstam, pers. comm.; Sladen et al. 1969; B. Koks, pers. comm.) with a migratory direction of  $60^\circ$  over the Kattegat,  $75^\circ$  over the NW Baltic,  $35^\circ$  over the Gulf of Finland,  $40^\circ$  over the White Sea and  $45^\circ$  over the Pechora Delta (Fig. 1)

#### Observations on migratory volume

Bewick's and whooper swans *Cygnus cygnus* stage in large numbers in the Gulf of Finland in April and May (V. A. Buzun, S. P. Rezvyi and G. A. Noskov, pers. comm.). Spring migration observations in the Gulf of Finland were performed at two Russian locations: in May 1994 and 1995, 86.5 and 79 observation hours were made on 10 and 11 days in Repino ( $60^\circ 10' N$ ,  $29^\circ 50' E$ ) and in May 1994, 1995 and 1996, 179, 255 and 229 observation hours were made on 18, 23 and 21 days in Vyborg ( $60^\circ 42' N$ ,  $28^\circ 45' E$ ), respectively. Out of 48 % of the passing swans identified, 94 % were Bewick's swans and only 6 % were whooper swans. We estimated the daily total numbers of each swan species by assuming that the unidentified portion had the same ratio of the two species as the identified portion on the same day. Since observation effort varied strongly between days ( $0.5-19.5 h.day^{-1}$ , average  $10 h.day^{-1}$ ), we extrapolated migratory volume to the maximum observation duration of 19.5 h day.

Spring migration of Bewick's swans was also observed from a 10 m high tower of a weather station at the southernmost tip of Mud'yug ( $64^\circ 52' N$ ,  $40^\circ 15' E$ ), an island in the Dvina Bay, White Sea, 30 km NNW of Arkhangelsk, Russia. It is a large fresh to brackish shallow water area with extensive fields of fennel pondweed *Potamogeton pectinatus* and eelgrass *Zostera marina* that attract large numbers of Bewick's swans every spring (Nolet et al. 2001). The Dvina Bay is the last major stop-over site for the swans before departure to the breeding grounds. The major stop-over site for



Bewick's swans preceding the White Sea is the Gulf of Finland, a direct distance of 800 km.

From Mud'yug, swan migration was observed from 7 to 31 May 1994, from 4 to 17 May 1995 and from 1 to 27 May 1996. Observations were conducted every day between 05:00 and 22:00 h. Swans were never noticed passing the observation point outside these times of day. In 1994 continuous counts were made. In 1995 and 1996, on days when few swans were passing the observatory, every two hours of observation was followed by a 1 hour pause. About 30 % of the swans passing were not identified to the species level. We used the observed ratio of Bewick's and whooper swans on a given day to assign the unidentified swans to the two species groups (more than 99 % of the identified swans were Bewick's swans). Of each group of passing swans, time of passage, group size and flight direction were noted. The number of passing birds was extrapolated to a 17 h day for those cases where observations were conducted for only part of the day.

For both Gulf of Finland and White Sea, a normal distribution was fitted to the number of swans passing the observatories each spring to assess the year-specific seasonal trend in migratory volume. The daily number of passing swans relative to the fitted seasonal trend in migratory volume ( $\Delta N$ ) was calculated by subtracting the expected number of swans for that specific day according to the fitted normal distribution ( $N_e$ ) from the actual daily numbers ( $N$ ).

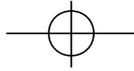
For the comparison of migratory volume of swans at Mud'yug with wind conditions, data were taken for May 1994, 1995 and 1996 over the Gulf of Finland and White Sea. Again, wind data for 10 m a.g.l., 1500 m a.s.l., and 3000 m a.s.l. were obtained from synoptic weather maps in the 'European Meteorological Bulletin'. For the swan counts from the observatories in the Gulf of Finland and the White Sea, we correlated migratory volume with wind data over Gulf of Finland and White Sea. Since in our view the number of birds profiting from wind assistance on a given day depends in part on the potential tailwind vectors in the foregoing period (see also Alerstam 1978), we calculated a relative tailwind vector ( $\Delta V_{tw}$ ,  $m.s^{-1}$ ) as the actual tailwind vector minus the average tailwind vector over the preceding three days. We thus correlated the relative number of passing swans (i.e. corrected for the seasonal trend) with the relative tailwind vectors (i.e. a change in wind conditions) measured at the same day (i.e.  $\Delta N_t$

with  $\Delta V_{tw_t}$ ) at 10 m a.g.l., 1500 m a.s.l. and 3000 m a.s.l. We also compared numbers passing the observatory in the White Sea with wind conditions in the Gulf of Finland. Bewick's swans could theoretically cover the distance between Gulf of Finland and White Sea within 12 h assuming an average ground speed of 20  $m.s^{-1}$ . However, our satellite tracking studies in Bewick's swans (Beekman et al. 2002) and those by Pennycook et al. (1996) on whooper swans indicate that swans rarely cover such distances in non-stop flight, but make regular landfalls instead. The actual speed of migration between major stop-over sites is therefore slower. We thus correlated relative number of swans passing Mud'yug (i.e.  $\Delta N_t$ ) with relative tailwind vectors from the three different altitudes measured over the Gulf of Finland on the same day (i.e.  $\Delta V_{tw_t}$ ), the previous day ( $\Delta V_{tw_{t-1}}$ ), two days before ( $\Delta V_{tw_{t-2}}$ ) and three days before ( $\Delta V_{tw_{t-3}}$ ). We tested for a year effect using a one-way analysis of covariance, with relative tailwind vector as the covariant and year as the factor. In all cases there appeared to be no year-effect (Table 1 and 2). Data from all years were thus pooled after which we conducted a linear regression analysis. To test for a positive slope between the relative number of swans passing Mud'yug and relative tailwind vector we subsequently used a one-tailed t-test. To test for a simultaneous effect of wind conditions at various altitudes on migratory volume we used stepwise multiple regression analyses.

## Results

### Satellite tracking

Over the whole journey from Denmark to the Pechora Delta (Fig. 1), we recorded 5 to 28 positions per individual (total 82) while flying (further referred to as 'in-flight trackings'). The average flight altitude was 165 (s.d. = 136) m a.s.l. with a maximum of 759 m (Fig. 2). We tested for the effect of individual bird and flying over sea or land on flight altitude using GLM ANOVA after the data were square-root transformed to avoid heteroscedasticity. Although there was a tendency for birds to fly lower over the sea (average = 102 m a.s.l., median = 89 m a.s.l., s.d. = 72,  $n = 43$ , max = 331) than over land (average = 156 m a.g.l., median = 115 m a.g.l., s.d. = 137,  $n = 39$ , max = 544;  $F_{1,66} = 3.13$ ,  $P = 0.081$ ),



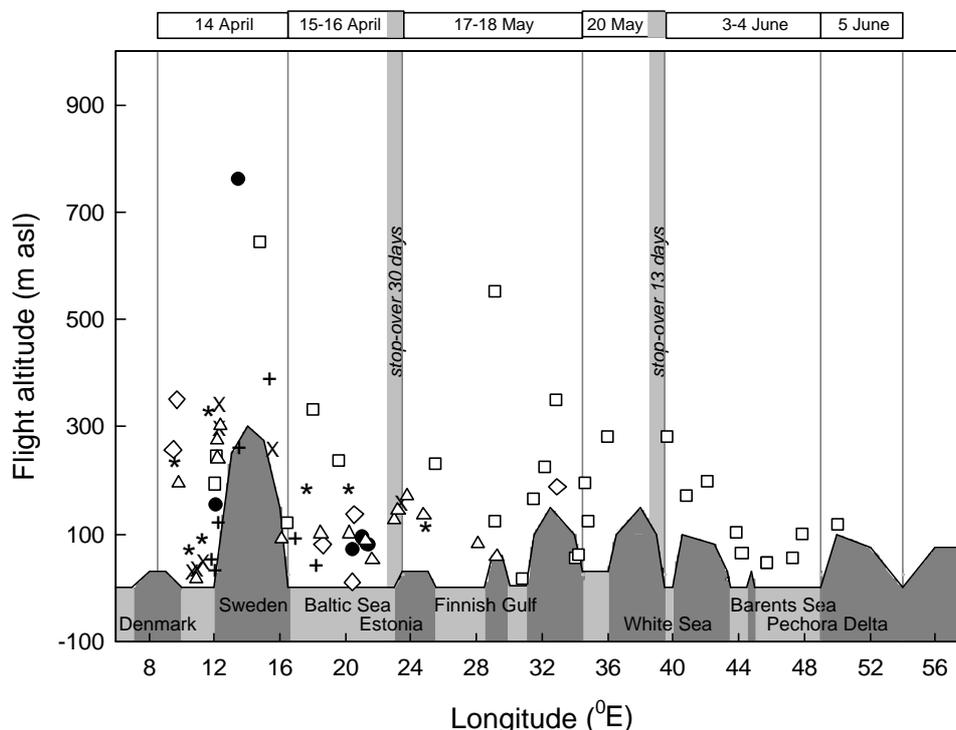
only a statistically significant effect of individual was found ( $F_{7,66} = 2.86$ ,  $P = 0.012$ ), i.e. some individuals flew higher than others.

Comparing the variation in tailwind vector at the three altitudes (Fig. 3) shows moderate and relatively stable tailwind vectors at 10 m a.g.l. at all sites. However, at 1500 m a.s.l. and 3000 m a.s.l. tailwind vectors were highly variable. At 3000 m a.s.l. the ground speed of a migrating Bewick's swan ranged from  $-11$  to  $40 \text{ m}\cdot\text{s}^{-1}$  or twice its air speed. In 77 % of the in-flight trackings where wind data were available ( $n = 63$ ), the tailwind vector at 1500 m a.s.l. was more favourable than at 10 m a.g.l. and in 75 % of the cases ( $n = 20$ ) it was even better at 3000 than at 1500 m a.s.l. However, there was no tendency for birds to fly higher with an increasing difference in tailwind vector between 1500 m a.s.l. and 10 m a.g.l. ( $r = -0.129$ ,  $n = 63$ ,  $P > 0.2$ ). Thus, in terms of exploiting optimal-tailwinds, in the majority of cases the Bewick's swans in this study were fly-

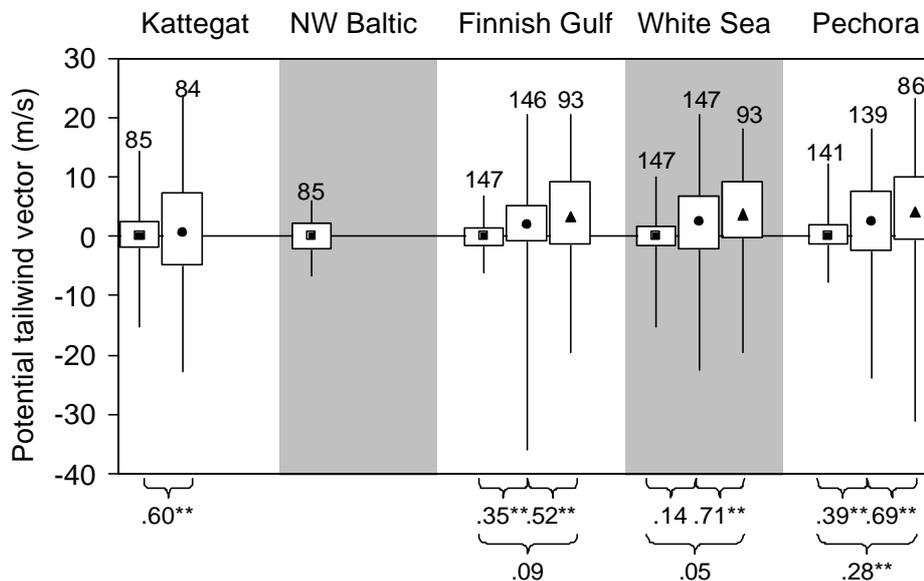
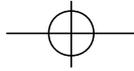
ing at a lower altitude than expected. The predictability of favourable tailwinds at high altitude may be problematic. That part of the variation in tailwind vectors at 3000 and 1500 m a.s.l. explained by tailwind vectors at 10 m a.g.l. ranged between 2 and 36 % and 0 and 8 %, respectively, for the different sites (Fig. 3).

### Observations of migratory volume

In 1994 and 1995 there was strong migration in the Gulf of Finland near Repino, but only weak migration was observed in Vyborg (a total of 1318 and 1100 Bewick's swans were observed migrating northwards in Repino in these respective years, compared with only 64 and 134 in Vyborg). In 1996 no observations were made in Repino. In Vyborg, very strong migration was observed (a total of 2076 Bewick's swans were observed migrating northward). We therefore used data from Repino during May 1994 and 1995 and from Vyborg during



**Figure 2.** Flight altitude of 8 Bewick's swans equipped with satellite transmitters in relation to their location (eastern longitude) along the spring migratory flyway from Denmark to the Pechora Delta in northern Russia (different symbols are used to indicate different individuals). Ground level is indicated with a thick line below which the location names are given (numbers with location names correspond with numbers in inset). At the top the dates of migration of the one bird that flew on schedule to the breeding grounds and from which we obtained most data ( $n = 26$  trackings; open squares) are indicated.



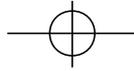
**Figure 3.** Potential tailwind vectors for Bewick's swans at 10 m a.g.l. (squares), 1500 m a.s.l. (dots) and 3000 m a.s.l. (triangles) at five weather stations along their spring migratory route. Symbols indicate the median, boxes the 25–75 % percentiles and bars the minimum and maximum values. The data presented are from May 1994 and 1995 (Gulf of Finland, White Sea and Pechora Delta only) and 15 March until 7 June 1996 (all stations). Sample sizes are indicated on top. Pearson correlation coefficients between tailwind vectors at 10 m a.g.l., 1500 m a.s.l. and 3000 m a.s.l. are indicated at the bottom of the graph (correlation coefficients significantly different from zero are marked \*\* ( $P < 0.01$ )).

May 1996 as a measure of spring migratory volume from the Gulf of Finland (Fig. 4).

On Mud'yug Island in the White Sea, counting efforts were more regular and a better impression was obtained of the spring migration pattern of Bewick's swans. In 1994, 1995 and 1996, respectively, 8750, 6790 and 13 040 Bewick's swans were observed passing the weather station on Mud'yug on a north-eastward course. Accounting for the observation gaps, approximately 9500 and 9100 Bewick's passed Mud'yug in 1994 and 1995, whereas in 1996 it was 19000 birds or 66 % of the estimated fly-way population (Beekman 1997). Although only in 1996 were counts made during virtually the whole of May, data from all years indicate low numbers during the first and last days of May and peak numbers occurring around mid-May (Fig. 4). Data for 1996 showed lower numbers of Bewick's swans passing Mud'yug during the first 10 days of May compared with numbers during the same period in May 1994 and 1995. This was probably related to a very slow advance of spring in 1996, as indicated by the date of ice break-up in the Dvina river which occurred on 8 May 1996, compared to 29 April 1994 and 23 April 1995. Ice

break-up in the shallow parts of the Dvina Bay around Mud'yug typically occurs one week after ice break-up in the Dvina river.

We compared the departure of swans from the Gulf of Finland with the timing of swans passing the observatory in the White Sea to discern the speed of migration over this stretch. Number of swans leaving Repino or Vyborg were correlated with numbers passing Mud'yug allowing for a duration of migration varying between 0 and 5 days. This analysis resulted in correlation coefficients for time lags of 0 to 5 days of  $-0.066$ ,  $0.459$ ,  $0.653$ ,  $0.439$ ,  $-0.142$  and  $0.298$ , respectively. This analysis thus indicates that most Bewick's swans probably cover the distance between the two sites in 1–3 days. A swan tracked on 17–20 May 1996 between western Estonia and the White Sea confirms this finding, making a one-day stop at Lake Onega on 19 May (Beekman et al. 1996). Another bird tracked in spring 1993 stopped for 22 days west of Lake Onega near Petrozavodsk (Beekman et al. 1996), but this location is known as a staging area of minor importance holding only some tens of birds annually (V. B. Zimin, pers. comm.).



**Table 1.** Results of ANCOVA and linear regression analyses testing the relationship between the relative number of birds passing Repino (in 1994 and 1995) and Vyborg (1996) at time  $t$  ( $\Delta N_t$ ) and the relative tailwind vector at 10 m a.g.l., 1500 m a.s.l. and 3000 m a.s.l. over Gulf of Finland at time  $t$  ( $\Delta Vtw_t$ ). Because the ANCOVAs showed no effect of year (F-tests; 2nd column), data from all years were pooled after which the linear regression analyses were conducted and the effects of the relative tailwind vectors were tested for a positive relationship with relative number of swans (one-tailed t-test; 3rd column).

