JOURNAL OF AVIAN BIOLOGY 32: 207–213. Copenhagen 2001

Age-related variation in wing shape of migratory and sedentary Blackcaps *Sylvia atricapilla*

Javier Pérez-Tris and José Luis Tellería

Pérez-Tris, J. and Tellería, J. L. 2001. Age-related variation in wing shape of migratory and sedentary Blackcaps *Sylvia atricapilla*. – J. Avian Biol. 32: 207–213.

In many passerines, juveniles have shorter and more rounded wings than adults. Given that (1) long and pointed wings improve endurance in migratory flights, (2) shorter and rounded wings improve manoeuvrability, and (3) juvenile birds are more vulnerable to predators than adults, it has been hypothesised that ontogenetic variation in wing shape results from a greater importance of predation avoidance relative to migration performance during the first year of life. If so, wing shape should not change with age in the absence of migration-related selection for longer and more pointed wings. We test this by studying the variation with respect to age in wing length and wing pointedness of migratory and sedentary Blackcaps wintering in southern Spain. Migratory Blackcaps had longer and more pointed wings than sedentary Blackcaps. Juveniles had shorter wings than adults in migratory populations, but not in sedentary populations. The variation with age in wing pointedness was less pronounced, and was found in migratory females only. These differences between the two traits could be related to a stronger selection for pointed wings than for longer wings with increasing distance of migration, and to an increased migratoriness of females in partially migratory Blackcap populations. We hypothesise that, in migratory Blackcaps, a shorter and more rounded wing in juveniles could be selected for if the decrease in predation rate compensated for the somewhat greater costs of the first migration attempt. On the other hand, there are no costs of migration in sedentary Blackcaps, which hence maintain a similar wing shape, giving high manoeuvrability, both as juveniles and as adults.

J. Pérez-Tris (correspondence) and J. L. Tellería, Departamento de Biología Animal I (Vertebrados). Facultad de Biología, Universidad Complutense. E-28040 Madrid, Spain. E-mail: jperez@eucmax.sim.ucm.es, telleria@eucmax.sim.ucm.es

Natural selection has shaped the wing morphology of birds for different kinds of flight, such as flapping or soaring, but has also resulted in more subtle differences among closely related species and even among different populations within species (Pennycuick 1989, Norberg 1990). For instance, wing shape fits particular needs of birds connected with different environments, feeding substrates or degrees of migratoriness (Leisler and Winkler 1985, Winkler and Leisler 1985, 1992, Rayner 1988, Norberg 1995, Norman 1997, Lockwood et al. 1998).

In passerines, one of the most impressive changes in wing shape is the increase in wing length and wing pointedness after the first complete moult. Alatalo et al. (1984) proposed that a shorter and more rounded wing in juveniles increases survival by improving their ability to evade predators. Several studies have shown that naivety makes juveniles more vulnerable than adults to the attacks of predators (Opdam 1978, Solonen 1997), and the view that slight differences in wing morphology could affect the escape ability of birds has been supported by a large body of empirical evidence. Shorter and more rounded wings allow birds to attain a higher velocity and a faster ascent after take-off (Pennycuick 1989, Norberg 1990, 1995), and recent studies suggest that take-off ability reduces the risk of being captured by predators (Kullberg et al. 1996, 1998, Lee et al. 1996, Lind et al. 1999). Observations of the hunting tactics of small raptors – the principal predators of passerines – corroborate this. Since these raptors usually rely on surprise (Rudebeck 1950, Newton 1986, Cresswell 1996), slight differences in take-off ability may make all the difference for their prey between escaping and ending up as a dinner (e.g., Bednekoff 1996). Therefore, and given that differences in juvenile survival account for a large amount of variation in fitness of birds (Newton 1989), a wing shape giving better manoeuvrability in the first year of life than in adulthood could be selected for.

