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The further the flight, the longer the wing: relationship between wing length and migratory distance in Old World reed and bush Warblers (Acrocephalidae and Locustellidae)

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We analysed how body mass, migration distance, taxonomic family and breeding on small islands vs. continents affect wing length in 72 species of closely related Old World reed and bush warblers (Acrocephalidae and Locustellidae), based on literature data. The species we analysed share similar morphology, habitat, food preferences, feeding habits and breeding systems, but their migratory behaviour varies from sedentariness to long-distance migration. The mean wing length of these species was strongly correlated with their body mass, migration distance and taxonomic family ($R^2 = 0.824$; $p = 3.2^{-26}$). The wing was on average 23.4% longer for each doubling of body mass and 2.7% longer for each 1,000 km of migration distance. Breeding on small islands was not significantly related to wing length. Species of Acrocephalidae had on average 11.7% longer wings than Locustellidae with the same body mass and migration distance. The relationship between migration distance and standardised wing length was identical in both families (difference between slope coefficients b: t-test: $t = 0.19$, $p = 0.85$). After we partly controlled for the effects of different habitats and behaviours, our results showed that at inter-specific level migration affects wing length in proportion to migration distance.

1. Introduction

Wing morphology affects the energetic efficiency of flight (Pennycuick 1989, Bowlin & Wikelski 2008). Many authors have shown the relationship between birds' wing length and pointedness and their migration distance, at the inter- and intra-specific level (Calmaestra & Moreno 2001, Pérez-Tris & Tellería 2001, Leisler & Winkler 2003, Fiedler 2005, Milá *et al.* 2008, Baldwin *et al.* 2010). Comparisons at the intra-specific level, between populations or subspecies, have shown that the migrants tend to have longer and more pointed wings, which helps in fast and efficient flight, than the sedentary birds, which tend to have shorter and more rounded wings for improved manoeuvrability (Pérez-Tris & Tellería 2001, Milá *et al.* 2008). However, comparisons of these wing features between species have not provided a clear pattern in these relationships. Some authors have shown that migrant species have longer wings than sedentary species (e.g. Marchetti *et al*. 1995, Milá *et al.* 2008), but others could not confirm this relationship or have shown only a weak correlation between wing length and migration distance (e.g. Mönkkönen 1995, Calmaestra & Moreno 2001, Baldwin *et al.* 2010).

This has led some authors (Marchetti *et al.* 1995) to conclude that wing length depends more on a species' ecology – such as habitat, food type, size of prey and feeding habits (Winkler & Leisler 1992, Swaddle & Lockwood 1998, Lockwood *et al.* 1998, Tornberg *et al*. 1999, Dawson 2005) – than on migration distance. The selective pressures of the different elements of birds' habitat or behaviour can have opposing effects on the wing length (James 1982, Alatalo *et al*. 1984) that lead to an equilibrium in which none of these factors' effects prevail over the others. Many authors have also shown that wing length can vary greatly because of weather and feeding conditions while the primaries are growing, and also because of age- and sex-dependent differences in the length of feathers (Björklund 1996, Dawson *et al.* 2000, Hall & Fransson 2000, Fiedler 2005, Milá *et al.* 2008, Baldwin *et al.* 2010, Polakowski & Jankowiak 2012). These numerous and insufficiently explored factors affecting wing morphology require multifactorial analyses to identify the relationships between wing length and the elements of behaviour typical of the species (including migratoriness or sedentariness) and of its habitat, or control of the remaining variables that could affect a conclusion (Baldwin *et al.* 2010). The need to consider the history of the species, or of its populations, is also emphasised, including the time during which different types of selective pressures have acted, such as the time during which a species and its ancestors had been sedentary (Baldwin *et al.* 2010). This history is reflected by relationships between different taxa.