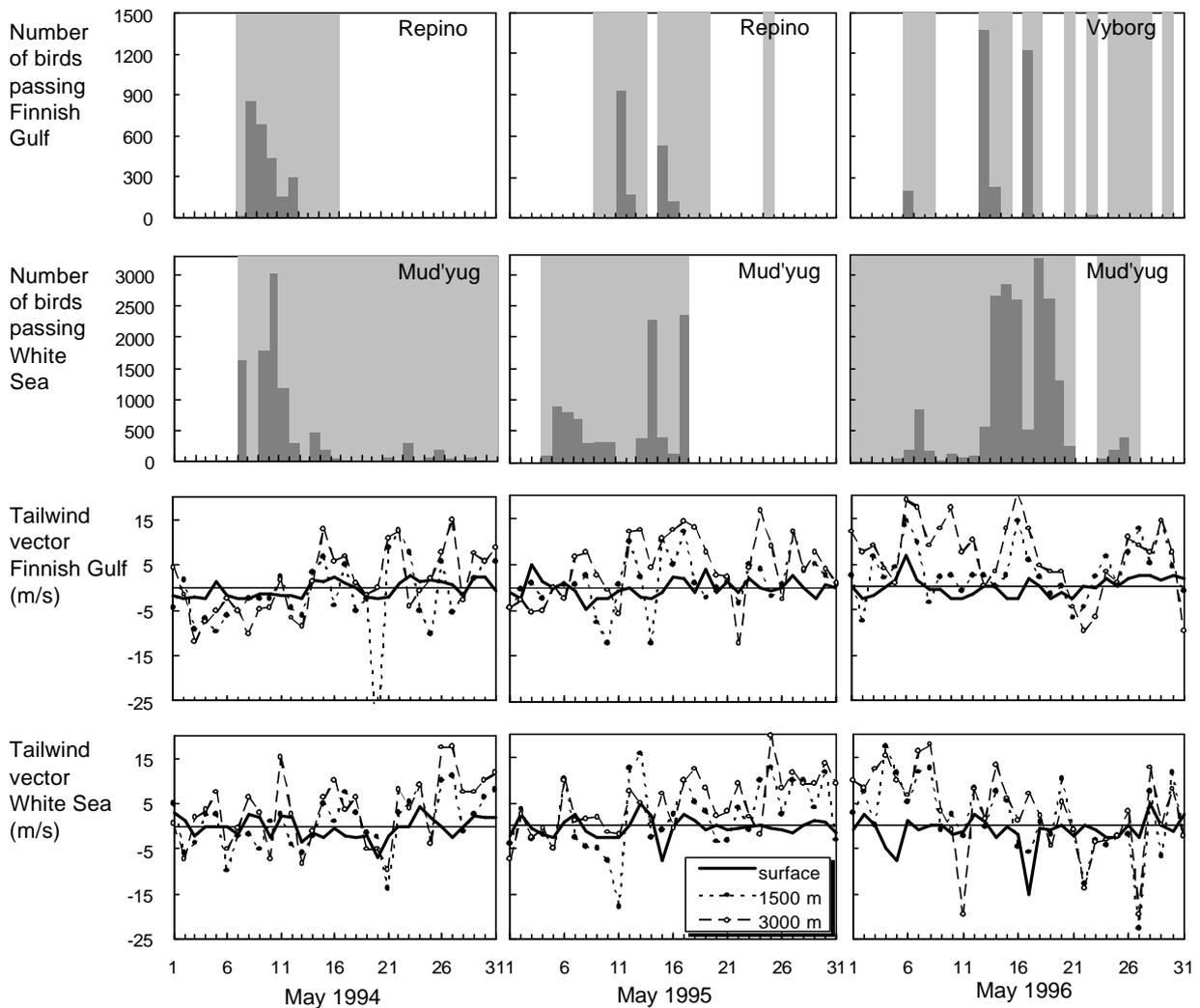
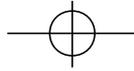
Covariate	Effect of year	Effect of covariate
Gulf of Finland $\Delta Vtw_t$ , 10 m a.g.l.	$F_{2,32} = 0.339$ , $P = 0.715$	$R = 0.287$ , $P = 0.045$
Gulf of Finland $\Delta Vtw_t$ , 1500 m a.s.l.	$F_{2,32} = 0.425$ , $P = 0.657$	$R = 0.175$ , $P = 0.154$
Gulf of Finland $\Delta Vtw_t$ , 3000 m a.s.l.	$F_{2,32} = 0.391$ , $P = 0.680$	$R = -0.388$

For both the Gulf of Finland and the White Sea, tailwind vectors vary considerably between days and altitudes (Fig. 4). If birds were to fly at any day in the months of May 1994, 1995 or 1996, the available tailwind-vector data for the Gulf of Finland and White Sea indicate that there was a 60 % chance that optimal conditions would prevail at 3000 m. There was less than 20 % chance that the most favourable winds would be found close to ground level. Average tailwind vectors would amount to 0, 1 and 4  $m \cdot s^{-1}$  over the Gulf of Finland and -1, 1 and 4  $m \cdot s^{-1}$  over the White Sea at 10 m a.g.l., 1500 m a.s.l. and 3000 m a.s.l., respectively.

When relating migratory volume in the Gulf of Finland to local changes in wind conditions a significant positive trend existed, but only between the relative number of departing Bewick's swans and the relative tailwind vector at 10 m a.g.l., and not with those at 1500 or 3000 m a.s.l. (Table 1). Similarly, a positive trend existed between the relative number of Bewick's swans passing the observatory on Mud'yug in the White Sea and the relative tailwind vector in that area on the same day at 10 m a.g.l. and not with those at 1500 or 3000 m a.s.l. (Table 2). None of the correlations between the daily estimates of the relative number of Bewick's

**Table 2.** Results of ANCOVA testing the relationship between the relative number of birds passing Mud'yug at time  $t$  ( $\Delta N_t$ ) and the relative tailwind vector at 10 m a.g.l., 1500 m a.s.l. and 3000 m a.s.l. over the White Sea and Gulf of Finland at time  $t$  ( $\Delta Vtw_t$ ) and over the Gulf of Finland at time  $t-1$  to  $t-3$  ( $\Delta Vtw_{t-1}$  to  $\Delta Vtw_{t-3}$ ). As the ANCOVAs showed no effect of year (F-tests; 2nd column), data from all years were pooled after which a linear regression analysis was conducted and the effects of the relative tailwind vectors were again tested for a positive relationship (one-tailed t-test; 3rd column).

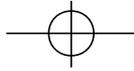
Covariate	Effect of year	Effect of covariate
White Sea $\Delta Vtw_t$ , 10 m a.g.l.	$F_{2,57} = 0.014$ , $P = 0.986$	$R = 0.236$ , $P = 0.033$
White Sea $\Delta Vtw_t$ , 1500 m a.s.l.	$F_{2,57} = 0.008$ , $P = 0.992$	$R = 0.125$ , $P = 0.170$
White Sea $\Delta Vtw_t$ , 3000 m a.s.l.	$F_{2,57} = 0.012$ , $P = 0.988$	$R = 0.032$ , $P = 0.405$
Gulf of Finland $\Delta Vtw_t$ , 10 m a.g.l.	$F_{2,57} = 0.013$ , $P = 0.987$	$R = -0.074$
Gulf of Finland $\Delta Vtw_t$ , 1500 m a.s.l.	$F_{2,57} = 0.017$ , $P = 0.983$	$R = -0.027$
Gulf of Finland $\Delta Vtw_t$ , 3000 m a.s.l.	$F_{2,57} = 0.005$ , $P = 0.995$	$R = 0.098$ , $P = 0.226$
Gulf of Finland $\Delta Vtw_{t-1}$ , 10 m a.g.l.	$F_{2,55} = 0.073$ , $P = 0.930$	$R = 0.293$ , $P = 0.013$
Gulf of Finland $\Delta Vtw_{t-1}$ , 1500 m a.s.l.	$F_{2,55} = 0.021$ , $P = 0.979$	$R = 0.024$ , $P = 0.428$
Gulf of Finland $\Delta Vtw_{t-1}$ , 3000 m a.s.l.	$F_{2,55} = 0.022$ , $P = 0.978$	$R = -0.004$
Gulf of Finland $\Delta Vtw_{t-2}$ , 10 m a.g.l.	$F_{2,53} = 0.047$ , $P = 0.954$	$R = 0.260$ , $P = 0.025$
Gulf of Finland $\Delta Vtw_{t-2}$ , 1500 m a.s.l.	$F_{2,53} = 0.002$ , $P = 0.998$	$R = 0.282$ , $P = 0.016$
Gulf of Finland $\Delta Vtw_{t-2}$ , 3000 m a.s.l.	$F_{2,53} = 0.002$ , $P = 0.998$	$R = -0.007$
Gulf of Finland $\Delta Vtw_{t-3}$ , 10 m a.g.l.	$F_{2,51} = 0.019$ , $P = 0.981$	$R = -0.023$
Gulf of Finland $\Delta Vtw_{t-3}$ , 1500 m a.s.l.	$F_{2,51} = 0.013$ , $P = 0.987$	$R = 0.044$ , $P = 0.374$
Gulf of Finland $\Delta Vtw_{t-3}$ , 3000 m a.s.l.	$F_{2,51} = 0.012$ , $P = 0.988$	$R = -0.105$



**Figure 4.** Daily migratory volume at the Gulf of Finland (Repino or Vyborg) and the White Sea (Mud'yug). Days on which counts were conducted are indicated by a shaded background. For each site and year tailwind vectors for Bewick's swans are depicted at 10 m a.g.l., 1500 m a.s.l. and 3000 m a.s.l. Average date of passing the observatory at Mud'yug in the White Sea is 11.1 (s.d. = 4.6), 12.0 (s.d. = 4.5) and 16.2 (s.d. = 3.8) May 1994, 1995 and 1996, respectively. Average date of departure from the Gulf of Finland is 9.3 (s.d. = 1.4), 12.7 (s.d. = 2.0) and 15.1 (s.d. = 2.8) May 1994, 1995 and 1996, respectively.

swans passing Mud'yug and the relative tailwind vectors at 10 m a.g.l., 1500 m a.s.l. and 3000 m a.s.l. measured over the Gulf of Finland on the same day as the counts was significant (Table 2). However, if we compare numbers passing Mud'yug with wind conditions at the site of departure (Gulf of Finland), taking a 1–3 day period to complete this migratory stretch into account, significant trends emerge. When we accounted for a 1-day time-lag between departure from the Gulf of Fin-

land and arrival in the White Sea a significant correlation was found between the tailwind vector at 10 m a.g.l. in the Gulf of Finland and the number of swans passing the observatory in the White Sea (Table 2). Taking a 2-day time-lag into account, significant correlations between both tailwind vector at 10 m a.g.l. and 1500 m a.s.l. in the Gulf of Finland and swans passing the observatory in the White Sea were obtained. In a stepwise multiple regression between relative number



of Bewick's swans passing Mud'yug and all relative tailwind variables given in Table 2, only the 1-day delayed relative tailwind vector at 10 m a.g.l. over the Gulf of Finland contributed significantly to the model.

In an attempt to estimate the advantage of flying with favourable winds we calculated the average tailwind vector that the swans enjoyed as:

$$\frac{\sum N \times V_{tw}}{\sum N}$$

and compared these with the average tailwind vector if the migratory volume at each day had exactly followed the seasonal trend:

$$\frac{\sum N_e \times V_{tw}}{\sum N_e}$$

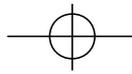
After subtracting the two we found for the four significant relations in Table 2 that on average the tailwind vector for the swans improved by 0.9, 0.6, 0.5 and 1.7 m.s<sup>-1</sup>, respectively, by selecting days with more favourable wind conditions.

## Discussion

For seven of the nine Bewick's swans with satellite transmitters that set off from Denmark for the breeding grounds in northern Russia the progress of migration was not according to expectation. The fact that many birds were delayed in their migratory timing casts doubt on the assumption that the swans show natural flight behaviour when fitted with satellite transmitters. Much smaller Black Brent *Branta bernicla nigricans* showed lower return rates and reduced breeding success when carrying transmitters (cf. Ward & Flint 1995). The swans that we equipped with satellite transmitters were caught at the end of the staging period in Denmark. Most staging birds in that area left within two days after the catches were made. The satellite birds, however, only left 2–3 weeks later. They apparently required some recovery time after being caught and it is therefore conceivable that they either temporarily lost their mates or missed the social stimulus of the flock to depart (Black 1988). This initial delay of two to three

weeks persisted during the rest of the spring migration, and some birds were later observed alone or in couples. However, of the nine birds that left Denmark, at least five were resighted (identification by neck collar) next winter. The depletion of food stocks at successive spring stop-overs may have prevented late-arriving swans from increasing fattening rates to compensate for time loss, and may also have prevented them from attaining full fuel reserves (Nolet & Drent 1998). However, we think that these indirect effects of catching the swans and equipping them with satellite transmitters would have had no impact on the flight altitude of the birds. The estimated flight altitudes of the one bird that flew on schedule to the breeding grounds and from which we obtained most data (n = 26 trackings), did not differ from flight altitudes obtained of the other birds (median test  $c_1^2 = 0.00$ , P = 1.00).

Even if Bewick's swans take wind conditions into account, this need not necessarily result in a correlation between tailwind vectors over the Gulf of Finland and migratory volume observed in the White Sea at Mud'yug, as intermittent stop-overs may occur between these two sites. Satellite-tracking studies have indicated that Bewick's swans stage in the area surrounding Lake Onega (63°N, 35°E; Beekman et al. 1996), 350 km south of the White Sea. In May however, foraging conditions between the Gulf of Finland and the White Sea are extremely poor due to ice-cover and especially in very late years, such as spring 1996 (J. H. Beekman and B. A. Nolet, pers. obs.), necessitating a virtually non-stop flight between these sites. Many of the birds arriving from the Gulf of Finland will land in areas of the White Sea closer by than the Mud'yug area, especially in the delta of the Dvina river. However, some of the swans fly directly as far as Mud'yug, as shown by one of the satellite tracked birds in 1996 (Nolet et al. 2001). In our opinion this justifies the correlation analysis we applied. Given the location of the observation points, counts at Repino and Vyborg relate to birds departing from the Finish Gulf, whereas at Mud'yug they relate to both arriving and departing birds. The latter might explain why, for the White Sea, positive correlations were obtained both between the relative number of swans and the local relative tailwind vector at 10 m a.g.l. on the same day, and between relative numbers and relative tailwind vector at 10 m a.g.l. over the Finish Gulf on the previous day. The first correlation might reflect departing and the latter arriving swans.



The results indicate that Bewick's swans tend to tune their migratory flight to favourable changes in wind conditions. By carefully selecting days with favourable (or less unfavourable) winds, Bewick's swans may be able to save considerably on energy costs for flight. For swans passing Mud'yug we calculated an average improvement of the tailwind vector following the four significant scenarios in Table 2 that varied between 0.5 and 1.7 m.s<sup>-1</sup>. Assuming an air speed of 20 m.s<sup>-1</sup> such wind assistance would lead to a reduction in flight cost per unit distance of 2.2–8.0 %. However, given the range of potential tailwind vectors (Fig. 3), there is potential for individual birds to save greatly on their costs of transport. The use of tailwinds has also been shown to be important for Bewick's swans on autumn migration (Beekman et al. 2002).

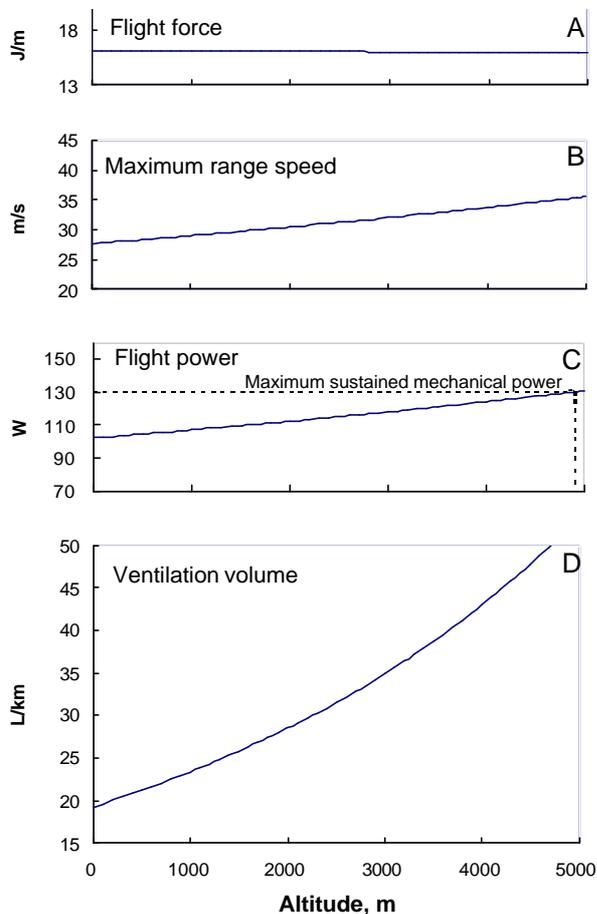
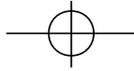
Our data suggest that Bewick's swans generally migrate at low altitudes. Other studies on selection of flight altitudes by northern swans confirm this suggestion. Bewick's, whooper and tundra swans *C. c. columbianus* usually fly at low altitudes, with some exceptions (Table 3). Thirty-nine radar trackings of Bewick's and whooper swans in the Baltic Sea area in southern Sweden indicate that low-altitude flights are common but that they regularly fly higher than 200 m over sea and higher than 700 m a.s.l. over land (T. Alerstam, unpubl. data). Bewick's swans departing from the Gulf of Finland usually fly at less than 100 m a.s.l., rarely 200 m a.s.l. (visual observations by JK). Radar tracking studies of east Siberian Bewick's swans and whooper swans also revealed that northward migration from Japan to Siberia over Sakhalin occurred at altitudes never exceeding 600 m a.s.l. (Ostapenko 1991). Tundra swans tracked by VHF radio and light aeroplanes were observed at altitudes ranging between 100 and 2,400 m a.g.l. (Sladen et al. 1969). Of eight whooper swans satellite-tracked while migrating over the Atlantic Ocean between Iceland and Scotland (Pennycuick et al. 1996, 1999), seven were flying at low altitudes (maximum altitude ranging between 68 and 387 m a.s.l., average = 228 m a.s.l.). However, one individual was tracked up to an altitude of 1856 m a.s.l. There is also one exceptional report of a flock of (probably whooper) swans that was encountered by an aeroplane at an altitude of 8200 m a.s.l. (Elkins 1979).