However, the disproportionate vulnerability of juveniles to predators due to their inexperience is not sufficient to explain age-related differences in wing morphology because the wing shape of adults should make them more vulnerable to predators than if they retained the juvenile wing shape. This means that age-related differences should only be maintained if adults obtain some benefit from their morphology. Alatalo et al. (1984) suggested that age-related differences in wing shape could reflect different optima resulting from changes with age in the relative impact of predation and migration-related selection. On the one hand, migratory birds should minimise the costs of migration (Alerstam and Lindström 1990, Alerstam 1991), which would be attained by a long and pointed wing that reduces energy expenditure and increases endurance during long-distance flights (Rayner 1988, Pennycuick 1989, Norberg 1990). On the other hand, a short and rounded wing reduces both energy expenditure and predation risk outside the migratory period, when short flights with frequent take-offs are the rule (Rayner 1988, Pennycuick 1989, Norberg 1990). Since juveniles are more vulnerable to predators, they could benefit from having shorter and more rounded wings than those optimal for undertaking migratory movements, whereas the balance would be shifted towards longer and more pointed wings in the more experienced adults (Alatalo et al. 1984). Up to now, however, this trade-off as an explanation for age-related differences in wing shape has not been convincingly tested.

In this paper, we study the age-related differences in wing morphology of migratory and sedentary Blackcaps *Sylvia atricapilla*. Genetic studies have shown that wing morphology is highly heritable in birds in general (Boag and van Noordwijk 1987) and in the Blackcap in particular (Berthold and Querner 1982). As sedentary Blackcaps do not face migration pressures that could affect their morphology (Tellería and Carbonell 1999), the comparison between migratory and sedentary populations will allow us to test the role of migration in the evolution of ontogenetic changes in wing shape. If the effects of predation rate were only expressed when opposing migration-related selection pressures, age-related differences should be found in migratory but not in sedentary populations. However, if migration played no role in determining age-related variation in wing shape, the same patterns should be found in both migratory and sedentary populations.

Methods

Populations under study

Our study site was located in the Campo de Gibraltar region, southern Spain (36°01′N, 5°36′W). Blackcaps occur in this area as year-round residents, remaining close to their breeding sites outside the breeding season (to the point that many of them are repeatedly captured at the very same site all around the year; Pérez-Tris et al. 1999). The morphological traits of these Blackcaps are consistent with their sedentary life style. They have a shorter and more rounded wing, as well as a longer tail, than the short-distance migratory populations inhabiting the Iberian Peninsula further to the north (Tellería and Carbonell 1999). In winter, large numbers of migratory Blackcaps from central and northern Europe occur in the area. In this season, both adult and first-year Blackcaps have a fresh plumage allowing a proper study of wing morphology (Jenni and Winkler 1994).

During both winters in the 1997 to 1999 period, we mist-netted 305 Blackcaps in an area of around 200 km^2. The fieldwork was initially designed to study the spatial distribution by sex and age of migratory and sedentary Blackcaps, so we did not use non-random sampling methods (such as supplying food or tape-luring) that could lead to bias with respect to population composition, body size or morphology of Blackcaps. We marked all individuals with standard aluminium rings to avoid using individuals more than once. Sexing and ageing criteria were based on plumage characters (Svensson 1992, Jenni and Winkler 1994). We differentiated between adults (individuals that had performed a complete post-nuptial moult) and juveniles (individuals that had retained juvenile feathers after their partial post-juvenile moult). Ageing was difficult in 26 cases (likely juveniles that had performed a very extensive partial moult, see Jenni and Winkler 1994), which we did not consider in our analyses. In order to avoid inter-personal bias, all individuals were aged and measured by one of us (JP-T). We measured tarsus length (to the most distal scale), bill length (from the skull) and bill height, to the nearest 0.01 mm with a digital calliper. We also measured the maximum wing chord, the length of the eighth primary feather (numbered descendantly and abbreviated P8) and the distances between the wing tip and the tip of each primary feather from the first to the ninth (primary distances 1 to 9), to the nearest half mm with appropriate rulers (Svensson 1992).