Bearing in mind the effects of habitat, behaviour and a species' history, for this analysis we selected Acrocephalidae and Locustellidae, two closely related families of passerines that share similar morphology, habitats and behaviour. Most species of these families show little sexual dimorphism, live in dense bush or reed habitats, feed on invertebrates and do not perform spectacular display flights (Kennerley & Pearson 2010). But the species in these families do present the whole spectrum of migratory behaviour, from complete sedentariness, through altitudinal or short-distance movements, to long-distance seasonal migration between continents. This makes them a suitable model to study the relationships between migration distance and wing morphology. Another important factor, which differs among these species, is that some breed on small islands in the Pacific or Indian Oceans, and most of those species are sedentary, but others breed and overwinter over vast land areas, such as large islands or continents (Kennerley & Pearson 2010). Living on small islands limits the likelihood of long movements during the breeding and wintering seasons, which considerably affects wing morphology (Senar *et al*. 1994, Desrochers 2010) and might even lead to flightlessness (Grant 1965, Olson 1973, Bicudo *et al.* 2010).

We aimed to identify the relationship between wing length and migration distance among passerines, while controlling for the effects of different habitat and feeding behaviour by choosing taxa of similar habits. We also aimed to identify the strength of this relationship and whether it is similar in bird groups of different phylogenesis, and to determine if breeding on small islands might affect this relationship.

2. Material and methods

This paper is based on the overview of biometric data published in Kennerley & Pearson (2010) for reed and bush warblers of the Old World. We analysed all 72 species of the families Acrocephalidae and Locustellidae for which that study provided the mean wing length and the mean body mass, and for which it was possible to determine an approximate migration distance (e.g. we did not include three species of partial migrants; see Appendix 1).

All the mean values of parameters such as migration distance, wing length and body mass, were the means for a species or a subspecies. When Kennerley & Pearson provided these values for a few subspecies, we used in our calculations the data for the subspecies that had the best-defined winter quarters or the most complete dataset (the largest sample size for which mean values were provided). If separate measurements were provided for males and females, we calculated the mean values for both sexes combined to standardise the data for comparisons with species in which the sexes were not distinguished. We used the body mass and the wing length for the population for which we could estimate the migration distance. For sedentary species, mainly tropical and subtropical, that do not show large seasonal changes in body mass, we used the mean body mass given by Kennerley & Pearson (2010), or the mean of minimum and maximum body masses where only those values were provided. For migrants, which show large differences in the body mass between the migration period and the rest of the year, we calculated the mean value using the mean body mass during migration and the mean body mass outside the migration period, allocating equal weights to both means. In this way we considered the effect of the body mass on the wing length in both periods of the migrants' life, but without assuming which of these periods was more crucial for this effect.

We estimated the migration distance as the distance between the middle of the breeding range and the middle of the wintering range of a species by the shortest line between these two points i.e., the orthodrome or great circle distance (Imboden & Imboden 1972). If Kennerley & Pearson (2010) described from which part of the breeding range the biometric data originated, we calculated the distance between the middle of this area and the middle of the wintering range of this population. To determine the effect of a species' breeding range being confined to a small island (hereinafter referred to as the "island factor") on the wing length, we divided all species into two groups: the "island group", species that breed on small islands (volcanic or coral reef) up to a dozen square kilometres, such as the Cook Islands inhabited by the Cook Island Warbler (*Acrocephalus kerearako*) and the Mariana Islands (Nightingale Warbler *Acrocephalus luscinius*); and the "continental group", species that breed on continental areas or large islands of at least 50,000 square kilometres, such as Ceylon (Ceylon Bush Warbler *Elaphrornis palliseri*), the Luzon Islands in the Philippines (Long-tailed Bush Warbler *Bradypterus caudatus*), or larger areas (for the importance of such a division, see Newton 2003). Appendix 1 presents the data we used in our analyses. We applied the logarithmic (ln) transformation to the biometic data before further calculations.