Why do Bewick's, as well as other swans, mostly fly at such a low altitude whereas more wind assistance is potentially available at higher altitudes? In part this

**Table 3.** Flight altitudes of northern swans.

Species	Flight altitude			Location and remarks	Reference
	Average ± s.d.	Usual range	Maximum		
Bewick's swan <i>Cygnus columbianus bewickii</i>	165 ± 136 m a.s.l. 102 ± 72 m a.s.l. 115 ± 137 m a.g.l.	Surface – 759 m a.s.l. Surface – 331 m a.s.l.	759 m a.s.l. 331 m a.s.l. 544 m a.g.l.	NW Europe <sup>4, a</sup> NW Europe <sup>1, 4, a</sup> NW Europe <sup>2, 4, a</sup>	This study This study This study
Tundra swan <i>C. c. columbianus</i>		Surface – 540 m a.s.l. < 100 m a.s.l. 100 – 2400 m a.g.l.	>540 m a.s.l. 200 m a.s.l. 2400 m a.g.l.	Sweden <sup>4, c</sup> Gulf of Finland <sup>3, e</sup> North America <sup>2, 4, b, d</sup>	T. Alerstam unpubl. J. Kontiokorpi unpubl. Sladen et al. 1969
Whooper swan <i>C. cygnus</i>	228 m a.s.l.	68 – 387 m a.s.l.	1856 m a.s.l. 8200 m a.s.l.	Iceland-Scotland <sup>1, 4, a</sup> Iceland-Scotland <sup>1, 4, c, d</sup>	Pennycuick et al. 1999 Elkins 1979
Bewick's and Whooper swans		150 – 300 m	600 m	Sakhalin Island <sup>4, c</sup>	Ostapenko 1991

<sup>1</sup>over sea  
<sup>2</sup>over land  
<sup>3</sup>at departure  
<sup>4</sup>mid-migration  
<sup>a</sup>satellite tracking  
<sup>b</sup>radio tracking  
<sup>c</sup>radar tracking  
<sup>d</sup>visual observation from aircraft  
<sup>e</sup>visual observation from ground



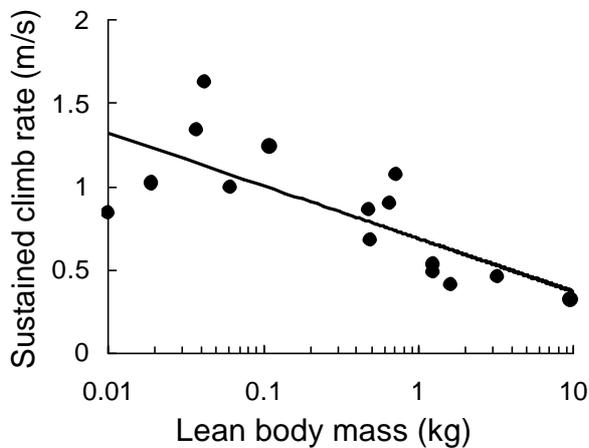
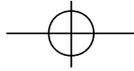
**Figure 5.** Predicted minimum mechanical costs per unit distance or flight force (A), maximum range speed (B), mechanical costs per unit time or flight power (C), and ventilation volume per unit distance (D) for a 6 kg Bewick's swan (see text). Calculations for A–C according to Pennycuick's (1989) model 1A and for D using the model presented by Klaassen et al. (1999). In C the maximum sustained flight power and the corresponding maximum flight altitude are indicated (for calculation see text). All y-axes in A–D are scaled to indicate identical relative changes in the parameters when flight altitude increases from 0 to 5000 m.

may be due to the low predictability of favourable tailwinds at high altitude from conditions on the ground (e.g. Piersma et al. 1990, this study). Flying at high altitude may also be problematic for large birds for aerodynamic and physiological reasons. According to aerodynamic theory, the power requirement for flight is a U-shaped function of flight speed. This relationship changes with increasing altitude because of a decrease in air density. Using Pennycuick's (1989) model 1A, we cal-

culated the mechanical power requirements for flight in relation to flight speed and air density for a 6 kg Bewick's swan with a wing span of 2.05 m, an aspect ratio of 8.67, and a body drag coefficient of 0.1. According to these calculations the minimum flight costs per unit distance remain virtually unchanged, decreasing by 0.7 % from sea level to 5000 m a.s.l. (Fig. 5a). However, the corresponding air speed at which these costs are minimal (i.e. the so-called maximum range speed,  $V_{mr}$ ) and, in conjunction, the mechanical power for flying at  $V_{mr}$  increased by almost 30 % from sea level to 5000 m a.s.l. Thus, despite only small changes in the energy costs per unit distance the energy costs per unit time increase dramatically with altitude (Fig. 5b–c).

With an increase in size, power requirements for flight as well as flight speed increase rapidly (Pennycuick 1989). Swans flying at low altitude may already be near the upper limit of what is physiologically possible. An increase in power output, for instance to enable flight at higher altitudes, may either not be attainable or would involve increased pathological risks or risk of injury. Pennycuick et al. (1996, 1999) found that whooper swans fly at speeds considerably below their maximum range speed (i.e. where flight costs per unit distance are lowest), suggesting that these swans avoid over-stressing of tendons, muscles and bones (i.e., reduce the risk of injury). The same phenomenon is apparent in Bewick's and tundra swans. Observed air speeds in these similar-sized species are approximately  $20 \text{ m}\cdot\text{s}^{-1}$ , which is substantially lower than the predicted maximum range speed at sea level of  $28 \text{ m}\cdot\text{s}^{-1}$  (Fig. 5b). The whooper swans that were reported flying at altitudes of 1856 m a.s.l. (Pennycuick et al. 1999), and even 8200 m a.s.l. (Elkins 1979) were probably carried to these high altitudes by lee waves (large scale air waves with upward movements; Pennycuick et al. 1996). It is likely that these birds use very little flapping to stay aloft, but instead use the upward lift for wave gliding as a mode of transportation, similar to Canada geese *Bran-ta canadensis* observed gliding at 5500 m over the Sierra Nevada (<http://www.silentflight.com/Gliding/Photos/photos.htm>).

While climbing, migrants probably fly at maximum power (Hedenström & Ålerstam 1992). The slow climbing rate in large birds such as swans is also an indication that their power requirements for cruising flight are close to the maximum and cannot be increased much further. Using data from Hedenström & Ålerstam



**Figure 6.** Sustained climb rate in relation to lean body mass for 15 species of birds. Data from Hedenström & Ålerstam (1992;  $y = 0.69 - 0.32 \text{ Log}_{10}(x)$ ,  $R^2 = 0.553$ ,  $P < 0.05$ ).

(1992) we compiled a relationship between lean body mass and the climb rate that the bird would be able to sustain for a long period of time (Fig. 6). According to this relationship, the predicted climb rate for a 6 kg Bewick's swan (with a lean mass of 4.8 kg) is  $0.47 \text{ m.s}^{-1}$  ( $1.7 \text{ km.h}^{-1}$ ), and for a 11 kg whooper swan (with a lean mass of 9 kg) is  $0.38 \text{ m.s}^{-1}$  ( $1.4 \text{ km.h}^{-1}$ ). At this rate of ascent the mechanical power requirements for a Bewick's swan to raise its weight against gravity are  $6 \text{ kg} \times 9.8 \text{ m.s}^{-2} \times 0.47 \text{ m.s}^{-1} = 28 \text{ W}$ . Adding this to the cruising power at sea level (102 W, Fig. 5c) yields a maximum sustained mechanical power output of 130 W. This maximum sustained mechanical power output level would permit flight at maximum range speed only at altitudes below 4900 m a.s.l. under normal air conditions.

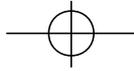
The mechanical power requirement for climb for our model Bewick's swan are approximately ( $28 \div 102 \text{ W} \times 28 \div 0.47 \text{ m.s}^{-1} =$ ) 16 times higher per unit distance than that in horizontal cruising flight. Because of muscle inefficiency, only about 23 % of the energy invested in gaining altitude is returned during descent. Thus, climbing costs may be an additional cause for Bewick's swans to remain flying at relatively low altitudes, although they have an insignificant impact on potential flight range.

Due to their high power requirements for flight and concomitant high rates of lung ventilation, large migrants especially may face problems of water imbal-

ance when flying at high altitude (Klaassen 1996). With an increase in altitude partial oxygen pressure decreases. Assuming oxygen extraction to remain unchanged, the ventilated volume of air through the lungs and therefore respiratory water loss (Carmi et al. 1992, Klaassen et al. 1999) will increase from sea level to 5000 m a.s.l. by as much as 175 % per unit distance flown and by 254 % per unit time flown (Fig. 5d). Dehydration may already be a problem for swans flying at low altitude. Migrating Bewick's swans are often observed to start drinking immediately upon arrival at stop-over sites (pers. obs.). A flock of whooper swans, one of which was carrying a satellite transmitter with a pressure sensor, flew close to sea level when making the crossing from Iceland to Scotland. Nevertheless, all members of this flock were seen to drink large amounts of fresh water upon arrival at the Scottish wintering grounds near Caerlaverock, just as nearly all arriving whooper swans are reported to do (Pennycuik et al. 1996). In contrast to whooper swans, Bewick's swans find abundant fresh water resources on their route and it may seem surprising that dehydration could be a problem for these birds. However a Bewick's swan, with a cruising altitude of 3000 m for maximal tailwind assistance, would need about two hours to regain its cruising altitude after a drinking pause. During normal flights of a few hundred kilometres, which can be covered in 4–6 hours, such a time loss makes climbing rather inefficient for seeking tailwind assistance.

We conclude that Bewick's swans probably mostly, though not exclusively, fly at low altitude because of mechanical and physiological limitations with respect to the generation of thrust for flight and to avoid rapid dehydration.

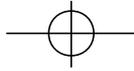
**Acknowledgements.** We are grateful to Bjarke Laubek, Jeroen Nienhuis, Erik Wessel, Stef van Rijn and Birte Hansen, for help during catching. Peter and Hanne Laubek are acknowledged for kindly hosting an entire Dutch catch- and film crew at their home in Denmark. We greatly benefited from information provided by our Russian colleagues in St. Petersburg and Petrozavodsk, notably V. A. Buzun, S. P. Rezvyi, G. A. Noskov and V. B. Zimin, about swan migration and ice conditions in spring in the Gulf of Finland and the great Karelian lakes Ladoga and Onega. We acknowledge the Meteorological Office, and in particular Pjotr A. Malygin of the Mud'yug weather station, for their hospitality and



permission to make use of the observation tower. We also thank Valery A. Andreev of the Committee of Environment Protection and Natural Resources of Arkhangelsk Region for his valuable co-operation. Rudi Drent paved the way for studying migratory waterfowl on Mud'yug Island. Anne Dekinga, Rudi Drent, Martin Epe, Anita Koolhaas, Oscar Langevoord, Martin Poot, Jeroen Nienhuis and Erik Wessel all spent long cold hours on the tower. Thomas Alerstam kindly allowed us access to his unpublished flight altitude data. Ten Dekkers, Harry Korthals and Melanie Paschke assisted in the careful analysis of the synoptic weather maps. Rudi Drent, Birgit Erni, Martin Green, Anders Hedenström and Felix Liechti gave valuable comments on earlier versions of the manuscript. This research was funded by the Netherlands Organization for Scientific Research (NWO-grant 047-002-008), the Beijerinck-Popping Fonds, the Groninger Universiteits Fonds and the Fonds voor Onderzoek der Natuur (FONA). This is publication xxxxx of the Netherlands Institute of Ecology and publication xxxxx of the Centre for Wetland Ecology.

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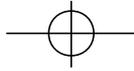
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## Sea crossing behaviour of falcons and harriers at the southern Mediterranean coast of Spain

Susanna K. Meyer, Reto Spaar and Bruno Bruderer

Using radar, we studied the migratory flight behaviour of harriers *Circus* spp. and falcons *Falco* spp. at the edge of a large water barrier. Arriving at the southern coast of Spain during autumn migration, raptors have to decide whether to cross the Mediterranean Sea by flapping flight (distance at least 150 km) or to fly a detour along the coast of the Iberian Peninsula (250 km) with the possibility of travelling by thermal soaring. In autumn, mean flight directions of falcons (228°) and harriers (229°) were similar, and the majority of falcons (57 %) and harriers (65 %) crossed the sea, preferably with support of following northwesterly winds. A higher proportion of Montagu's harriers *Circus pygargus* (74 %) than of the larger marsh harriers *C. aeruginosus* (50 %) crossed the sea. In spring, 65 falcons and 5 harriers approaching the coast from the sea had mean flight directions of 10° and 16°, respectively, and none of them was observed in strong northerly, i.e. opposing winds. In autumn, harriers slightly decreased air- and ground-speed as well as flight altitude when crossing the coast seawards, whereas falcons showed no change in flight behaviour. In spring, falcons approaching the coast from the sea decreased flight altitudes towards land, but no landings were observed within the 8 km range of the radar. The high proportion of birds crossing the sea, even during twilight and at night, and with little change in flight behaviour when crossing the coast seawards in autumn and landwards in spring, indicate that these small raptors are well adapted to cross relatively large water bodies on migration. By selecting following winds and stable weather conditions for sea crossing they reduce flight time to cross the sea and reduce the risks, in particular the potential hazard of sudden weather changes.

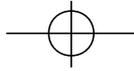
Key words: Migration, barrier, sea crossing, *Falco*, *Circus*, Mediterranean Sea, Spain

Swiss Ornithological Institute, CH-6204 Sempach, Switzerland; corresponding author: reto.spaar@vogelwarte.ch

Barriers such as the Alps, the Mediterranean Sea and the Sahara play an important role in the Eurasian-African bird migration system (Moreau 1972, Bruderer & Jenni 1990, Bruderer & Liechti 1995). Various adaptations in migratory birds as well as the actual migratory routes and flight strategies reflect the selection processes related to these obstacles.

Flight behaviour varies greatly among raptor species of different size and shows additional variability within species in response to varying environmental conditions (Kerlinger 1989, Spaar & Bruderer 1997a, Spaar 1999). Large raptor species such as eagles, buzzards and kites migrate predominantly by thermal soaring

and are therefore bound to fly over land as far as possible. This leads to concentrations at the geographic bottlenecks between Eurasia and Africa, such as the Strait of Gibraltar on the western flyway or the Bosphorus and other locations in the Middle East on the eastern flyway (Bijlsma 1987). Thermal convection enhances cross-country speed in soaring flight, and many species maximize cross-country speed by adopting thermal-dependent airspeeds according to optimal flight theory (Spaar & Bruderer 1997a, Spaar et al. 1998, Spaar 1999). Smaller raptors may additionally use flap-gliding (Spaar 1997). Thus, when arriving at a sea coast, they have the option of choosing between a



sea crossing and flying along the coast. Flying across a large water body implies powered flight and thus high energy expenditure, but may considerably reduce the time needed for the journey. Deterioration of weather conditions during a sea crossing may induce increased risks. Flying along the coast allows energy saving by soaring flight and reduces the risk of bad weather, but may require large detours. Relatively low numbers of small raptors observed at the Strait of Gibraltar (Cortes et al. 1980) indicate that many of them opt for a sea crossing.

In order to study decision-taking of small raptors at a sea coast we tracked harriers *Circus* spp. and falcons *Falco* spp. in autumn at the southern coast of Spain where this coast runs E–W and is not expected to induce any concentration. We hypothesized that (a) the proportion of sea crossings would be higher in smaller raptors; (b) the proportion of sea crossings would be higher in following than in opposing winds; and (c) unstable (low-pressure) weather conditions would lead to reduced numbers of sea crossings.

Most studies on water crossing behaviour of raptors have been carried out at concentration points such as the Strait of Gibraltar, Delaware Bay and Lake Superior, or on islands like Sicily and Malta (e.g. Evans & Lathbury 1972, Beaman & Galea 1974, Agostini & Logozzo 1995). Such studies emphasised the importance of land bridges and stepping-stones, while other studies showed that small raptors regularly migrate over large water barriers (e.g. Bannermann & Bannermann 1971, Beaman & Galea 1974, Thiollay 1977, Thake 1982, 1983, Galea & Massa 1985, Fuller et al. 1998). Nevertheless, exact measurements of flight parameters in such situations are rare.

The second part of this study deals, therefore, with the diurnal pattern of sea crossings and with reactions in flight behaviour when birds cross the coast seawards in autumn and landwards in spring. A reluctance of birds to fly offshore has been supposed to result in reduced flight speed combined with an increase in flight altitude above the unfamiliar habitat or even in return flights, particularly at dusk.

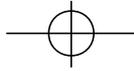
## Methods

### The study site

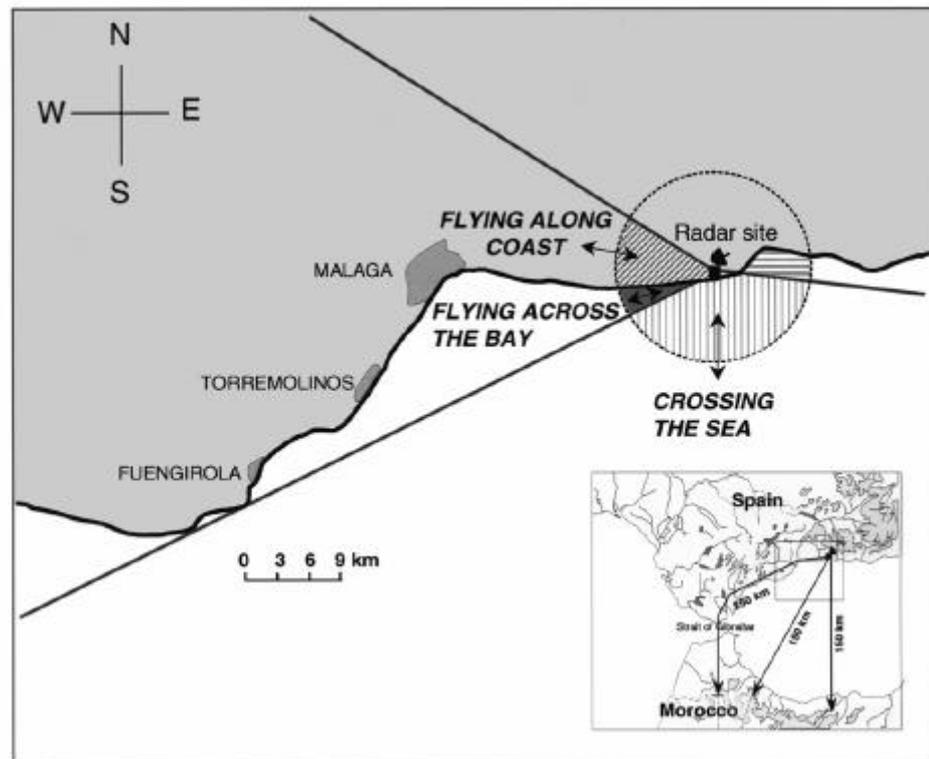
We studied raptor migration by radar at the south coast of the Iberian Peninsula (Spain), 25 km east of Malaga and 140 km northeast of Gibraltar (Fig. 1). The radar was situated about 300 m from the coast and about 50 m above sea level. The topography was not expected to have a concentration effect, as for example at the Strait of Gibraltar; but it might have a leading-line effect for soaring migrants following the coastline in autumn. The nearest point of the African coast across the Mediterranean Sea is at a distance of approximately 150 km and invisible for a migrant; the distance across land via Gibraltar from the radar station to a similar latitude is approximately 250 km (Fig. 1).

### Data recording

Data were collected from 10 August to 24 October 1996 and 22 March–25 May 1997. A tracking radar ('Superfledermaus') was used to track the birds' trajectories. It allows tracking of a single medium-sized raptor for up to about 8 km (for details see Bruderer et al. 1995). Targets for tracking were selected arbitrarily, and aimed to obtain long flight tracks. The birds' exact positions (x, y and z co-ordinates) were recorded every 1 s, and the flight path and wing-beat patterns were visualised on a computer monitor. The data were estimated by linear regression over consecutive intervals of 10 s. If possible, the bird species was identified using a 12.5x telescope mounted parallel to the radar beam. The flight behaviour of the birds was visually observed and recorded during the whole track. Visual observation of migrating raptors lasted from 0800 h to about 2000 h local time (UTC + 1 h). During the entire night, wing-beat patterns of an average of 280 tracked targets were stored electronically and allowed classification of various bird types (Liechti & Bruderer 1995). This method allows identification of raptors migrating at night (Stark & Liechti 1993, Spaar et al. 1998; see below). A daily break of two hours, alternately between 12–14 h and 14–16 h was needed for operational reasons such as data backup or radar maintenance. Wind speeds and directions at all flight levels were obtained from pilot balloons released and tracked every four hours up to 3000–4000 m above ground level.



**Figure 1.** Location of the radar and classification of migratory directions of falcons and harrisers in autumn (for details see Methods): 'crossing the sea' (flight directions  $95^{\circ}$ – $240^{\circ}$ ); 'flying across the bay' ( $240^{\circ}$ – $270^{\circ}$ , i.e. birds flying at least partially above sea); 'flying along the coast' ( $240^{\circ}$ – $300^{\circ}$ , birds flying above land). The circle indicates the range of the radar for tracking medium-sized raptors.