We distinguished between migratory and sedentary Blackcaps by using a discriminant function that combines three morphological traits: P8, tail length, and a simple index of wing pointedness (the difference between the primary distances 1 and 9). This method (Pérez-Tris et al. 1999) allowed the correct classification of 91% of Blackcaps captured at different latitudes in the Iberian Peninsula (including the sedentary population studied in this paper), whose migratory habits were well known (Tellería and Carbonell 1999). This discriminant function will classify individuals even more accurately during winter, as the traits related to a migratory habit are more pronounced in central and northern European Blackcaps – the largest fraction of migratory Blackcaps at the study site – than in the Iberian migratory populations (for further details, see Pérez-Tris et al. 1999).

The analysis of wing morphology

In passerines, wing length and wing pointedness are good correlates of flight speed and manoeuvrability. However, they must be scaled to body size if a sound analysis of their variation is to be conducted (Norberg 1990, Senar et al. 1994). Otherwise, differences in wing morphology could simply reflect variation in overall body size, which differs between the populations studied (Tellería and Carbonell 1999). We used the first component extracted by a Principal Components Analysis (PCA) from body measurements as an index of structural size (Rising and Somers 1989). Usually, this component explains most of the variation in the traits studied, as larger individuals have larger values for all body dimensions. In our case, all measurements but wing length showed high positive loadings on the first component (bPC1), which explained 32.7% of variation (Table 1). By contrast, wing length showed a high negative loading on bPC2, which accounted for a similar amount of variation (26.1%). This pattern of variation was clearly influenced by the fact that sedentary Blackcaps are larger but have shorter wings than migratory ones (Tellería and Carbonell 1999), causing wing length to vary independently of body size in a mixed sample.

We conducted another PCA with primary distances to obtain a measure of wing pointedness of Blackcaps (Chandler and Mulvihill 1988, Senar et al. 1994, Tellería and Carbonell 1999). However, wing shape could be more dependent on wing size than on body size, which varied almost independently from one another. For example, the wings of sedentary Blackcaps might not be large enough to manifest the same variation in wing shape as the wings of migratory Blackcaps. In addition, the increase in wing length does not affect all primaries equally (Senar et al. 1994). To control for these effects, we standardised primary distances with respect to wing size and allometry, for which we used the expression:

Table 1. Coefficients of correlation between the body measurements used in the study of body size and the principal components extracted by PCA (bPC1 and bPC2). The bPC1 was used to measure structural size.

Body measurements	Factor loadings	
	bPC1	bPC2
Tarsus length	0.67***	0.18**
Wing length	0.03	−0.86***
Bill length	0.72***	0.28***
Bill height	0.64***	0.06
Tail length	0.51***	−0.67***
Eigenvalue	1.63	1.30
Variance explained (%)	32.7%	26.1%

** $P<0.01$; *** $P<0.001$.

Table 2. Coefficients of correlation between primary distances (standardised with respect to wing size and allometry between primary lengths and wing length) and the principal components extracted by PCA (wPC1 and wPC2). The wPC1 was used to measure wing pointedness.

	Factor loadings	
Primary distances	wPC1	wPC2
Distance 9	−0.49***	0.73***
Distance 8	−0.53***	0.70***
Distance 7	0.66***	−0.09
Distance 6	0.86***	0.04
Distance 5	0.94***	0.12
Distance 4	0.96***	0.13
Distance 3	0.95***	0.16
Distance 2	0.95***	0.17**
Distance 1	0.91***	0.21**
Eigenvalue	6.14	1.17
Variance explained (%)	68.2%	13.0%

** $P<0.01$; *** $P<0.001$.

$$P^*_{ji} = P_{ji}\left(\frac{l_0}{l_i}\right)^{b_j}$$

where P_{ji} is the original primary distance j in the individual i, P^*_{ji} is the standardised value, l_i is the wing length of the individual i, l_0 is a standard wing length to which all individuals are reduced or increased (which we conventionally set at 73 mm, the average value in the population), and b_j is the allometry coefficient of the primary j according to the growth model: $P_{ji} = a_j l_i^{b_j}$, where a_j is a parameter (for further details, see Senar et al. 1994).