We used the body mass and the migration distance as continuous variables, and the taxonomic identity (the family) and the island factor as class variables in our analyses of the factors that might affect the wing length (response variable) of the studied species. We compared all 16 possible models with different combinations of the factors using Bayesian Information Criteria (BIC) to calculate the relative weight of each model m as "penalised" likelihood: $L(m) = \exp\{-0.5\ \mathrm{BIC}(m)\}$ and to estimate posterior probabilities $P(m) = L(m) / \Sigma_m L(m)$ (Congdon 2006, Lunn *et al.* 2012). We chose the model that had the highest posterior probability in further analyses by linear multiple regression.

We checked if the regression lines for both families were parallel by testing the difference between the slope coefficients *b* using Student's *t*-test.

3. Results

BIC's ranking of models with different combinations of factors showed that the three-factorial model with the body mass, migration distance and taxonomic identity used as explanatory variables (factors) was the best-fitting model. The probability that this model was best fitted to the data was higher than 95% ($p = 0.955$, Table 1), so we chose it for further calculations. The second-best model, which considered all four explanatory variables (including the island effect), had a probability of almost 5%, a few orders higher than all the remaining models (Table 1). All other models with different sets of factors had low probabilities ($p < 0.001$, Table 1), and thus could be ignored from further consideration.

The three-factorial linear regression showed a high correlation between the three factors we analysed and the wing length (total corrected $R^2 = 0.824$; $p = 3.2e^{-26}$). Body mass was the factor most significantly correlated with wing length, and the

Table 1. BIC ranking of models with different numbers of explanatory variables. We show the four models with the highest probability. Model rank – rank of the model according to the best fit, factors – explanatory variables used in the models (1 – island factor, 2 – taxonomic family, 3 – body mass, 4 – migration distance, "–" – absence of a factor in the model), *N* – the number of species that were included in the model, *P* – probability of the model (the sum of the probabilities for all the possible models = 1).

Model rank	Factors	*N*	*P*
1	– 2 3 4	72	0.955
2	1 2 3 4	72	0.045
3	1 – 3 4	72	< 0.0001
4	– – 3 4	72	< 0.0001

slope coefficient *b* for this parameter indicated that the heavier the species, the longer its wing; and with a doubling of body mass the wing length increased by 23.4% (Table 2). The second-most significant factor was the migration distance. The longer the migration distance, the longer the wing, by 2.7% for each 1,000 km of migration on average (Table 2, Fig. 1). With the same body mass and the same migration distance the Acrocephalidae had on average 11.7% longer wings than the Locustellidae. This meant that a sedentary Acrocephalid would have a wing of the same length as a Locustellid of the same body mass that migrated 4,100 km.

This showed that the species of Acrocephalidae and Locustellidae differed in wing length even after we considered the differences in their body mass and their migration distance. Thus we also tested if the relationship between migration distance and wing length was similar within each family. The regression lines between the migration distance and the standardised wing length for Acrocephalidae and Locustellidae were parallel. Their slope coefficients *b* were almost identical (difference only 0.1% of wing length / 1,000 km; *t*-test: $t = 0.19$, $p = 0.85$).

4. Discussion

Our results showed that size (expressed as body mass), migration distance and family explained most of the inter-specific variation in wing length among Old World reed and bush warblers. These effects were so strong that these factors were statistically significant though we used only approximate migration distances and body measurements, provided in the literature. The effect of migration distance on wing length was almost identical in Acrocephalidae and Locustellidae, as shown by almost parallel regression lines, but this relationship settled at a different level in each family. This pattern suggested that the selective pressure of migration distance increased gradually with distance. The energy saved by wings with appropriate aerodynamic properties for long-distance flight (such as length and pointedness) increases with migration distance (Bowlin & Wikelski 2008).