## Analysis

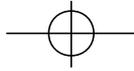
The digitised and visual records were used to quantify the proportions of gliding, soaring and flapping flight at a resolution of 10 s (Spaar 1997). Airspeed and heading direction while gliding were calculated by subtracting the wind vector at the respective flight altitude from the measured track vector (Liechti 1993). Air- and groundspeed are the mean velocities in gliding, soaring or flapping, relative to the air and ground, respectively. The tailwind component is the wind speed in the track direction. Horizontal flapping-gliding flight was assumed if vertical speeds of a straight flight did not exceed  $0 \pm 0.5 \text{ m}\cdot\text{s}^{-1}$ . Flight altitude of a bird is the mean altitude per track. Circular statistics are based on Batschelet (1981). To test whether raptors preferred or avoided migrating under particular wind conditions, we compared the distribution of wind directions at the individual bird's flight altitude (using the temporally nearest wind measurement) with the directional distribution of all available winds, the latter including the wind measurements at 8 h, 12 h and 16 h local time in 200 m intervals up to 2600 m a.s.l.

## Classification of migratory routes

We classified the autumn flight paths according to track direction and position relative to topography (Fig. 1): 'flying along the coast' comprises flights above land with track directions of  $240^{\circ}$ – $300^{\circ}$ , while 'flying across the bay' are tracks partly above sea with directions of  $240^{\circ}$ – $270^{\circ}$ . Raptors 'crossing the sea' flew out to the sea with directions of  $95^{\circ}$ – $240^{\circ}$ . To separate 'crossing the sea' and 'flying across the bay' we took the direction from the radar site towards the visible coastal tip near Fuengirola ( $240^{\circ}$ , distance approx. 50 km) which is a possible leading point under good atmospheric conditions (Fig. 1). North- or eastwards flying birds ( $300^{\circ}$ – $95^{\circ}$ ) were not included in the analysis. In spring, birds crossing the sea arrived with directions of  $275^{\circ}$ – $60^{\circ}$ .

## Reactions in flight behaviour when crossing the coast

To analyse reactions in flight behaviour when crossing the coastline, we subdivided long tracks of sea-crossing birds into three sections 'above land' and 'above sea'



(for both distances to the coastline  $>750$  m), and 'above coast' (distance to the coastline  $<750$  m). For each section, mean flight altitude, vertical speed, and horizontal air- and groundspeed were calculated. Only flight tracks containing all three sections were included in the analysis in Table 2. Mean track length of these flight paths was 500 s (range 410–930 s) in falcons and 550 s (310–960 s) in harriers.

We estimated the duration of Mediterranean Sea crossings according to the measured groundspeeds of the birds in Table 1, but including tracks with vertical speeds between  $0 \pm 1$  m.s<sup>-1</sup>. We assumed a constant flight speed while over water and a crossing distance of 150 km.

### Species and numbers recorded

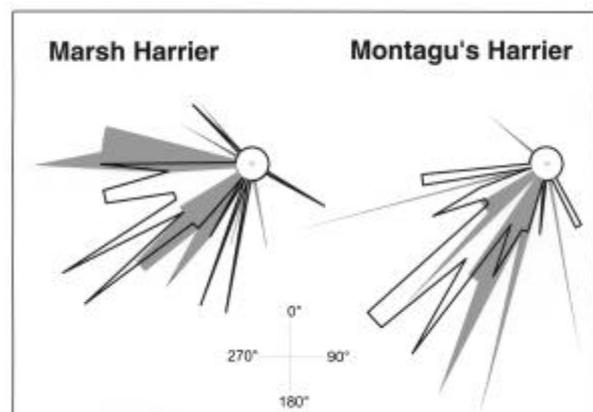
The following numbers of tracked birds of prey do not represent real numbers of migrating raptors passing the radar station, because birds were tracked for as long as possible to document eventual reactions in flight behaviour when confronted with the coast. The passage of other raptors during that time was therefore not recorded. In autumn 1996, 144 tracks of falcons were recorded (2 peregrines *Falco peregrinus*, 16 common kestrels *Falco tinnunculus*, 10 hobbies *Falco subbuteo*, 8 lesser kestrels *Falco naumanni*, and 108 unidentified *Falco* spp.). In spring, 65 falcons were tracked (1 peregrine, 4 hobbies, 9 kestrels and 51 unidentified). The high number of unidentified falcons was due to large observation distances and/or bad light conditions.

One hundred and two harrier tracks were recorded in autumn (26 marsh harriers *Circus aeruginosus*, 15 Montagu's harriers *Circus pygargus*, 18 Montagu's or hen harriers *Circus cyaneus*, and 43 unidentified *Circus* spp.). In spring, only five tracks of harriers were recorded (3 marsh harriers, 1 Montagu's harrier, and 1 unidentified). Females and juveniles of Montagu's and hen harriers are very similar in plumage, and identification of the two species is possible only under optimal conditions (Gensbøl 1997). They have distinct migratory periods, however, Montagu's harriers migrating from the end of August until the middle of September, and hen harriers starting migration at the beginning of October (90 % limits of observations at Gibraltar, Bernis 1980). The 18 female or juvenile Montagu's or hen harriers were observed before the end of September and were therefore probably Montagu's harriers. These

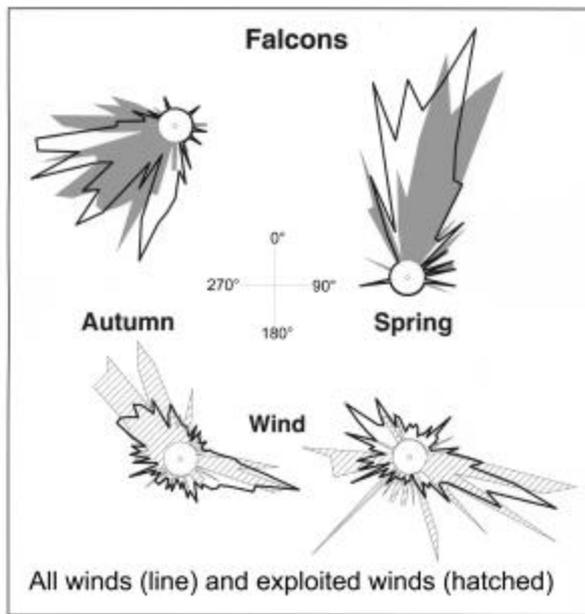
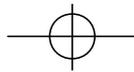
birds were pooled with identified Montagu's harriers for further analysis.

### Nocturnal migration of raptors

It is possible to identify raptors at night by their characteristic wing-beat patterns (Stark & Liechti 1993, Spaar & Bruderer 1997b, Spaar et al. 1998). To distinguish other species groups from small falcons and sparrowhawks *Accipiter* spp. at night, Stark & Liechti (1993) set the upper limit of the wing-beat frequency to 5.5 Hz (to exclude alpine swifts *Apus melba*) and the lower limit to 4.0 Hz (to exclude gulls *Larus* spp. with frequencies of 3–4 Hz; B. Bruderer & A. Boldt pers. comm.). In Spain, the wing-beat frequency of visually identified raptors was  $3.4 \pm 0.3$  Hz in harriers (mean  $\pm$  s.d.;  $n = 64$ , range 3.0–4.3 Hz) and  $5.1 \pm 0.4$  Hz in falcons ( $n = 162$ , range 3.8–6.2 Hz). It was therefore not possible to separate harriers from gulls electronically. Taking the same frequency limits as Stark & Liechti (1993), we electronically identified 23 falcons in autumn and 30 in spring at night and during twilight, among them 11 and 15 falcons crossing the sea, respectively (see also Fig. 4).



**Figure 2.** Circular distribution of track (line) and heading (shaded) directions of marsh and Montagu's harriers in autumn. Tracks and headings of Montagu's harrier were significantly more southerly compared to marsh harriers.



**Figure 3.** Circular distribution of track (line) and heading (shaded) directions of falcons in autumn and spring. The distributions are given of wind directions when tracking the birds (hatched) and all available winds (bold line; for details see Methods).

**Results**

**Migratory directions and sea crossing**

In autumn, the average track and heading directions of harriers and falcons were southwesterly, both with a large variance (Fig. 2 and 3). Flight directions did not differ statistically between falcons and harriers (mean  $\pm$  s.d.; falcons, track  $228^\circ \pm 36^\circ$ , heading  $240^\circ \pm 35^\circ$ ,  $n = 144$ ; harriers, track  $229^\circ \pm 31^\circ$ , heading  $231^\circ \pm 34^\circ$ ,  $n = 102$ ; Watson-Williams test; track,  $F_{1,242} = 0.01$ , n.s.;

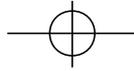
heading,  $F_{1,242} = 3.22$ , n.s.). Mean track and heading directions differed significantly, however, between marsh and Montagu's harriers (marsh harrier: track  $238^\circ \pm 34^\circ$ ,  $n = 26$ , heading  $250^\circ \pm 40^\circ$ ,  $n = 26$ ; Montagu's harrier: track  $220^\circ \pm 26^\circ$ ,  $n = 32$ , heading  $214^\circ \pm 28^\circ$ ,  $n = 30$ ; Watson-Williams test, track  $F_{1,56} = 4.76$ ,  $P < 0.05$ , heading  $F_{1,54} = 12.98$ ,  $P < 0.01$ ; Fig. 2). A higher proportion of the heavier marsh harriers followed the coast compared to Montagu's harriers (Montagu's harrier: 74 % crossing the sea, 16 % flying along coast and 10 % flying across the bay; marsh harrier: 50 %, 29 % and 21 %, respectively). Sixty five percent of all harriers and 57 % of all falcons directly crossed the sea. Seven out of the 16 tracked common kestrels (43 %) flew along the coast and eight (50 %) directly crossed the sea. The smaller hobby and lesser kestrel mainly crossed the Mediterranean Sea (7 out of 10 hobbies, and 5 out of 8 lesser kestrels), while only one individual of each species flew along the coast.

In spring, mean track and heading directions of falcons were  $10^\circ \pm 29^\circ$  and  $15^\circ \pm 40^\circ$  ( $n = 65$ ), respectively. Track directions were more concentrated than in autumn, because only raptors arriving from the sea were observed at the radar site (Mann-Whitney test,  $Z = 3.7$ ,  $P < 0.001$ ; Fig. 3). Only five harriers were tracked in spring (track  $16^\circ \pm 17^\circ$ , heading  $19^\circ \pm 19^\circ$ ).

Wind distributions were bimodal in spring and autumn, as northwesterly and easterly winds prevailed (Fig. 3). Distributions of available winds and winds exploited by the birds differed significantly for falcons in autumn and spring (autumn: available winds  $129^\circ \pm 74^\circ$ ,  $n = 637$ , exploited winds  $340^\circ \pm 63^\circ$ ,  $n = 144$ , Watson's  $U^2$  test = 1.68,  $P < 0.001$ ; spring: available winds  $27^\circ \pm 79^\circ$ ,  $n = 602$ , exploited winds  $161^\circ \pm 63^\circ$ ,  $n = 65$ ,  $U^2 = 0.85$ ,  $P < 0.001$ ) and for harriers in autumn (available winds  $129^\circ \pm 74^\circ$ ,  $n = 637$ , exploited winds  $14^\circ \pm$

**Table 1.** Flight characteristics in horizontal flapping-gliding flight (vertical speed  $0 \pm 0.5$  m.s<sup>-1</sup>) of falcons and harriers crossing the sea. Harriers include Montagu's harrier, marsh harrier and unidentified harriers. Mean  $\pm$  s.d. Number of tracks are in brackets.

	Falcons		Harriers	Montagu's harrier	Marsh harrier
	spring	autumn	autumn	autumn	autumn
Groundspeed (m.s <sup>-1</sup> )	12.9 $\pm$ 3.5 (44)	13.7 $\pm$ 2.3 (27)	11.6 $\pm$ 2.3 (44)	11.6 $\pm$ 2.3 (14)	12.7 $\pm$ 3.2 (8)
Airspeed (m.s <sup>-1</sup> )	11.3 $\pm$ 2.6 (44)	11.7 $\pm$ 1.8 (26)	11.0 $\pm$ 1.8 (43)	10.7 $\pm$ 2.2 (13)	11.5 $\pm$ 2.3 (8)



**Table 2.** Changes in flight parameters of sea crossing birds flying seawards in autumn and landwards in spring, respectively. Long tracks were divided into three sections: 'above land', 'above coast' and 'above sea'. Sequence of flight sections were in autumn from 'above land' to 'above coast' to 'above sea', and in spring from 'above sea' to 'above coast' to 'above land'. Only tracks including all three sections were included (for details see methods). 'Above coast' = distance to coast line <750 m; 'above sea' and 'above land' = distance to coast line >750 m.

	Flight direction			Friedman ANOVA
	above land	above coast	above sea	
<i>Falcons</i>				
Autumn (n = 32 tracks)				
Flight altitude (m a.s.l.)	1392 ± 467	1359 ± 467	1325 ± 471	$\chi^2_{2,30} = 1.75$ , P = n.s.
Vertical speed (m.s <sup>-1</sup> )	-0.18 ± 0.63	-0.29 ± 0.79	-0.02 ± 0.55	$\chi^2_{2,30} = 1.68$ , P = n.s.
Groundspeed (m.s <sup>-1</sup> )	13.4 ± 4.7	13.3 ± 3.7	13.5 ± 3.7	$\chi^2_{2,30} = 0.82$ , P = n.s.
Airspeed (m.s <sup>-1</sup> )	11.8 ± 3.2	11.6 ± 2.6	11.7 ± 2.7	$\chi^2_{2,30} = 1.93$ , P = n.s.
Spring (n = 33 tracks)				
Flight altitude (m a.s.l.)	1040 ± 642	1110 ± 673	1152 ± 698	$\chi^2_{2,31} = 22.6$ , P < 0.001
Vertical speed (m.s <sup>-1</sup> )	-0.85 ± 1.43	-0.52 ± 0.76	-0.30 ± 0.48	$\chi^2_{2,31} = 5.5$ , P < 0.07
Groundspeed (m.s <sup>-1</sup> )	13.7 ± 3.5	14.0 ± 2.9	14.0 ± 3.1	$\chi^2_{2,31} = 1.15$ , P = n.s.
Airspeed (m.s <sup>-1</sup> )	12.7 ± 3.6	12.9 ± 2.8	12.8 ± 2.6	$\chi^2_{2,31} = 2.96$ , P = n.s.
<i>Harriers</i>				
Autumn (n = 25 tracks)				
Flight altitude (m a.s.l.)	1177 ± 379	1157 ± 386	1137 ± 421	$\chi^2_{2,23} = 13.04$ , P < 0.002
Vertical speed (m.s <sup>-1</sup> )	-0.22 ± 0.79	-0.19 ± 0.44	-0.20 ± 0.45	$\chi^2_{2,23} = 1.04$ , P = n.s.
Groundspeed (m.s <sup>-1</sup> )	11.9 ± 2.7	11.0 ± 2.6	11.2 ± 2.3	$\chi^2_{2,23} = 6.08$ , P < 0.05
Airspeed (m.s <sup>-1</sup> )	11.2 ± 2.7	10.3 ± 2.6	10.0 ± 2.4	$\chi^2_{2,23} = 7.28$ , P < 0.03

71°, n = 102,  $U^2 = 0.78$ , P < 0.001). In spring, the five tracked harriers were observed in southerly winds (192° ± 53°, n = 5). Thus, falcons and harriers preferably migrated in northwesterly winds in autumn (i.e. following side winds) and winds with a southerly component in spring, and they avoided crossing the sea in opposing winds (Fig. 3).

#### Flight speeds of raptors crossing the sea

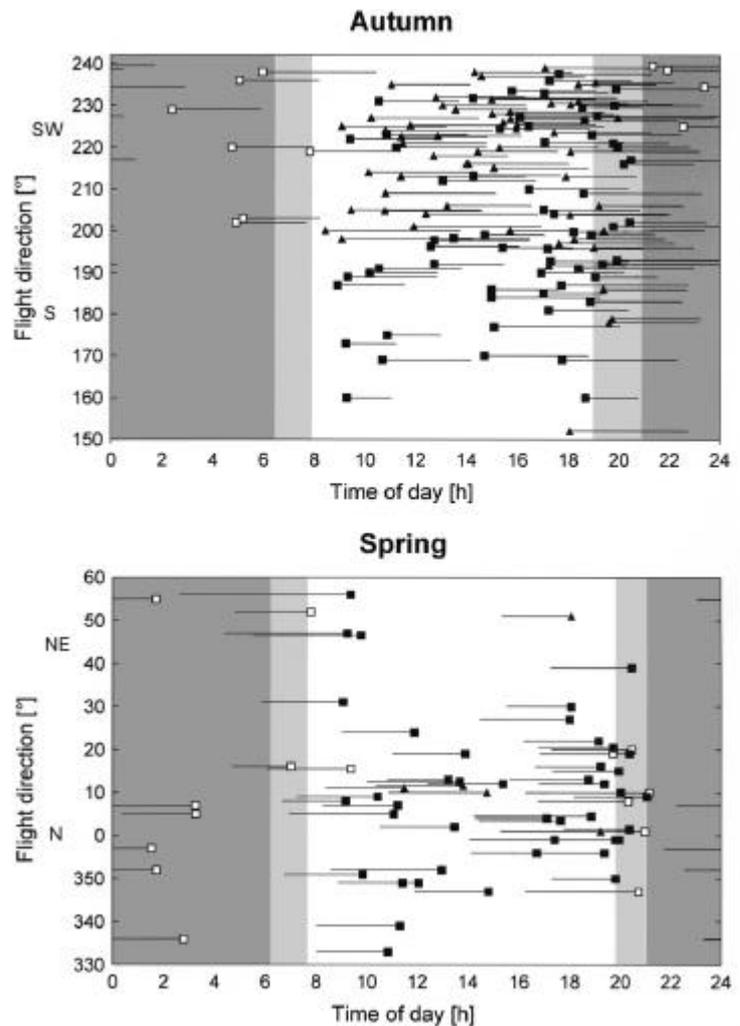
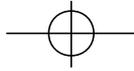
Among birds crossing the sea in horizontal flapping-gliding flight (vertical speed  $0 \pm 0.5$  m.s<sup>-1</sup>), falcons had significantly higher groundspeeds than harriers in autumn (Table 1;  $t = -2.1$ , P < 0.05). This difference was mainly due to a higher tailwind support for falcons (tailwind-components: 2.8 m.s<sup>-1</sup> in falcons v. 1.4 m.s<sup>-1</sup> in harriers;  $t = -2.1$ , P < 0.05). Airspeeds did not differ between the two groups ( $t = -0.56$ , n.s.). For marsh and Montagu's harriers, no inter-specific difference was found in ground- and airspeeds (groundspeed,  $t = 0.97$ , n.s.; airspeed,  $t = 0.79$ , n.s.). In falcons, ground- and air-

speed did not differ between autumn and spring migration (groundspeed,  $t = -0.97$ , n.s.; airspeed,  $t = -0.83$ , n.s.).