Our results concur with studies on the Blackcap (*Sylvia atricapilla*), in which different populations or subspecies present a plethora of migration behaviours, from complete sedentariness to transcontinental migrations of about 7,000 kilometres, and show an associated difference of up to 7.8 mm in wing length, which gives an increase in wing length of about 1 mm for each 1,000 km of migration distance (Pérez-Tris *et al.* 1999, Fiedler 2005). Other authors who have analysed intra-specific variation in wing length have also shown that the migration distance of different populations

Table 2. Regression coefficients for the three-factorial linear regression of the best fitted model 1 (see Table 1). *b* – slope coefficient, SE b – standard error of the slope coefficient, *p* – statistical significance of the effects of each factor (explanatory variable).

Factor	Mean	*b*	SE *b*	*p*
Constant	65.0	3.15	0.06	< 0.0001
Mass (ln)	15.9	0.337	0.020	< 0.0001
Distance	0.075	0.0268	0.0029	< 0.0001
Taxon	–	0.110	0.014	< 0.0001

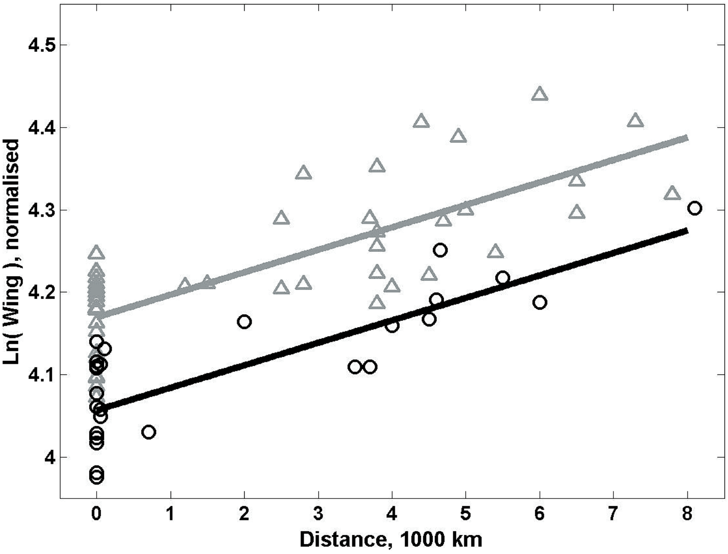

Fig.1. Correlation of wing length and migration distance in the Acrocephalidae (grey symbols) and Locustellidae (black symbols). Data values for Ln(Wing) were adjusted for mass using the formula Ln(Wing)–0.337 × [Ln(Mass)–LM0], where LM0 is the mean of (Ln(Mass). The regression lines were calculated for each taxon separately with the common constant value of Ln(Mass) = LM0.

or subspecies significantly affects their mean wing length (e.g. Milá *et al.* 2008). These results refer to intra-specific variation, but our results are similar, though we examined inter-specific variation.

Our results and those of other authors can be explained well by a hypothesis that wing length is shaped by contradictory selection pressures (Milá *et al.* 2008). A long wing is more energy-efficient in migratory flight than a short one (Pennycuick 1989, Bowlin & Wikelski 2008, Newton 2008), and so it is favoured by natural selection in migrants. But the same bird could face opposing selection pressures when moving through dense vegetation and when evading predators on breeding, stopover and wintering grounds, where the manoeuvrability provided by shorter and rounder wings would be favoured (Alatalo *et al.* 1984, Keast *et al.* 1995, Marchetti *et al.* 1995, Swaddle & Lockwood 2003). Therefore birds that do not migrate over longer distances usually have short rounded wings (Senar *et al.* 1994, Pérez-Tris & Tellería 2001, Milá *et al.* 2008). One could assume that these opposing pressures act differently on populations of the same species that differ in their migration distance or habitat as well as on the inter-specific level (Marchetti *et al.* 1995, Milá *et al.* 2008).