#### Reactions in flight behaviour when crossing the coast

To analyse reactions in flight behaviour of birds crossing the coast seawards in autumn and landwards in spring, we subdivided tracks of falcons into sections above land, coast and sea (for details see methods). In autumn, falcons showed no changes in flight behaviour when starting towards the sea: horizontal ground- and airspeed, vertical speed and flight altitude did not differ between the land, coast and sea sections (Table 2). Harriers decreased horizontal air- and groundspeeds as well as flight altitudes from land towards the sea in autumn (Table 2).

In spring, falcons approaching the coast after crossing the sea tended to increase sinking rates towards land and flight altitudes consequently decreased signi-



**Figure 4.** The diurnal pattern of sea crossings of visually identified falcons (squares) and harriers (triangles), and electronically identified falcons (?), for details see Methods). Symbols indicate observation times at the radar site, and lines show the expected durations of sea crossings calculated according to the observed groundspeeds. Sunset and sunrise variation during the season are indicated by light grey areas. Assumptions: Crossing distance is 150 km, and groundspeeds do not change during the sea crossing.

ificantly towards land (Table 2). For harriers, no analysis could be performed because only five were observed in spring.

#### Diurnal pattern of Mediterranean Sea crossings

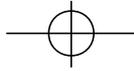
The majority of falcons and harriers crossed the Mediterranean Sea during daytime (Fig. 4). However, some birds started sea crossing before sunrise or after sunset and flew across the sea at least partly during the night. Nocturnal passages of falcons occurred during the whole night as indicated by the electronically identified falcons (Fig. 4); this was observed during the whole migratory period. We estimated crossing time based on the observed groundspeeds (for details see methods): in autumn, it was  $199 \pm 52$  min ( $n = 57$ ) for

visually and  $208 \pm 37$  min ( $n = 11$ ) for electronically identified falcons (Fig. 4). Corresponding values for spring were  $190 \pm 37$  min ( $n = 42$ ) and  $203 \pm 43$  min ( $n = 15$ ), respectively. Visually identified harriers flew  $226 \pm 44$  min ( $n = 53$ ) in autumn and  $204 \pm 31$  min ( $n = 5$ ) in spring.

## Discussion

### Flight directions and sea crossing

Earlier studies at the same point on the E–W aligned coast of southern Spain showed that soaring species like black kites *Milvus migrans* and honey buzzards *Pernis apivorus* migrated mainly along the coast (Meyer et al.



2000). In contrast, more than half the harriers and falcons tracked during the autumn season of the present study flew offshore. There was no significant difference in average directions between the harriers and the falcons, but within the two families the smaller species showed the expected higher preference for sea crossings compared to their larger relatives.

The difference between smaller and larger raptors is also obvious at other barriers. The tendency of raptors to cross the Alps decreases with the species-specific proportions of soaring flight (Bruderer & Jenni 1990), and small sparrowhawks *Accipiter nisus* are more prone to cross the Alps than the larger common buzzards *Buteo buteo* (Schmid et al. 1986).

Harriers were much more abundant in autumn than in spring. It seems that harriers choose another flight route in spring compared to autumn. Our data may support the idea of García & Arroyo (1998) that the main migratory route of harriers in spring is more easterly via Sicily and Italy, including a sea crossing of at least 140 km. In Sicily, both marsh and Montagu's harriers are more common migrants in spring than in autumn (Iapichino & Massa 1989).

#### Flight conditions and behaviour when crossing the coast

Sea crossing at the Malaga coast, like most raptor migration, occurred predominantly during daytime. However, there was a considerable number of birds that crossed the sea at least partly during the night. Flight characteristics did not differ between diurnal and nocturnal migrants. According to the measured ground-speeds, birds had to fly about three to four hours to cross the 150 km wide water body. Maintaining migratory direction without deviation or hesitation when arriving at a sea coast more or less perpendicular to the innate direction, and with the opposite shore invisible, requires a very strong adherence to this shortest flyway. Off-shore flights at nightfall in birds known as 'diurnal migrants' underline the importance of this straight flight strategy.

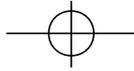
Several studies report nocturnal migration in falcons and harriers, but usually they fail to show the amount of nocturnal compared to diurnal migration (Casement 1966, Beaman & Galea 1974, Gatter 1984, Russel 1991, Spaar & Bruderer 1997b). Nocturnal migration of raptors can be quantified by identifying the wing-

beat patterns of migrants. In this way, Spaar et al. (1998) estimated that about 5–10 % of the total population of Levant sparrowhawks *Accipiter brevipes* pass Israel by nocturnal migration. In this study, five out of 11 electronically identified falcons in autumn and five out of 15 in spring crossed the Mediterranean sea during darkness. These are 3 % and 6 % of the 155 and 81 visually and electronically identified falcons in autumn and spring, respectively. Including also the visually and electronically identified birds that flew across the sea at least partly during night, these proportions in autumn and spring rise to 33 % and 34 % for falcons and to 15 % and 20 % for harriers. Thus, nocturnal crossing of the Mediterranean Sea is a common phenomenon in these small raptor species.

Birds flying seawards in autumn and landwards in spring showed only minor reactions in flight behaviour when crossing the coast. This confirms again their low reluctance to fly across a coast line. In contrast to a hypothesised increase in flight altitude when moving towards an unfamiliar habitat, harriers flying offshore in autumn showed a slight decrease in flight speed and altitude. In spring, falcons approaching the coast from the sea increased slightly their sinking rates, thus in line with the hypothesis that they should moderately reduce flight altitudes. There was, however, no indication that birds attempted to land when reaching the coast.

Favourable winds were rare during our study periods; winds were usually from NW or ESE. Among the winds exploited for migration NW and NNW directions were preferred for sea crossings in autumn, in spite of the fact that these were side winds, but at least with a following component. ESE winds favoured coasting towards the west. Similarly, spring arrivals occurred with following wind components, though in most cases it was a side wind with a following component instead of a tailwind. Considering that no tailwinds occurred for sea crossing, our hypothesis suggesting a preference for following winds for sea crossing was at least partially supported.

Unstable weather conditions may influence decisions on whether to cross the sea or to follow the coast. During and after the passage of several cold and warm fronts in mid-September, we observed about a dozen harriers and falcons migrating along the coast against strong northwesterly opposing winds. As these winds could be following side winds for sea crossing birds, but



were not used by the birds in such way, we assume that these birds hesitated to cross the sea because of unstable weather, thus accepting increased energy expenditure in favour of reduced weather risks.

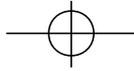
### Conclusions

Falcons and harriers readily cross the 150 km wide water barrier during day and night, showing only minor reactions to the coast line and no tendency to land after a sea crossing. This suggests that straight flights across barriers are an integral part of their migratory strategy, particularly in the smaller species. They follow this strategy even if winds are only partially favourable. Time saving seems to have a high priority as long as offshore flights in unstable weather or against the wind can be avoided.

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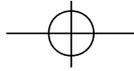
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## Population regulation in birds: is there anything new since David Lack?

Ian Newton

This paper examines the development of ideas about population regulation in birds over the past 50 years. The main issues addressed include the roles of (1) territorial and other dominance behaviour; (2) other density dependent processes, and (3) external factors, such as food or predators, in limiting bird numbers.

The role of territorial behaviour as a proximate mechanism influencing bird breeding densities has been confirmed by removal experiments. In 60 experiments on 43 species, removed birds were replaced in the same spring by other individuals, often known to derive from a non-territorial surplus. Within species, territorial behaviour can limit breeding densities at different levels in different areas or in years, according to prevailing food supplies.

Density dependence has proved hard to demonstrate in bird populations, partly because of the confounding influence of density independent factors, and partly because the resources over which birds compete often vary greatly in abundance from year to year. In the latter situation, density is best measured as numbers per unit of resource, rather than as numbers per unit of area. None-the-less, evidence for density dependence is now available for a wide range of bird populations.

More than 100 field experiments have been done to test the role of different external factors in limiting bird breeding densities. These experiments provide confirmation that all main potential limiting factors (food-supplies, nest-sites, predators, parasites and competitors) do indeed limit breeding densities in one species or another. They also reveal that particular species might be limited by different factors in different areas.

Key words: Population regulation, territorial behaviour, density dependence, limiting factor.

Ian Newton, Monks Wood Research Station, Abbots Ripton, Huntingdon, Cambs. PE28 2LS, United Kingdom; email: ine@ceh.ac.uk

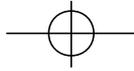
No other person has had more influence on the development of ideas on population regulation in birds than David Lack (1910–1973). As one of his small number of students, I was in a good position over six years to absorb his approach and ideas.

David Lack's views on population regulation in birds were laid out in two books: *The Natural Regulation of Animal Numbers* (1954) and *Population Studies of Birds* (1966). In the later book, he encapsulated his ideas in two simple sentences: (1) The reproductive rate, evolved through natural selection, is that which results in the greatest number of surviving offspring per pair. (2) Population density is regulated by density de-

pendent mortality, in most species by food shortage outside the breeding season.

These are two firm statements which, after 50 years, we might judge as still partly correct, but in need of considerable modification.

Population limitation is now a large and thriving research field, and in this paper I shall pick out three aspects, in order to show how knowledge and ideas have advanced since Lack's time. These include: (1) the role of territorial and other dominance behaviour as proximate mechanisms in the regulation of breeding density; (2) the role of density dependent processes in the dynamics of bird populations; and (3) the role of



**Table 1.** Summary of findings from removal experiments done to test the role of territorial behaviour in limiting bird breeding densities<sup>1</sup>.

	Species	Experiments	Replacement of one sex <sup>2</sup>	Replacement of both sexes
Song birds	23	34	21	8
Grouse	7	12	6	5
Raptors	3	3	0	3
Ducks	5	5	1	3
Waders	2	3	0	2
Seabirds	3	3	0	3
Totals	43	60	28	24

<sup>1</sup>Based on a review by Newton (1998), in which the original references may be found.

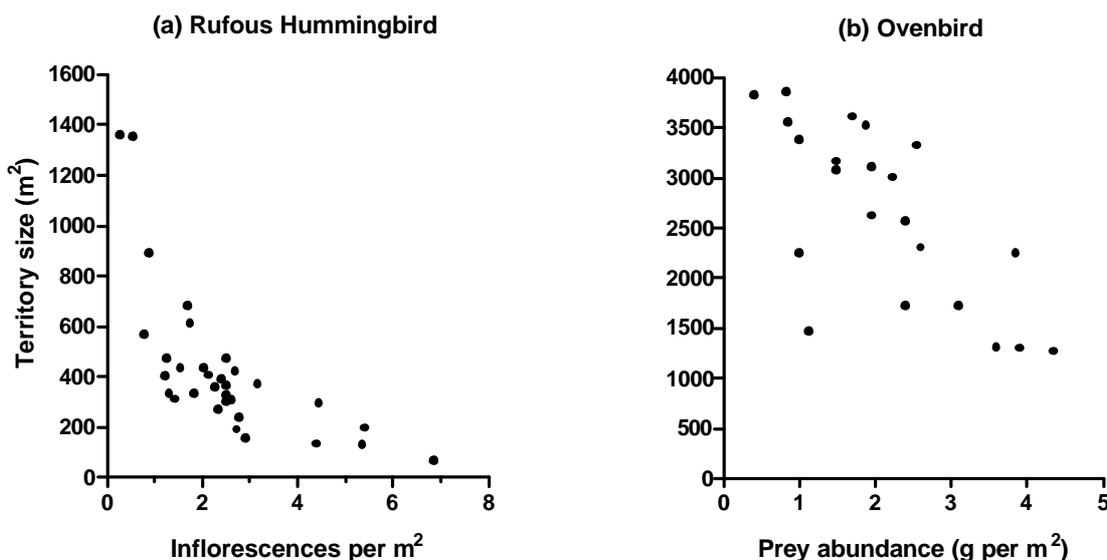
<sup>2</sup>In some experiments only one sex was removed, whereas in others both were removed but only one was replaced.

external factors, such as food-supply, predation and parasitism, in limiting bird numbers. Examples are drawn mainly from Newton (1998), in which further details may be found.

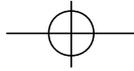
#### Territorial behaviour

Through their territorial behaviour, birds space themselves through suitable habitat. Lack appreciated that this spacing provided a possible mechanism through

which density could be limited, but concluded that, in practice, this did not happen. He thought that birds which survived until the end of winter simply divided the available habitat between them. If there were few birds, they had large territories; if there were many, they had small territories. However, at that time, the existence of surplus non-territorial birds was largely unknown (or unappreciated), and there had been no good experimental studies demonstrating the role of territorial behaviour in density limitation.



**Figure 1.** Examples of the inverse relationship between territory size and local food density in birds. (a) Rufous hummingbird *Selaphorus rufus* which fed on *Castilleja* flowers in a meadow. Redrawn from Gass 1979. (b) Ovenbird *Seiurus aurocapillus* which fed on invertebrates from among forest ground litter. Redrawn from Smith & Shugart 1987.



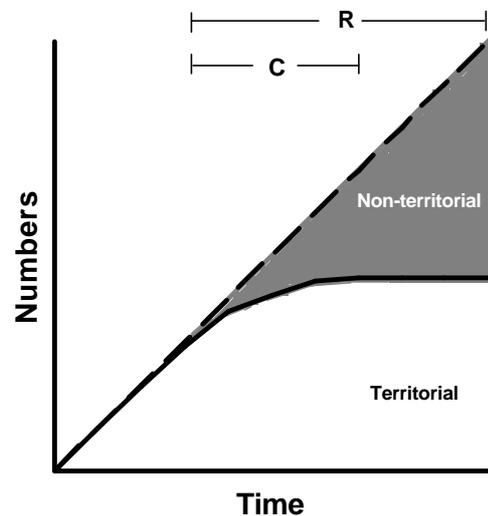
So-called 'removal experiments' played a crucial role in changing these ideas. The procedure was as follows. You waited in spring until birds had settled on their territories and density had stabilised, and then removed some of the territorial individuals. If these birds were replaced in the same spring by other individuals, so that overall density was maintained, then territorial behaviour limited density. If, in addition, you could prove that the replacement birds had been drawn from a non-territorial sector, rather than from other territories, this would further show that territorial behaviour contributed to the existence of a non-territorial, non-breeding sector. In this case, territorial behaviour, as well as limiting breeding density, also prevented some birds from reproducing, and thus limited the breeding output of the population as a whole.

Some years ago, I summarised the findings from removal experiments in birds (Newton 1992, 1998). The 60 experiments involved 43 species, ranging from passerines to auks (Table 1). In about 80 % of these experiments, removed birds of one or both sexes were rapidly replaced. In many of the experiments, the replacement birds were ringed, and known to derive from a non-territorial sector. Evidently, the limitation of breeding density by territorial behaviour is widespread among birds. This does not mean that the densities of all territorial bird populations are limited in this way everywhere every year. For one reason or another, many might not achieve densities at which their territorial behaviour would become limiting.

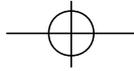
In many bird species, territories vary in size in relation to local food supplies. Two examples from North America are given in Figure 1. In both species territory sizes decline with increase in food densities, and in the hummingbird, territory sizes changed from week-to-week, or even day-to-day, according to changes in their nectar food supply, as flowers opened or died. So here we have a simple behavioural mechanism through which changes in food supply are translated into changes in bird densities, with excluded individuals having to move elsewhere or being relegated to marginal habitats, where their survival chances are lower.

The manner in which territorial behaviour might limit bird densities is depicted in the model in Figure 2. As birds arrive in their breeding areas in spring, their numbers steadily rise. The first birds to arrive get territories, because space is plentiful. But later arrivals have increasing difficulty in squeezing in, and after a certain

point, territories can be compressed no further, and territory densities stabilise. Any additional birds, which arrive after this time, must either replace existing territorial birds, accumulate locally as a non-territorial surplus, or move elsewhere. This behavioural mechanism could thus provide powerful density dependent control of territorial density and, if only territorial birds are able to breed, it also provides density dependent control over reproduction. This could perhaps be one of the strongest and most widespread regulatory mechanisms operating in many bird populations. It was missed by David Lack because, on the evidence available to him, he



**Figure 2.** Model showing how the numbers of territorial and non-territorial birds might change according to change in the total numbers of potential settlers. C shows the range of total numbers over which territories could be compressed under pressure from further contenders, and R shows the range of total numbers over which replacement of dead (or removed) territorial birds could be expected. At low numbers, all individuals can establish a territory, and territorial behaviour serves merely to space out birds within the habitat. At higher numbers (zone C), an increasing number of birds can establish territories, but an increasing proportion is excluded from doing so, providing a mechanism for the regulation of local density. Territorial behaviour can thus limit density from the start of zone C, even though higher densities can be reached (to the end of zone C) under pressure from further rise in the number of contenders. Beyond C, no further increase in territorial numbers occurs, despite further rise in the number of contenders. At this high level, for every additional territorial bird that settles, one must die or leave. From Newton 1998.



could not accept that territorial behaviour limited density. This was partly because, in the species of most interest to him, territorial density varied greatly from year to year. It had not occurred to him that territory sizes might vary from year to year in relation to prevailing food supplies (and perhaps other local conditions) and that limitation might occur at different densities in different years.

Territorial behaviour is not the only proximate mechanism that can regulate bird densities. Any kind of dominance behaviour, including fighting, supplanting and avoidance behaviour, frequently seen in flocking birds, can do the same. This is because, in any competitive situation, some individuals get more (or better) resources than others, and through such interactions, densities become adjusted to local resource levels, and birds which cannot meet their needs must leave or die. Good examples of social interactions (involving interference and depletion of food supplies) acting in this way are provided by Murton (1968) in woodpigeons *Columba palumbus* and by Goss-Custard et al. (1982, 1984) in oystercatchers *Haematopus ostralegus*. So territorial and other dominance behaviour, evolved for the benefit of individuals, has emerged as a major proximate mechanism through which bird numbers are adjusted to resource levels. Compared to the situation 40 years ago, this represents a major advance in understanding, because it elucidates the spacing and dominance behaviour of birds, and reveals its consequences in density regulation.