Baldwin *et al.* (2010) emphasised the importance of a species' history on the present morphology of its flight apparatus. The extent of time since the last significant change of a species' habitat or life strategy, such as a transition from migratory to sedentary behaviour or the opposite, is of particular importance (Fiedler 2005, Baldwin *et al.* 2010). Our results confirmed the influence of a species' history on its wing length, and showed that this is stronger than has been suggested so far. The differences in the standardised wing length between species of Acrocephalidae and Locustellidae (Fig. 1) cannot be explained only by the time that has passed since they reached their current level of migratoriness (as measured by the mean migration distance). Both groups contain tropical birds that have been sedentary for a long time, such as many species of the genus *Acrocephalus*, and among Locustellidae of the genus *Bradypterus* (Kennerley & Pearson 2010), as well as species whose migration patterns were shaped only after the last ice-age (Newton 2003, 2008). Certainly species of the two families differ to some extent in their lifestyles and chosen habitats, which might influence the morphological differences we found. But these variations also occur within each of these families, and the general differences between species of Acrocephalidae and Locustellidae are smaller than the differences within these families (Leisler *et al.* 1989, Kennerley & Pearson 2010). The difference in the increment of the regression lines, showing the level at which the relationships we analysed settled for these two families (Fig. 1), suggested that the morphology of the species that were ancestral to each family considerably affected the current wing morphology of the current species. We hypothesise that the ancestral species of the Acrocephalidae and Locustellidae had some properties of their skeleton, musculature, feather structure etc. that predisposed or limited further evolutionary changes and in that way they shaped the morphological features of the current species of both families. This could apply in more general terms to other bird taxa.

Our study did not clearly show any effect of the "island factor" on wing length, but the occurrence of this factor in the second-best model in our ranking (Table 1) suggested that it might be of some importance. Whether the effect of the "island factor" is significant or not, we concluded that it did not bias the relationship between migration distance and wing length for the species of Acrocephalidae and Locustellidae included in our study. No effect, or weak effect, of the "island factor" on the wing length is intresting in the light of our related studies on wing shape (in preparation), which show that the "island factor" has a highly significant effect on the wing shape.

Summing up, our results showed at the interspecific level that migration affects the wing length in proportion to migration distance, when we partly controlled for the effect of different habitat and behaviour. This has not yet been well demonstrated at the inter-specific level. We showed that this effect is similar in Acrocephalidae and Locustellidae. The "island factor" has little or no effect on wing length, and this issue requires further study.

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Mitä pidempi muuttomatka sitä pidempisiipisempi laji

Analysoimme lajitasolla miten ruumiinpaino, muuttoetäisyys, taksonomia (heimo) ja saaripopulaatiostatus (saarilaji/mannerlaji) vaikuttivat siiven pituuteen 72 lajilla, heimoissa Acrocephalidae ja Locustellidae. Aineisto perustui kirjallisuustietoon. Tarkastelluilla lajeilla on samankaltainen morfologia, elinympäristö, ravinto, ruokailutottumukset ja pesimäbiologia, mutta niiden muuttokäyttäytyminen vaihtelee paikkalinnuista pitkän matkan muuttajiin. Siiven keskimääräinen pituus oli näillä lajeilla voimakkaasti korreloitunut ruumiinpainon, muuttoetäisyyden ja taksonomian kanssa ($R^2 = 0.824$; $p = 3.2^{-26}$). Siipi oli keskimäärin 23,4 % pidempi ruumiinpainon kaksinkertaistuessa ja 2,7 % pidempi jokaista 1 000 km muuttomatkaa kohti. Muuttomatkan ja siivenpituuden suhde ei eronnut heimojen välillä. Saarilla esiintyminen ei selittänyt siiven pituutta tilastollisesti merkitsevästi. Acrocephalidae heimon lajeilla oli keskimäärin 11.7 % pidemmät siivet kuin heimolla Locustellidae, korjattuna ruumiinpainolle ja muuttoetäisyydelle.

References

Alatalo, R.V., Gustafsson, L. & Lundberg, A. 1984: Why do young passerine birds have shorter wings than older birds? — Ibis 126: 410–415.