### Density dependence

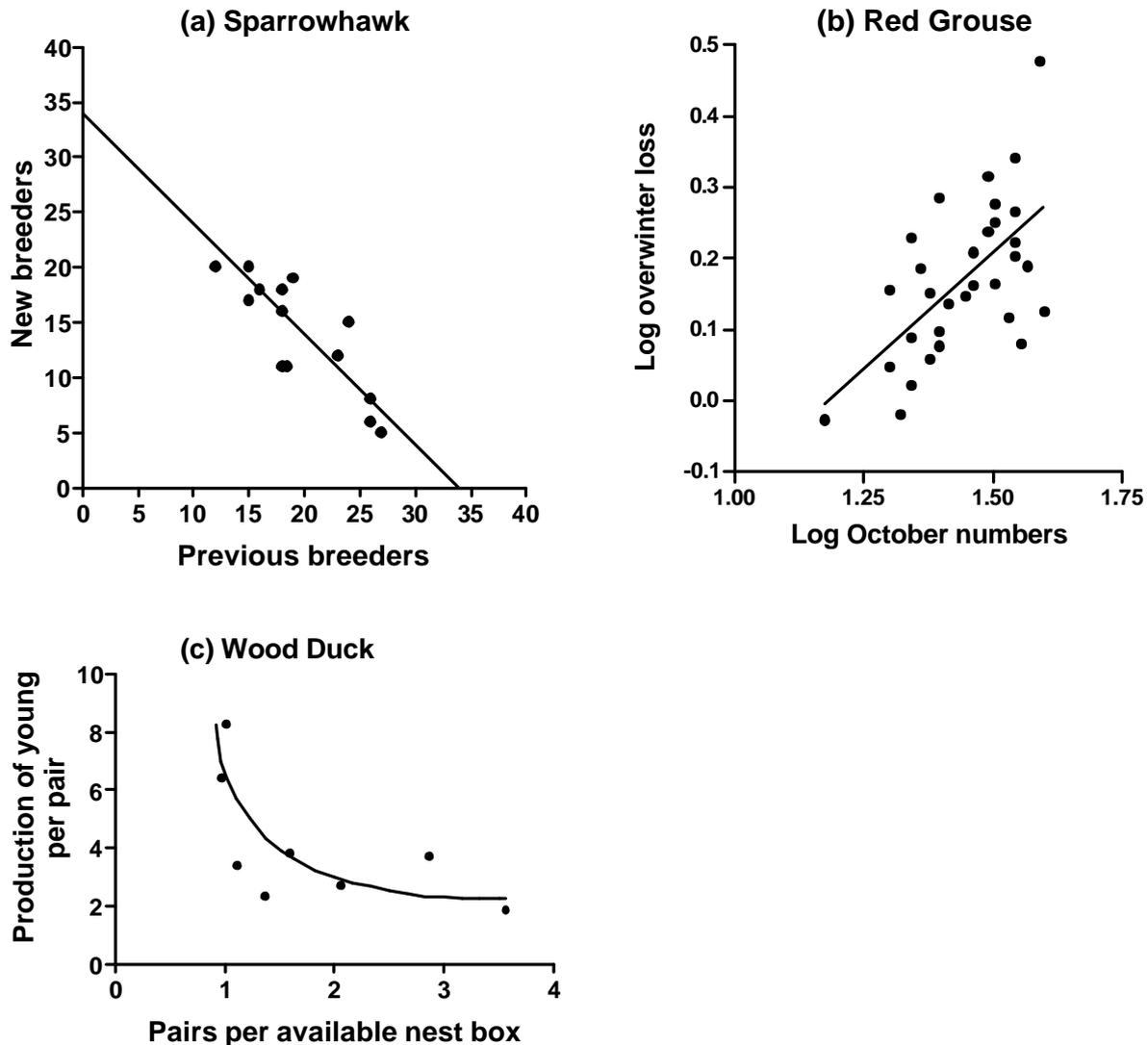
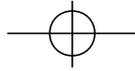
Lack appreciated that most bird populations normally fluctuate between much narrower limits than are theoretically possible, and hence that densities must be regulated by factors which remove increasing proportions of individuals as their numbers rise, and decreasing proportions as their numbers fall. He was clear, too, that density dependence could arise through competition for food or other resources, through predation, or through parasitism by infectious disease agents. His argument for the importance of density dependence was based almost entirely on logic, as this was the only way in which he could conceive that the relative stability of bird densities could be explained. It was an act of faith on his part, for no good field evidence was available for birds (except for slight density dependence in the clutch-size

of tits, which Lack thought was insufficient to stabilise densities). In addition, there was a counter view, championed by Andrewartha & Birch (1954), who claimed that weather and other density independent factors were of over-riding importance in limiting animal numbers.

It took more than 20 years for any substantial body of evidence on density dependence to accumulate for bird populations. There were two major problems. First, the numbers of birds are of course influenced by both density dependent and density independent controlling factors. So in any run of data, such as annual counts or breeding rates of birds, it was hard to separate the density dependent signal from density independent noise. One needed long runs of data collected over many years, and sophisticated statistical methodology, neither of which were available to David Lack. Secondly, food-supplies (and other resources which affect the carrying capacity of habitats) vary greatly in abundance from year to year, so measurements of density were being made against a continuing changing baseline. This problem could have been overcome if density had been measured, not as numbers per unit of area, but as numbers per unit of food (or whatever other resource the birds were competing for).

But then, as now, few observers measured resources as well as bird numbers and performance, so density was almost always measured on the basis of area.

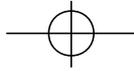
Despite these problems, evidence for density dependence in bird populations is now available for a wide range of species (Newton 1998). Figure 3 gives three examples to illustrate different points. In the sparrowhawk *Accipiter nisus*, breeding density remained fairly stable from year to year, with nest numbers over a 26-year period fluctuating no more than 15% on either side of the mean level. Stability in breeding density was achieved by density dependent recruitment of new breeders, with the numbers added each year approximately matching the numbers of established breeders lost from the population since the previous year (Figure 3a). This situation arose because the numbers of territories in this 200 km area was more or less fixed, which kept a somewhat flexible ceiling on breeding density (Newton 1991). A similar mechanism is also apparent in species whose breeding densities fluctuate much more from year to year than those of the sparrowhawk, except that the ceiling is much more flexible.



**Figure 3.** Examples of density dependence in bird populations. (a) Density dependent recruitment of a breeding population of sparrowhawks *Accipiter nisus*, 1975–89. The breeding population remained fairly stable during this period, and the numbers of new breeders recruited each year were inversely related to the numbers of established breeders remaining from the previous year. Population stability was itself the consequence of a fairly stable territorial system, in which the landscape was occupied to a similar level each year. From Newton 1991. (b) Overwinter losses of red grouse *Lagopus l. scoticus* in different areas of moorland, in relation to initial (October) numbers in each area. Areas that started with the highest densities showed the greatest losses, mainly due to predation. From Redpath & Thirgood 1997. (c) Relationship between density and breeding success among wood ducks *Aix sponsa* competing for nest-sites. Failures were due to females fighting and laying in the same nests, giving rise to desertions and reduced hatching success. From Jones & Leopold 1967.

The second example illustrates spatial density dependence. At the start of winter (October), the densities of red grouse *Lagopus l. scoticus* varied greatly on different areas of moorland in south Scotland (Redpath & Thirgood 1997). Overwinter losses of grouse (between

October and April) were greatest in those areas that had the highest October densities (Figure 3b). These losses were caused primarily by predation, but the fact that the two areas with the lowest October densities gained the most birds overwinter indicated that movements were also



involved. Nevertheless, differential overwinter loss led to spatial stabilisation in the densities of grouse by the following breeding season.

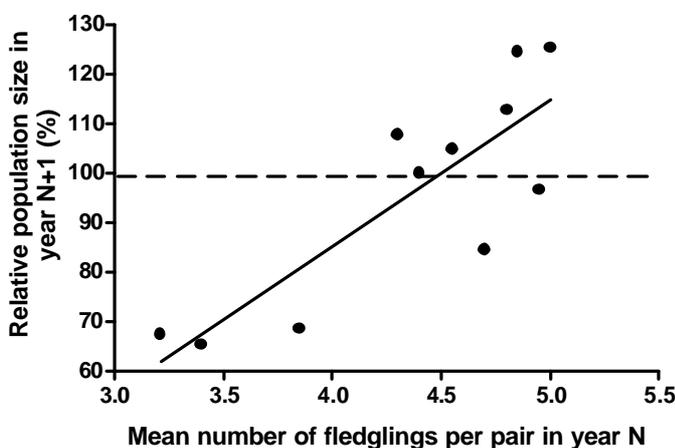
The third example shows the effects of competition for a resource in limited supply. In the area concerned, the numbers of wood duck *Aix sponsa* pairs in some years exceeded the number of available nest boxes. In consequence, different pairs interfered with one another, which led to density dependent reduction in breeding success (Jones & Leopold 1967). As in many competitive situations, however, the relationship between productivity and density was not linear, but curvilinear. This illustrates another difficulty in measuring density dependence: over one part of the density range in Figure 3c the density dependence is readily apparent, but over another part it is not. In other words, the chance of detecting density dependence could depend greatly on the range of densities experienced during the study.

Following the publication of Lack's books, one priority was therefore to collect evidence for density dependence in bird populations. But as such evidence has accumulated over the years, the emphasis has shifted to determining the shape of the relationship (whether linear or curvilinear) for use in population models. It has also shifted towards assessing the relative importance of density dependent, as opposed to density independent, processes in influencing population levels. It may be added that not all forms of density dependence are stabilising. Inverse density dependence or delayed density-dependence can lead to fluctuations in density, but these aspects are outside the scope of this review (for examples see Newton 1998).

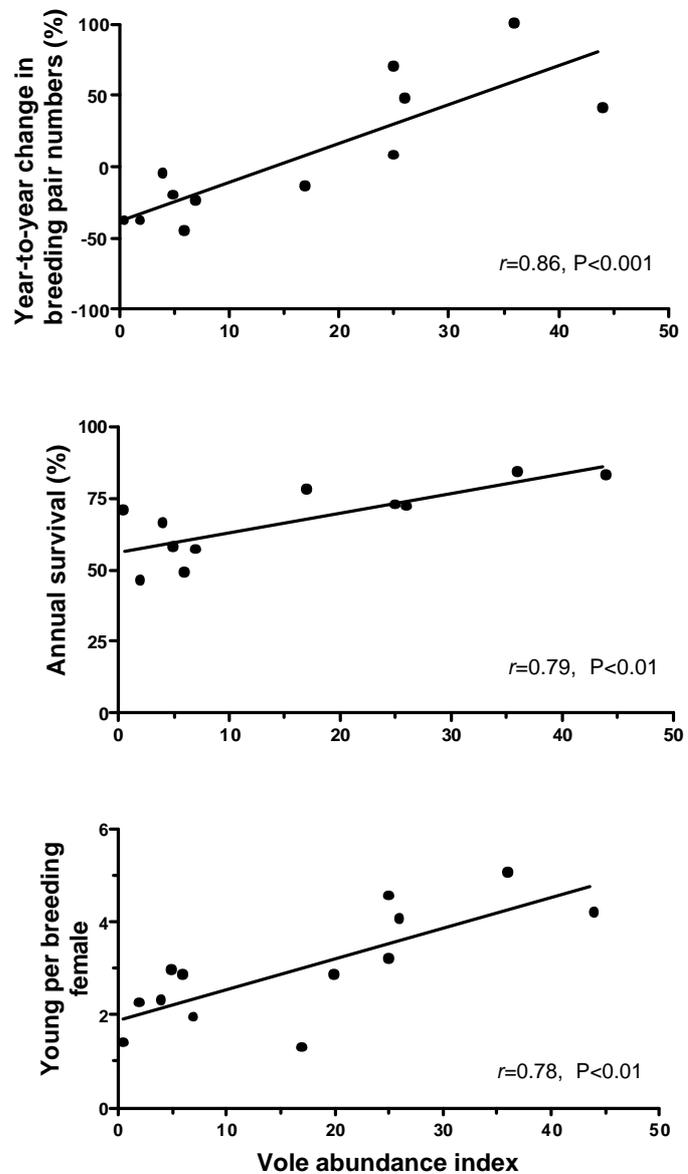
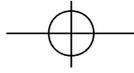
### Limiting factors

Lack (1954) was well aware of the potential importance of food shortage, predation and disease in limiting bird populations. He saw food shortage as of over-riding importance, acting in winter, and as causing direct starvation. He acknowledged that predation was of widespread occurrence, but thought that it was important in limiting the numbers of relatively few species, notably gallinaceous birds. Disease was also of widespread occurrence, and caused occasional large-scale losses, especially in waterfowl, but otherwise was unimportant in limiting numbers. Another potential limiting factor, adverse weather, Lack saw as acting chiefly through the food-supply, with extremes making food more or less available. The evidence available to Lack was skimpy, and virtually none was experimental.

In light of more recent information, Lack's views need substantial modification. Firstly, although Lack knew that provision of nest boxes could increase the local breeding densities of hole-nesting birds, in my view he greatly under-estimated the importance of nest-sites in limiting bird breeding densities. Such limitation is apparent not only in tree-cavity nesters, but in all other species that require special places for their nests – sites that are not abundantly available in all landscapes, such as cliffs, caves, islets in lakes, and so on. Secondly, predation and parasites have emerged as important in limiting the numbers of a much wider range of species than those envisaged by Lack, acting in some species to hold breeding densities well below the level that food supplies would permit. Thirdly, different factors often act in combination to limit numbers, interact-



**Figure 4.** Relationship between breeding output and annual change in breeding density of pied flycatchers *Ficedula hypoleuca*. From Virolainen 1984.

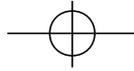


**Figure 5.** Numbers, survival and breeding success of barn owls *Tyto alba* in relation to abundance of field voles *Microtus agrestis* in different years. In the study area, immigration and emigration were slight, and year-to-year changes in numbers were due mainly to local changes in survival and breeding success, in turn related to vole densities. From Taylor 1994.

ing in such a way as to cause bigger reductions in numbers than would be caused by one factor alone. For example, food-shortage might predispose predation, in that hungry birds become less 'shy', and allow a much closer approach by humans and other predators. Likewise, the mere presence of predators might prevent birds from feeding in certain places, and thereby reduce their food supply; or it might restrict many birds to nesting in especially safe sites, thereby limiting the range of sites available to them. Many other examples of such interactions are given by Newton (1998). Fourthly, in populations limited by food, shortage often acts in ways

other than starvation. I have already mentioned the link in some species between territory size and food supply, as a result of which excluded birds may die in various ways, not necessarily including starvation. Moreover, food supply can affect population levels at any time of year, not just in winter, as envisaged by Lack.

In some short-lived birds, that breed in their first year of life, food supply in one breeding season can affect breeding numbers in the next breeding season, as in Figure 4. In this population of pied flycatchers *Ficedula hypoleuca*, increases in breeding numbers followed good breeding years, when the production of young per

**Table 2.** Summary of field experiments concerned with external factors limiting bird breeding densities.

	Grade of experiment <sup>1</sup>			Total	Number showing increase in breeding density
	1	2	3		
Food provision	5	11	10	26	15 (58 %)
Nest site provision	37	5	4	46	44 (96 %)
Predator reduction	4	7	6	17	10 (59 %)
Parasite reduction	3	0	1	4	3 (75 %)
Competitor reduction	3	5	4	12	11 (92 %)
Totals	52	28	25	105	83 (79 %)

<sup>1</sup>Grade 1: before-and-after comparison in a single area; Grade 2: single treatment area and single control area; Grade 3: replication by reversal of treatments in two areas, or by several simultaneous treatment and control areas.

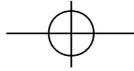
pair was high, while decreases in breeding numbers followed poor breeding years (Virolainen 1984). Food supplies in summer influenced breeding success, which in turn influenced population change to the next breeding season. There was a lag of one year between the food supply and its manifestation in breeding density. The pied flycatcher is a migrant, which winters in tropical Africa, yet year-to-year changes in the breeding density of this Finnish population were influenced primarily by events in breeding areas, rather than by events in winter, as found in some other migrants (e.g. den Held 1981, Peach et al. 1991). Similar relationships between breeding success and year-to-year change in breeding densities have emerged in some resident species, too, including the great tit *Parus major* in southern England (Perrins 1979).

Another example is provided by the barn owl *Tyto alba*, which resides in the same areas year round, and normally takes the same type of rodent prey year round. In this species, food supply influences performance throughout the year (Figure 5). In years of high vole densities, both annual breeding and annual survival rates of Barn Owls are higher than in years of low vole densities, so not surprisingly, year-to-year changes in owl densities are also related to vole densities. In this species, therefore, food supply influences performance not just in summer, nor just in winter, but throughout the year. Year-round limitation by food supply may be less frequent, or less easy to detect than in the Barn Owl, in species that switch from one type of food to another during the course of the year, as do many passerines.

### Experiments on limiting factors

When Lack wrote about limiting factors, he drew his conclusions from what little information was available then. The most important subsequent development is in the growth of experimental evidence. In the past 40 years, more than 100 field experiments have been done to test the role of food supply, nest sites, predators, parasites or competitors in limiting bird breeding densities. The commonest type of experiment involves the single area treatment, in which breeding numbers are monitored for several years, then something is changed (perhaps nest boxes are added or predators are removed), and then numbers are monitored for several further years, giving a before-and-after comparison in the same area. The weakness of this type of experiment is that, without a control, one cannot be certain that numbers have not changed for some other reason, independent of the experiment. The second type of experiment involves two areas, with the treatment applied in one area but not the other, which provides the control. The third type involves some degree of replication, either a reversal of treatments, so that after a period of years the experimental becomes the control area, and vice versa, or a duplication of areas, with several experimental and several control areas studied concurrently. In terms of reliability and robustness of conclusions, these three types of experiments could be graded 1–3, poor to good.

The findings from 105 relevant experiments from the scientific literature are summarised in Table 2. Some involved the provision of extra winter food or nest sites, while others involved the removal of preda-



tors, parasites or competitors. They reveal four main points.

(1) Although the experiments varied in design and quality, taken together they provide confirmation that all the main potential limiting factors, whether resources or natural enemies, do indeed limit breeding densities in one species or another. They also reveal that particular species might be limited by different factors in different areas or different years. In the great tit, for example, winter food proved limiting in some areas, but nest sites in other areas.

(2) While some experiments lasted up to ten years, most lasted only 1–3 years (the usual duration of a grant), and in many experiments breeding numbers were still increasing when the work stopped, so it was not possible to tell the full impact of the treatment on breeding density. Nevertheless, most experiments resulted in at least a doubling of breeding density compared with the control. However, nest-box studies resulted in much bigger increases, sometimes giving more than 20-fold increases in the densities of target species. In some experiments, the provision of nest sites attracted species into the study area that were previously absent there. Hence, for many species that require special nest sites, shortage of such sites emerged as an especially potent factor in limiting both abundance and distribution.

(3) For each species, experiments were done on whatever factor previous observational evidence had suggested was limiting. If it looked like food was important, food was provided. If it seemed that predation was important, predators were removed. While this is a perfectly legitimate procedure, it means that, as a group, existing experiments may be biased towards giving positive results. If species for the different experiments had been selected at random from the local avifauna (in practice not possible), rather than on the basis of prior knowledge, the number of positive results may well have been much lower than the 79 % recorded overall.

(4) In all the experiments, only a single factor was manipulated, as none was concerned with the interactive effects of two or more limiting factors acting together. Such experiments are likely to prove expensive, but they could provide a fruitful field for future research.

## Concluding remarks

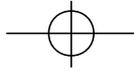
Compared to when Lack wrote, we now have much more understanding of the role of territorial and other dominance behaviour as proximate mechanisms in the regulation of bird densities in relation to resource levels. We have much more evidence on density dependent processes, and their role in relation to density independent processes in influencing year-to-year population changes. We also have experimental confirmation that the breeding densities of birds can be influenced by all the potential limiting factors, including food supplies, nest-sites, predators, parasites and competitors.

So what are the main developments that have got us where we are now, and have helped to develop our understanding of population limitation in birds over the past half century? First, there is the obvious point that we now have much more information than was available to Lack. This information has come from a much wider range of bird species, and from a much wider range of areas in different parts of the world. It has also come from a range of different schools, using different approaches, and having different ways of addressing problems. Secondly, ideas have been abundantly tested experimentally in field conditions. This has been especially important in elucidating the role of territorial behaviour as a proximate mechanism in regulating bird densities, and the role of resources and natural enemies as ultimate limiting factors. Thirdly, there have been technological advances, particularly in the development of statistical methodology (important in detecting density dependence in time series), and in computing power (important in handling multiple variables in large data sets), both of which have given us the means to assess and weigh evidence much more reliably than in the past. Perhaps the most important factor of all, however, was the legacy of stimulating synthesis and ideas left to us by David Lack.

**Acknowledgments.** I am grateful to Professor C. M. Perrins, for helpful comments on the manuscript.

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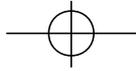
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## Spatial behaviour of radio-tagged Eurasian bitterns *Botaurus stellaris*

Luca Puglisi, M. Claudia Adamo and N. Emilio Baldaccini

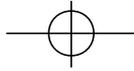
Because Eurasian bitterns *Botaurus stellaris* are secretive by nature and live in densely vegetated marshes, the home range and movements of this non-colonial heron are still poorly known. This study describes the size and structure of the home range of radio-tagged bitterns during the breeding season and subsequent summer months at Lake Massaciuccoli, Italy. A total of 11 males and one female were radio-tagged and their movements estimated by means of minimum convex polygon, cluster and kernel analyses. The bitterns' home range proved to be multinuclear, during the breeding and post-breeding seasons. The size of the most frequently used areas was comparable in both periods, though during the post-breeding season these areas were scattered over a significantly larger total area. Bitterns repeatedly visited the same spots within their home ranges, both during the same and in different years, as revealed by the individuals captured and tagged in successive years. Individual experience appears to play an important role in the shape of home ranges. Contrary to other herons, the bittern's individual feeding, roosting, and nesting areas seem to coincide, and each individual moves about solitarily. This may represent a behavioural strategy to best exploit food resources in densely vegetated marshes.

Key words: Eurasian bittern, home range, radio-tracking, Mediterranean wetland, ardeids.

Dipartimento di Etologia, Ecologia ed Evoluzione, Università di Pisa, I-56126 Italy; e-mail: lpuglisi@discau.unipi.it

The Eurasian bittern *Botaurus stellaris* is a poorly known heron that lives in vegetated marshy areas, whose populations are in general decline mainly because of the destruction or deterioration of their habitats. The species is considered particularly vulnerable in Europe (Tucker & Heath 1994), especially in western European countries where most national populations are less than a few hundreds (Kushlan & Hafner 2000). Due to the bittern's secretive nature and closed habitat, most observations are limited to direct sightings of birds at the edge of vegetation or in sub-optimal patches (e.g., Mädlow & Semisch 1987). During the reproductive period, males can be detected by their far-carrying, low-frequency vocalisations (Bibby et al. 1992, Kushlan & Hafner 2000). Females are usually impossible to observe unless they perform foraging flights to feed their young (Whiterby et al. 1939, Ké-

rautret 1969, Mallord et al. 2000). After the breeding season, male bitterns become silent, so their vocalisations cannot be used to locate birds. Consequently, knowledge of the characteristics of the home ranges and movements of this species is generally lacking. Most data on their use of space are limited to the density estimates of booming males at different sites (e.g., Puglisi et al. 1995, Hagemeyer & Blair 1997, Kaiser et al. 1998, Piskorski 1999). Although an animal's use of space is best understood through direct observation, when this is precluded, such as in the case of species difficult to find and monitor visually such as the bittern, radio-telemetry can fill an important gap (Kernohan et al. 2001). Thus, in 1997 we undertook a radio-tracking study in a Mediterranean marsh, with the aim of describing the movements and home range of bitterns during the breeding and post-breeding seasons.



## Methods

### Study area

The study was carried out within marshes around Lake Massaciuccoli (Central Italy, 43° 49' N, 10° 21' E, Fig. 1), that lie within the Regional Natural Park of Migliarino-San Rossore-Massaciuccoli. The largest marshy area (800 ha) is located north of the lake, and the vegetation beds are divided into well-defined sectors by wide canals and basins created by the extraction of sand (Fig. 1). The vegetation is made up of mixed beds of saw-sedge *Cladium mariscus* and common reed *Phragmites australis*. Water depths fluctuate yearly, reaching maximum levels in autumn and spring, and minimum levels during summer droughts when most vegetation beds become dry.

### Bittern population, capture and radio-tracking methods

Bitterns re-colonised the marshes of Lake Massaciuccoli during the 1980s and the population increased continuously for about 15 years: numbers of booming males reached their peak in 1998 (22–25 birds), after which, for reasons that are still unclear, the population

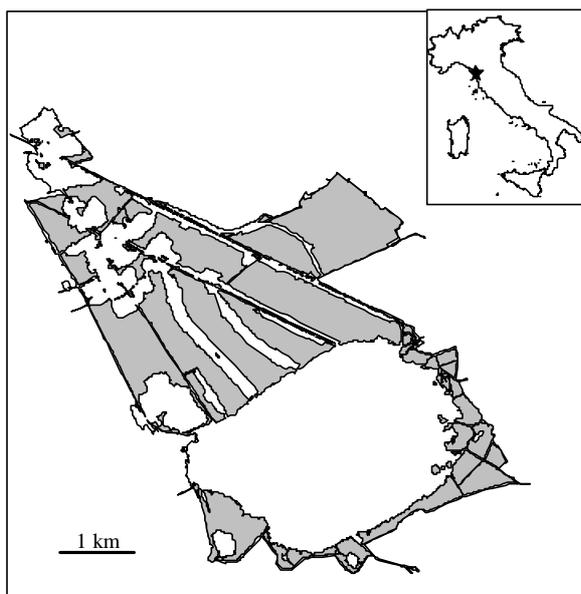
declined sharply to 7–8 booming males in 2000 and 2001 (L. Puglisi, unpubl. data).

Male bitterns were captured during spring over the years 1997–2000. Birds were located within the vegetation by means of their vocalisations, uttered either spontaneously or in response to audio playbacks. Their responses to playbacks were scored according to the following scale: 3 = the bird increases its calling rate and approaches the loudspeaker; 2 = the bird increases its calling rate but does not approach the loudspeaker; 1 = no apparent reaction; 0 = the bird stops calling. In most cases, bitterns reacted to our approach by freezing in the so-called 'bittern stance', allowing us to catch them with a landing net. One female was captured near her nest. Individual captures took from 30 min to 8 hr.

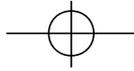
The captured bitterns were sexed and aged, following Baker (1993), and each was fitted with a 6-g radio-tag (TW-4, Biotrack Ltd, U.K.) fixed to a leg by means of a leather strap. The detection range of the tags in the dense marshy vegetation was up to 300 m at ground level. However, depending on the animal's location or when the tag was submerged, the radio signal was temporarily suppressed.

The bitterns' positions were pinpointed from a boat. Two to four bearings were taken for each fix, depending on the bird's distance from the boat and the shape of the vegetation beds. The average location accuracy as tested using hidden tags was 13.2 m ( $\pm 4.8$  s.d.,  $n = 10$ ). Because of the tags' limited range, we often searched for displaced birds from a motorised hang-glider (Fig. 2). In this case, we flew at about 150 m above the ground holding the antenna downwards; when the signal was detected, its direction was verified by rapidly moving the antenna. We then flew in tighter and tighter circles centred on the signal direction to locate the bittern, which was finally checked with two perpendicular passages crossing over the estimated position of the bird.

Position fixes were obtained throughout the day. Because the analysis of more intensively collected preliminary data revealed that the birds tended to spend all day in the same spot ( $0.4 \pm 0.2$  ha,  $0.6 \pm 0.5$  ha, mean daily minimum convex polygon size  $\pm$  s.d. for two birds;  $n = 9$  and 4 days, respectively), radio-tagged individuals were located once every two days. Furthermore, each individual was located at least three times at night in order to determine if they roosted in areas different from the diurnal foraging sites.



**Figure 1.** Study area (marshes surrounding Lake Massaciuccoli, Italy) and its location (box).



**Figure 2.** Radio-tracking bitterns from the glider.

### Data analysis

Home ranges were estimated using three methods. First, in order to estimate the size of the areas visited by individual birds, the minimum convex polygon (MCP, Kenward 1987) was computed. The areas where the birds actually spent the most time were instead estimated by means of cluster analysis (Kenward 1987, Badyaev et al. 1996, Rohner 1997) and kernel analysis, using 50 %, 75 % and 95 % of the total locations (hereafter indicated as CA50, CA75, CA95, and KA50, KA75, KA95, respectively). We used the fixed kernel analysis method (Worton 1989), determining the smoothing factor via the least-squares cross validation method (Seaman & Powell 1996, Seaman et al. 1999). The Ranges V package (Kenward & Hodder 1996) was utilised for the MCP and cluster analyses, while the kernel analysis was performed with the 'Animal Movement' package in Arcview (Hooge & Eichenlaub 1997). In the case of kernel analysis (all percentages) and cluster analysis with 95 % of fixes, unsuitable areas such as the lake or large or deep canals were nearly always included. Thus, most of the analyses of ranging behaviour were based on the cluster analysis with 75 % of locations (CA75).

In order to compare the movements of different individuals and their positions relative to each other, we divided the vegetation beds visited by the bitterns into numbered 10 ha plots (mean size: 10.9 ha  $\pm$  1.9, n = 53);

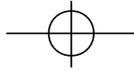
neighbouring plots within each sector were assigned consecutive numbers. For the most part, plots were delimited arbitrarily, though whenever possible their borders were made to coincide with canals or ditches.

Separate analyses were conducted for the breeding and post-breeding periods: the first was assumed to coincide with the booming season for the males and with the nesting period for the female, while the second covered the interval from the end of the breeding season until the tags stopped transmitting.

The individual home ranges were calculated only for individuals with long enough periods of tracking (at least 30 days); thus the sample sizes may be different for the breeding and post-breeding periods. Data on the same individual from different years were pooled if no considerable change in home-range size and location, number of nuclei and movements between nuclei was observed, otherwise data from consecutive years were treated separately. Unless otherwise specified, the median (inter-quartile range) is reported. Due to the non-normal distribution of most variables, non-parametric statistics have been used.

### Results

A total of 11 males (out of 15 trapped) and one female were radio-tagged (Table 1). Three males were recap-



**Table 1.** Radiotracking of Eurasian bitterns at Massacciucoli marsh, Italy. Study times for each of 15 cases, showing for each bird (M = males, n = 11 individuals; F = female, n = 1 individual) the study year, its age class (1-y: bird born the preceding spring; ad: older than 1 year), tracking time and number of fixes during the breeding and post-breeding season. In bold type are indicated the recaptured individuals and the number of fixes when used to calculate the home range during the breeding or post-breeding periods.

Individual	Age	Year	Breeding season		Post-breeding season	
			Tracking time	No. of fixes	Tracking time	No. of fixes
<b>M971</b>	ad	1997	4 Apr–4 Jun	<b>93</b>	5 Jun–16 Dec	<b>43</b>
M972	ad	1997	11 Apr–26 May	<b>51</b>	27 May–4 Nov	<b>26</b>
M973	ad	1997	11 Jun	1	12 Jun–30 Sep	<b>26</b>
<b>M971</b>	ad	1998	31 Mar–3 Jun	<b>19</b>	4 Jun–11 Nov	<b>30</b>
<b>M981</b>	ad	1998	31 Mar–27 May	<b>17</b>	28 May–9 Jun	3
M982	ad	1998	1 Apr–17 Jun	<b>28</b>	18 Jun–29 Jun	3
<b>M983</b>	1-y	1998	6 Apr–17 Jun	<b>27</b>	18 Jun–8 Jul	6
M984	ad	1998	5 May–21 May	<b>15</b>	22 May–31 Jul	<b>33</b>
M985	ad	1998	6 May–12 Jun	9	13 Jun–17 Nov	<b>23</b>
M991	ad	1999	23 Mar–20 May	<b>21</b>		
M992	1-y	1999	24 Mar–31 May	<b>23</b>	1 Jun–20 Aug	<b>32</b>
M993	ad	1999	6 Apr–31 May	<b>18</b>	1 Jun–17 Sep	<b>32</b>
<b>M981</b>	ad	1999	7 Apr–24 May	<b>16</b>	25 May–28 May	2
F991	ad	1999	17 May–28 May	<b>71</b>	29 May–27 Sep	<b>39</b>
<b>M983</b>	ad	2000	14 Apr–16 May	<b>30</b>	17 May–15 Sep	<b>90</b>

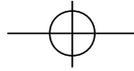
tured, two of them in successive years (M971 and M981), the third one two years later (M983), totalling of 15 tracking datasets. When first captured, male M983 was one of the two one-year-old adults trapped. Capture dates ranged from 23 March to 12 June. The mean yearly tracking period for an individual was  $135.6 \pm 63.0$  days (s.d.; n = 15), while the mean number of fixes was  $55.5 \pm 39.7$  days (n = 15).

The efficiency of the capture method for males varied with the strength of their response to playback, which was highest during the first study year and decreased thereafter (average response score: 1997 = 2.3, 1998 = 1.3, 1999 = 1.3, 2000 = 0.8) and was seemingly related to overall booming activity. During the study years, in fact, the length of the booming season (presence of booming males in the study area) progressively decreased, from about 150 days in 1997 (from January to late June) to 115 in 1998 and 1999, and 75 in 2000 (from mid March to late May). The booming activity of tagged males was not synchronised: the end of an individual's booming period varied between 16 May and 17 June (Table 1).

### Breeding season

For males, the estimated size of any given year's home range was not correlated with the number of fixes (no. fixes v. KA50max:  $r_s = 0.54$ , n.s., n = 12 cases). The three recaptured males had similar home ranges in both years. Regarding the home range structure and size (Table 2; see also Fig. 3), only the MCP of bird M971 was larger in 1998 than in 1997 (24.1 and 5.4 ha, respectively), despite the virtually identical tracking times. Therefore, for calculation of the overall median home range, data on the same individual for different years were averaged.

Male bitterns' MCPs ranged from 5.4 to 120 ha (median: 34.4 ha, interquartile range: 15.1–62.4) and included more than one marsh sector in 6 out of 9 cases. The lowest values (5.4 and 9.4 ha) were observed in 1997, i.e. the last year in which population increased (see Methods), though the small sample size for each year did not allow us to analyse the annual variations in home range features. At all analysis levels, the home ranges proved to be multinuclear by both cluster and kernel analyses: the CA75 home ranges of males varied from 2 to 16 ha and were divided into 1–4 nuclei, i.e.



covering only 19.1 % (16.8–21.4 %) of the total area visited (MCP). The CA75 surface area was correlated with that of the MCP ( $r_s = 0.67$ ,  $P < 0.05$ ,  $n = 9$  individuals), but not the number of nuclei ( $r_s = -0.08$ , n.s.,  $n = 9$ ). The higher the number of nuclei, the higher was the number of movements among nuclei ( $r_s = 0.90$ ,  $P < 0.01$ ,  $n = 9$  individuals). Each male boomed not only in each CA75 nucleus of his breeding home range, but also at scattered locations within the MCP.

The percentage area of the MCP shared by simultaneously studied males (maximum number individuals/year = 5) was higher than for the sharing of CA75 or KA75 nuclei (MCP: 13.0 %, inter-quartile range 10.4–22.1 %; CA75: 0 %, 0–3.9 %; KA75: 0 %, 0–12.6 %, ( $n = 9$  individuals). However, the two birds that shared the highest percentage of CA75 and KA75 nuclei were never present at the spot simultaneously.

The only female studied lost her brood progressively when the young were about 15 days old (this species hatches asynchronously), so we could track her only for 11 days during the reproductive period ( $n = 70$  fixes). During the first 8 days, she fed almost exclusively within about 50 m of the nest, later moving on to another feeding ground 600 m away: her overall MCP extended

for 8.5 ha, but her CA75 for only 0.5 ha, centred on the nest (Fig. 3). This CA75 nucleus was between two CA75 nuclei of male M991. She shared 54 % of her MCP with that male.