Baldwin, M.W., Winkler, H., Organ, C.L. & Helm, B. 2010: Wing pointedness associated with migratory distance in common-garden and comparative studies of stonechats (*Saxicola torquata*). — Journal of Evolutionary Biology 23: 1050–1063.

Bicudo, J.E.P.W., Buttemer, W.A., Chappell, M.A., Pearson, J.T. & Bech, C. 2010: Ecological and environmental physiology of birds. — Oxford University Press, Oxford.

Björklund, M. 1996: The effect of male presence on nestling growth and fluctuating asymmetry in the Blue Tit. — Condor 98: 172–175.

Bowlin, M.S. & Wikelski, M. 2008: Pointed wings, low wingloading and calm air reduce migratory flight costs in songbirds. — PLOS ONE 3: e2154. DOI: 10.1371/journal.pone.0002154

Calmaestra, R.G. & Moreno, E. 2001: A phylogenetically-based analysis on the relationship between wing morphology and migratory behaviour in Passeriformes. — Ardea 89: 107–415.

Congdon, P. 2006: Bayesian statistical modelling. 2nd ed. — John Wiley & Sons, Ltd., Chichester.

Dawson, A. 2005: The scaling of primary flight feather length and mass in relation to wing shape, function and habitat. — Ibis 147: 283–292.

Dawson, A., Hinsley, S., Ferns, P., Bonser, R. & Eccleston, L. 2000: Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. — Proceedings of the Royal Society B 267: 2093–2098.

Desrochers, A. 2010: Morphological response of songbirds to 100 years of landscape change in North America. — Ecology 91: 1577–1582.

Fiedler, W. 2005: Ecomorphology of the external flight apparatus of blackcaps (*Sylvia atricapilla*) with different migration behavior. — Annals of the New York Academy of Sciences 1046: 253–263.

Grant, P.R. 1965: The adaptive significance of some size trends in island birds. — Evolution 19: 355–367.

Hall, S. & Fransson, T. 2000: Lesser Whitethroats under time-constraint moult more rapidly and grow shorter wing feathers. — Journal of Avian Biology 31: 583–587.

Imboden, C. & Imboden, D. 1972: Formel für Orthodrome und Loxodrome bei der Berechnung von Richtung und Distanz zwischen Beringungs und Wiederfundort. —Vogelwarte 26: 336–344.

James, F.C. 1982: The ecological morphology of birds: a review. — Annales Zoologici Fennici 19: 265–275.

Keast, A., Pearce, L. & Saunders, S. 1995: How convergent is the American Redstart (*Setophaga ruticilla*, Parulinae) with flycatchers (Tyrannidae) in morphology and feeding behavior? — Auk 112: 310–325.

Kennerley, P. & Pearson, D. 2010: Reed and bush warblers. — Christopher Helm, London.

Leisler, B. & Winkler, H. 2003: Morphological consequences of migration in Passerines. — In Avian Migration (ed. Berthold, P., Gwinner, E. & Sonnenschein, E.): 175–186. Springer-Werlag, Berlin.

Leisler, B., Ley, H.-W. & Winkler, H. 1989: Habitat, behaviour and morphology of *Acrocephalus* warblers: an integrated analysis. — Ornis Scandinavica 20: 181–186.

Lockwood, R., Swaddle, J.P. & Rayner, M.V. 1998: Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. — Journal of Avian Biology 29: 273–292.

Lunn, D.J., Jackson, C., Best, N., Thomas, A. & Spiegelhalter, D. 2012: The BUGS book: a practical introduction to Bayesian analysis. — Chapman & Hall/CRC Texts in Statistical Science.

Marchetti, K., Price, T. & Richman, A. 1995: Correlates of wing morphology with foraging behaviour and migration distance in the genus *Phylloscopus*. — Journal of Avian Biology 26: 177–181.

Milá, B., Wayne, R.K. & Smith, T.B. 2008: Ecomorphology of migratory and sedentary populations of the yellow-rumped warbler (*Dendroica coronata*). — The Condor. 110: 335–244.

Mönkkönen, M. 1995: Do migrant birds have more pointed wings?: a comparative study. — Evolutionary Ecology 9: 520–528.

Newton, I. 2003: The speciation and biogeography of birds. — Academic Press, London.

Newton, I. 2008: The migration ecology of birds. — Academic Press, London.

Olson, S.L. 1973: Evolution of the Rails of the South Atlantic Islands (Aves: Rallidae). — Smithsonian Contributions to Zoology 152: 1–53.

Pennycuick, C.J. 1989: Bird flight performance: a practical calculation manual. — Oxford University Press, New York.

Pérez-Tris, J. & Tellería, J. 2001: Age-related variation in wing shape of migratory and sedentary Blackcaps (*Sylvia atricapilla*). — Journal of Avian Biology 32: 207–213.

Pérez-Tris, J., Carbonell, R. & Tellería, J.L. 1999: A method for differentiating between sedentary and migratory Blackcaps *Sylvia atricapilla* in wintering areas of south Iberia. — Bird Study 46: 299–304.

Polakowski, M. & Jankowiak, Ł. 2012: Timing of autumn migration and biometric characteristics of migrating populations of European Robin (*Erithacus rubecula* L. 1758) in north-eastern Poland. — Polish Journal of Ecology 60: 797–804.

Senar, J.C., Lleonart, J. & Metcalfe, N.B. 1994: Wing-shape variation between resident and transient wintering Siskins *Carduelis spinus*. — Journal of Avian Biology 25: 50–54.

Swaddle, J.P. & Lockwood, R. 1998: Morphological adaptations to predation risk in passerines. — Journal of Avian Biology 29: 172–176.

Swaddle, J.P. & Lockwood, R. 2003: Wingtip shape and flight performance in the European Starling *Sturnus vulgaris*. — Ibis 145: 457–464.

Tornberg, R., Mönkkönen, M. & Pahkala M. 1999: Changes in diet and morphology of Finish goshawks from 1960s to 1990s. — Oecologia 121: 369–376.

Winkler, H. & Leisler, B. 1992: On the ecomorphology of migrants. — Ibis 134: 21–28.

Appendix 1. Data used in the analyses (based on Kennerley & Pearson 2010). Island factor (ISL): I – "island" species whose breeding range is confined to small islands, C – "continental" species whose breeding and wintering ranges extend across a continent or large islands. Other variable listed are Migration distance (DIST; 1,000 km), mean wing length (WING; mm) and mean body mass (MASS; g).