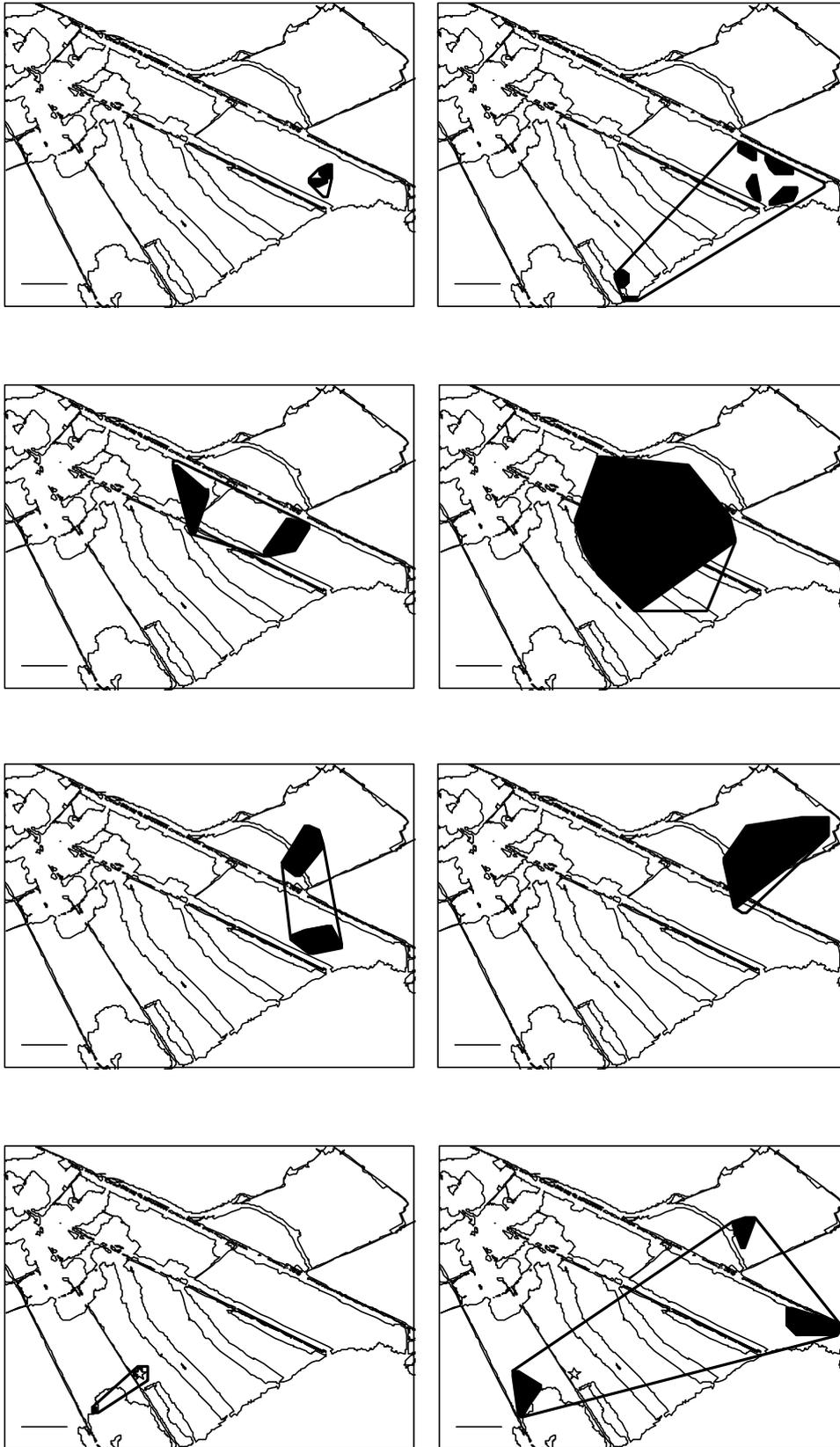
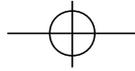
#### Post-breeding period

For some birds, the transition from the breeding to the post-breeding period coincided with a significant displacement within the first 2–3 weeks: three males (including M971 in both years) and the female moved as far as 1.5–2 km away, while M981 disappeared in both years, probably leaving the marsh. The other males ranged almost wholly within or very close to their breeding MCP.

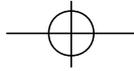
Eight males were tracked for at least two months (one, M971, for two years). The median date of last fix was 30 September (inter-quartile range: 15 September–4 November;  $n = 9$  cases). A sufficiently long tracking time was attained for M983 only during the second year, when it left the Massaciuccoli marsh, so he is treated separately. Therefore median values relative to male post-breeding home range refer to only seven individuals (Table 2).

**Table 2.** Home range characteristics of Eurasian bitterns (area in hectares and number of nuclei) at Massaciuccoli marsh, Italy, during the breeding and post-breeding seasons, as measured by kernel (KA) and cluster (CA) analyses with increasing percentages of fixes (50 %, 75 % and 95 %) and minimum convex polygon (MCP). Median values (interquartile intervals) are reported for males ( $n = 9$  and 7 individuals, during breeding and post-breeding periods, respectively); male M983 was excluded from calculation of the median post-breeding home range (see text for explanation).

		Breeding season		Post-breeding season	
		ha	# nuc	h	# nuc
Males	KA50	4.9 (3.6–11.1)	1.5 (1–1.5)	31.7 (20.2–46.6)	1 (1–2)
	KA75	19.1 (7.4–35.9)	1.5 (1.5–2)	95.0 (44.6–110.1)	2 (1–2.5)
	KA95	43.5 (27.0–108.7)	2 (2–2)	215.7 (142.9–280.2)	2 (1.3–2.5)
	CA50	2.6 (2.0–3.5)	2 (1–3)	3.7 (2.9–4.5)	4 (2.5–4)
	CA75	5.7 (4.9–7.8)	2 (2–2.5)	10.3 (6.3–18.5)	3 (1.5–4.8)
	CA95	25.9 (8.8–30.1)	2 (1–2)	50.1 (27.6–62.7)	2 (1–2.5)
	MCP	35.4 (15.1–62.4)		167.6 (131.3–198.8)	
Female	KA50	1.4	1	68.7	2
	KA75	2.6	1	183.8	2
	KA95	7.0	2	482.4	2
	CA50	0.5	1	2.0	2
	CA75	0.8	1	5.9	3
	CA95	1.0	2	11.5	3
	MCP	9.1		325.4	



**Figure 3.** Home range of four selected individual Eurasian bitterns studied in different years at Lake Massaciuccoli: M971 in 1997 in the first row, M984 in the second, M993 in the third and F991 in the fourth. The panels in each row refer to the same individual during the breeding (left) and post-breeding periods (right). The line encompasses the MCP, while the nuclei identified via the cluster analysis with 50, 75 and 95 % fixes are indicated by black, crossed and striped areas, respectively. For the only female, F991, the nest position is indicated by a star. The solid line in each panel (bottom left) indicates 500 m.



The estimated size of the home range in any given year was not correlated with the number of fixes (no. fixes v. MCP size: max  $r_s = -0.37$ , n.s.,  $n = 8$  cases). The extent of male M971's range was very similar for both years at all analysis levels, so the average was used. The post-breeding locations of males (Table 2; see also Fig. 3) were spread over 70–270 ha (median: 167.6 ha; interquartile range 131.8–198.8;  $n = 7$  birds). At all analysis levels, the home range was divided into different nuclei covering a limited portion of the overall MCP. For example, the CA75s were 5–35 ha in area (10.3 ha, 6.3–18.5 ha;  $n = 7$ ), distributed throughout 1–5 nuclei (3, 1.5–4.8;  $n = 7$ ), i.e. 7.6 % (4.6–12.7 %) of the total MCP area visited. The size of the CA75 area was not correlated with either MCP size or the number of nuclei ( $r_s = 0.18$ , n.s.;  $r_s = -0.15$ , n.s.,  $n = 7$ , respectively). Regarding the number of moves between CA75 nuclei, male M971 exhibited a different pattern in the two years of study, moving about much more in 1997 than in 1998 (19 and 8 displacements, respectively), so these data were treated as independent. The number of moves between nuclei was positively correlated with the number of nuclei ( $r_s = 0.71$ ,  $P < 0.05$ ,  $n = 8$ ).

In late May 2000, just after the end of the booming season, male M983 left the marsh for another 40 ha marsh located 15 km north of Massaciucoli, where he spent 3 months, wandering in a single 9-ha CA75 nucleus (about half of the area of this marsh that remains wet in summer). He moved back to Massaciucoli in mid-September, just before the battery died.

The percentage overlap of the MCPs of simultaneously studied individuals (maximum number individuals/year = 3) was higher for MCP than for the CA75 or KA75 nuclei (MCP: 36.9 %, 12.63–76.4 %; CA75: 0.3 %, 0–0.9 %; KA75: 24.7 %, 15.3–31.4 %).

The MCP area was significantly larger during the post-breeding period than during breeding ( $150.0 \pm 57.7$  ha v.  $38.4 \pm 30.5$  ha,  $n = 7$  birds,  $T = 4.15$ ,  $P < 0.01$ , Wilcoxon test) though this difference was not found for the CA75 ( $15.4 \pm 10.5$  ha v.  $7.6 \pm 5.4$  ha,  $n = 7$  birds,  $T = 1.7$ , n.s.). The median breeding MCP covered 11.5 % (interquartile range 3.1–23.5 %) of the post-breeding area, while the breeding CA75 did not cover any (0 %; 0–15.5 %) of the post-breeding area. Figure 3 shows the home ranges of three individuals.

The female visited a larger area than the males (MCP = 325 ha), occupying several nuclei extending over a total of just a few hectares (e.g., CA75 = 6 ha; Table 2,

Fig. 3). She moved six times between three different CA75 nuclei, and her MCP overlapped 22 % with those of two males, though her CA75 nuclei were exclusive.

### Site fidelity and movement patterns within the Massaciucoli marsh

Four males were recaptured (though one of them was radio-tagged only in the second year) within 150–400 m from the first capture site. The three re-tagged birds occupied almost the same areas during the two reproductive seasons studied (Fig. 4). The only male that was also tracked also during the post-breeding periods in both years, M971, showed a very similar displacement pattern, with only slight timing differences after the end of the booming season. During the summer months of both years, he visited different parts of the same sectors. The breeding home ranges of M981 during the two years were virtually coincident, and M983 occupied the same area in the initial part of the booming season.

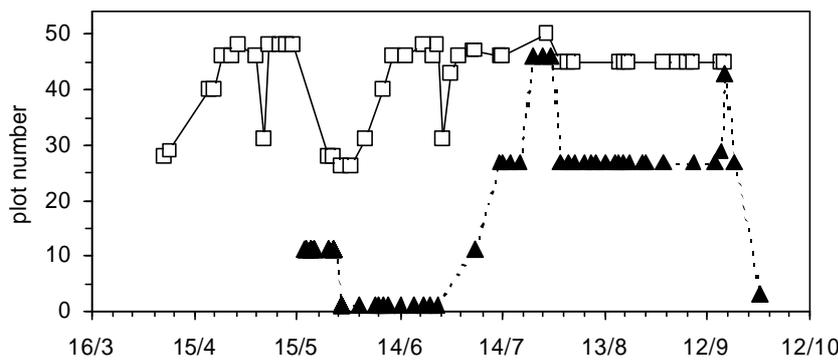
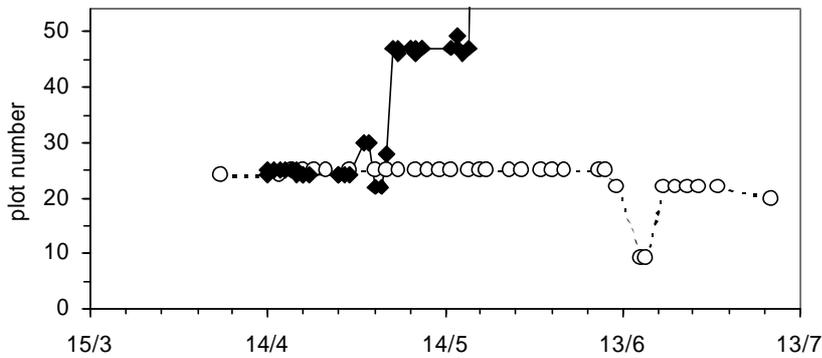
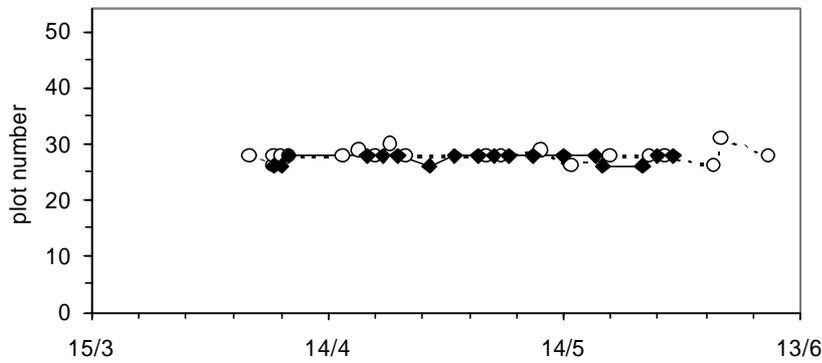
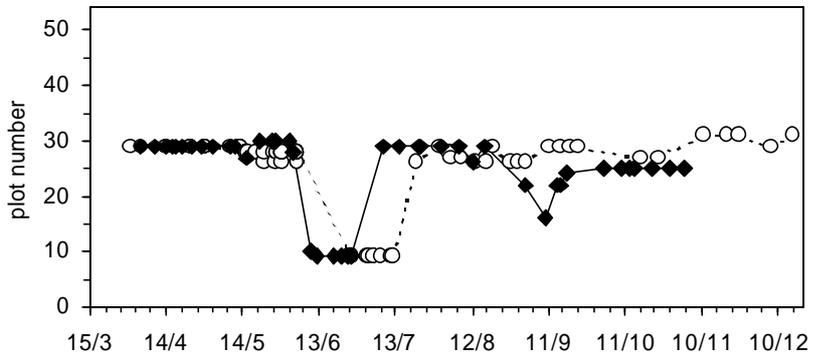
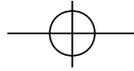
Figure 4 shows the movement patterns of the males M971, M981 and M983 during two years of study and of the female F991 and male M993 during a single year of study. In most cases, during the summer months the birds were located in a different marsh area from that of the breeding season. The same plot was not occupied continuously over the entire study period, but visited several times. All movements between distant areas occurred at night. When bitterns spent several consecutive days in the same spot, their night locations coincided with those in the preceding afternoon ( $n = 3$  comparisons for each bird).

### Causes of death

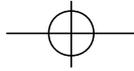
Although the Massaciucoli bittern population decreased markedly during the course of the study, we found only two dead birds, both in September 1999. M994 male died for unknown reasons, while the F991 female was the victim of illegal hunting.

### Discussion

This study provides the first documentation of bittern home range size and structure during both the breeding and post-breeding periods. The new information gathered on the ranging behaviour of the species outside the



**Figure 4.** Displacements of selected radio-tagged Eurasian bitterns at Lake Massaciuccoli. The graphs show the dates of presences within numbered, arbitrarily selected 10 ha plots (ordinate); the distances actually travelled cannot be deduced directly. The first three panels show the movements of males M971, M981 and M983 in the first (solid dots and broken line) and second year of study (solid diamonds and solid line). The bottom panel indicates the movements of the female F991 (solid triangles and broken line) and male M993 (solid squares and solid line). Only movements within the Massaciuccoli marsh are reported for the M983 male.



breeding period, when bitterns are never heard and rarely seen, is particularly important. Some behavioural modifications we observed during the study, such as the reduction of booming season, are related to the decline of the population, as already observed at other sites (Gilbert et al. 1994, Fontanelli et al. 1995), rather than to a fieldwork-induced disturbance.

The bitterns' home ranges were typically multinuclear during both the breeding and post-breeding seasons. Bitterns spent all day on virtually the same spot, where they carried out all their activities, without marked differences between feeding and roosting sites. Various scattered locations within a larger area were visited repeatedly: bitterns appear to move mainly between areas they already know, travelling far during the post-breeding period, while ignoring other suitable surrounding and nearby locations, which are sometimes exploited by other individuals. Four birds were re-caught very close to their first capture site. Three re-tagged males showed similar or partially coincident displacement patterns in both study years, using the same or nearby patches. Individual experience, rather than occasional active searches for favourable locations, appeared to play the major role in the layout of bitterns' home ranges. No correlation was found among the number of patches used during either the reproductive or post-breeding period and the total extent of the area visited, since small but highly fragmented home ranges were observed. Tagged birds used intensively those areas which were probably exclusive, although we could not discount the possibility that some untagged birds could have been sharing the same grounds. Maximum convex polygons, on the other hand, exhibited large inter-individual overlaps.

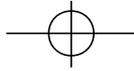
Many behavioural traits, such as solitary feeding and roosting, male booming vocalisations, polygyny and uniparental care, distinguish bitterns from other heron species (Del Hoyo et al. 1992). The observed movement patterns also differ considerably from other herons, whose home ranges centre on the colony during the reproductive period and on the roosting site afterwards, and who travel long distances (up to 30 km or more) to feeding grounds shared with individuals of the same or different species (Custer & Osborn 1978, van Vessem et al. 1984, Draulans & van Vessem 1985, Marion 1989, Smith 1995, Strong et al. 1997). Colonial herons often change feeding grounds over short time intervals, probably in response to variations in the dis-

tribution of food resources, even though the colony or roosting site remains stable (e.g., Dugan et al. 1988, Kersten et al. 1991, Hafner et al. 1993).

In the case of the bittern, whose feeding, nesting and roosting habitats coincide, each individual seems to move solitarily within areas varying individually in size (MCP). This may be an advantageous strategy to exploit a habitat where basic resources, such as food, are distributed in a predictable fashion, but not exploitable by aggregated individuals. A direct observational study of squacco herons *Ardeola ralloides* revealed that feeding success within the vegetation cover diminished if other individuals were nearby (Hafner et al. 1980), probably because prey, disturbed by the other herons, were less easily caught. Bitterns usually forage for aquatic prey within the vegetation cover, where they may benefit by solitarily searching for food and profiting from individual experiences of favourable patches where prey is abundant and where intraspecific competition is reduced or absent. Thus, individual experience and/or their ability to defend favourable patches may be important factors affecting the size of the single areas visited and exploited.

The total extent of the areas where bittern males concentrated their activity was similar during breeding and post-breeding periods, indicating that at the Massaciucoli marsh the patch size required to maintain an individual is 5–20 ha (CA75) during both spring and summertime, although the areas in question need not coincide.

During the breeding season the various home range nuclei were not occupied continuously, but visited on different days by male bitterns, who boomed in each one. Bittern males' movements were restricted to a decidedly smaller area than in the post-breeding months. This difference in displacement area between the breeding and post-breeding period may be linked to the less favourable conditions in summer, when the drop in water level drastically reduces the availability of feeding grounds. However, it is worth noting that several individuals moved away by late May or early June just after they stopped booming, one month before the summer drought. Possible factors involved in such a strategy may be the depletion of food resources consequent to continuous feeding in the same area, as observed for other herons or wading birds (Rogers & Nesbitt 1979, Dugan et al. 1988, Custer & Galli 2002), as well as the different social pressures at play during the two periods.



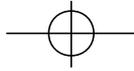
During the breeding period, the single female studied fed almost exclusively very close to her nest. Given this species' uniparental care of young, nesting within profitable feeding areas could be very important in determining the time budget of breeding females (M.C. Adamo et al., unpubl. data) and reproductive success (L. Puglisi & V. Bretagnolle, unpubl. data). During the post-breeding period, her home range had a structure similar to the males, but with smaller nuclei scattered over a larger area.

This study provides some basic background information on which to build further studies of the behavioural adaptations of bitterns to their closed marshy habitat, in particular to the interactions between vocalisations, male spatial behaviour and female mating choice. The radio-tracking data reveal that during the post-breeding period bitterns move to areas unexploited during the breeding period, even to other marshes some distance away. Thus, management strategies based exclusively on their distribution during the reproductive period, as inferred from studies of booming males, may lead to incorrect assessments of the key factors in the maintenance of resident populations.

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