No	Species	ISL	DIST	WING	MASS
Acrocephalidae					
1	*Acrocephalus aequinoctialis*	I	0	73.85	25
2	*Acrocephalus agricola*	C	2.8	57.55	11.25
3	*Acrocephalus arundinaceus*	C	6.5	94.55	28
4	*Acrocephalus baeticatus*	C	1.5	59.60	10.5
5	*Acrocephalus bistrigiceps*	C	3.8	55.20	8.75
6	*Acrocephalus brevipennis*	I	0	65.65	16
7	*Acrocephalus concinens*	C	2.5	55.10	9.25
8	*Acrocephalus dumetorum*	C	4.5	62.15	12.5
9	*Acrocephalus familiaris*	I	0	63.00	18.3
10	*Acrocephalus griseldis*	C	4.9	82.25	18.5
11	*Acrocephalus kerearako*	I	0	77.00	22.5
12	*Acrocephalus luscinius*	I	0	87.30	33.1
13	*Acrocephalus melanopogon*	C	1.2	58.45	10.7
14	*Acrocephalus newtoni*	C	0	68.20	17.8
15	*Acrocephalus orientalis*	C	3.7	83.15	25.25
16	*Acrocephalus paludicola*	C	5.4	62.90	12
17	*Acrocephalus palustris*	C	7.8	68.50	13
18	*Acrocephalus rimitarae*	I	0	83.15	26.5
19	*Acrocephalus rodericanus*	I	0	61.70	12.1
20	*Acrocephalus rufescens*	C	0	73.20	20
21	*Acrocephalus schoenobaenus*	C	6.5	65.95	15.5
22	*Acrocephalus scirpaceus*	C	5	66.25	13.375
23	*Acrocephalus sechellensis*	I	0	66.85	16
24	*Acrocephalus sorghophilus*	C	3.8	57.70	8.1
25	*Acrocephalus stentoreus*	C	0	79.15	25
26	*Acrocephalus taiti*	I	0	80.85	24.3
27	*Acrocephalus tangorum*	C	4	54.10	8
28	*Acrocephalus vaughani*	I	0	79.00	25
29	*Calamonastides gracilirostris*	C	0	61.80	10.6
30	*Hippolais icterina*	C	7.3	78.10	14.75
31	*Hippolais languida*	C	4.4	75.90	13.68
32	*Hippolais olivetorum*	C	6	86.60	18.5
33	*Hippolais polyglotta*	C	4.7	65.35	14
34	*Iduna (Hippolais) caligata*	C	3.8	60.20	8.9
35	*Iduna (Hippolais) opaca*	C	2.8	69.20	10.5
36	*Iduna (Hippolais) pallida*	C	3.8	66.35	9.5
37	*Iduna (Hippolais) rama*	C	2.5	61.15	9
38	*Iduna natalensis*	C	0	61.95	10.7
39	*Iduna similis*	C	0	58.65	11.1
40	*Nesillas aldabranus*	I	0	67.00	19.2
41	*Nesillas brevicaudata*	I	0	65.00	16.1
42	*Nesillas lantzii*	C	0	62.10	17.5
43	*Nesillas mariae*	I	0	61.00	15.6
44	*Nesillas typica*	C	0	63.95	18.1
45	*Phragamaticola aedon*	C	3.8	80.15	25.9
Locustellidae					
1	*Bradypterus accentor*	C	0	59.40	14
2	*Bradypterus alfredi*	C	0	58.90	15.8
3	*Bradypterus baboecala*	C	0.05	59.65	14
4	*Bradypterus bangwaensis*	C	0	63.05	21

No	Species	ISL	DIST	WING	MASS
5	*Bradypterus barratti*	C	0.05	62.70	18.8
6	*Bradypterus carpalis*	C	0	69.90	22.3
7	*Bradypterus castaneus*	C	0	56.00	19
8	*Bradypterus caudatus*	C	0	62.00	22.9
9	*Bradypterus cinnamomeus*	C	0	62.15	17.5
10	*Bradypterus davidi*	C	3.5	53.00	10.1
11	*Bradypterus grandis*	C	0	65.80	18.5
12	*Bradypterus graueri*	C	0	57.95	16.9
13	*Bradypterus lopezi*	C	0	61.75	18.9
14	*Bradypterus mandelli*	C	0.05	53.10	12.2
15	*Bradypterus sylvaticus*	C	0	59.80	21
16	*Bradypterus tacsanowskius*	C	3.7	55.60	11.4
17	*Bradypterus thoracicus*	C	0.1	54.60	10.8
18	*Elaphrornis palliseri*	C	0	61.30	11.5
19	*Locustella certhiola*	C	4.5	64.55	15.1
20	*Locustella fasciolata*	C	6	80.60	27.1
21	*Locustella fluviatilis*	C	8.1	75.50	19
22	*Locustella lanceolata*	C	4	56.65	11.15
23	*Locustella luscinioides*	C	4.65	70.15	17.5
24	*Locustella naevia*	C	5.5	63.75	14.25
25	*Locustella ochotensis*	C	4.6	70.35	18
26	*Locustella pleskei*	I	2	71.00	20
27	*Locustella pryeri*	C	0.7	54.95	13.55