We conducted the PCA with the standardised primary distances. As usual in this type of studies (for a review see Lockwood et al. 1998), the first component (wPC1), which explained far more than half of the variation in primary distances (Table 2), was a good index of wing pointedness. The higher the wPC1 scores, the more concave the proximal portion of the wing (as indicated by the positive loadings for inner primaries) and the more pointed the wing tip (as shown by the negative loadings for outer primaries in this component).

Controlling for body size, neither migratory nor sedentary Blackcaps showed sexual dimorphism in wing length (ANCOVA: Sex $F_{1,276} = 0.007$, $P = 0.93$; Population $F_{1,276} = 224.43$, $P < 0.0001$; Interaction $F_{1,276} =$

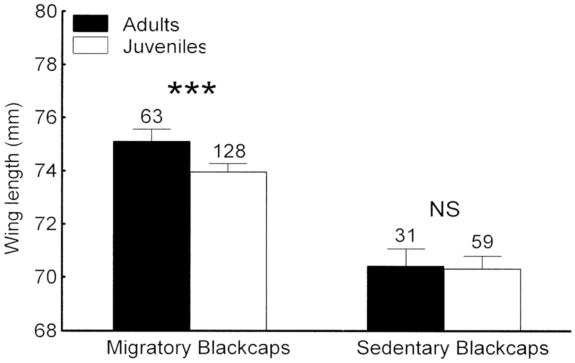

Fig. 1. Variation in wing length in relation to age in migratory and sedentary Blackcaps. Means adjusted by structural size (bPC1), standard errors and sample sizes are shown. Results of Tukey's tests for differences between age classes are also given (NS: $P > 0.98$; ** $P < 0.0001$).

0.27, $P = 0.60$; covariate structural size $F_{1,276} = 31.73$, $P < 0.0001$). Hence, we pooled the sexes in the analyses of wing length to increase sample size. There was, however, an almost significant interaction between sex and population for wing pointedness (Sex $F_{1,276} = 0.10$, $P = 0.75$; Population $F_{1,276} = 326.36$, $P < 0.0001$; Interaction $F_{1,276} = 3.90$, $P = 0.050$; structural size $F_{1,276} = 0.19$, $P = 0.66$). Since this could affect the differences between age classes, we tested for the interactions involving sex and population in the analysis of wing pointedness. Given that changes in wing pointedness were independent of body size, we did not consider this factor in the analysis of age-related variation.

Results

Once the body size of individuals was controlled for, migratory Blackcaps had longer wings than sedentary ones, and, on average, adults had longer wings than juveniles. However, an *a posteriori* evaluation of differences between means revealed that the difference between age classes was significant in the migratory population but not in the sedentary one (Fig. 1), resulting in a significant population by age interaction (Table 3).

Table 3. Results of the two-way ANCOVA comparing wing length of adult and juvenile Blackcaps in migratory and sedentary populations, controlling for structural size (all tests for interactions between factors and the covariate with $P > 0.26$). Adjusted means are shown in Fig. 1.

Source of variation	$F_{1,276}$	P
Effects		
Population	242.09	<0.0001
Age	5.95	0.015
Population × Age	4.34	0.038
Covariate		
Structural size (bPC1)	26.96	<0.0001

Table 4. Results of the general linear model comparing wing pointedness of adult and juvenile Blackcaps in migratory and sedentary populations, controlling for the different effect of sex in each population. Means are shown in Fig. 2.

Source of variation	$F_{1,274}$	P
Population	347.47	<0.0001
Age	4.71	0.031
Population × Age	2.27	0.133
Sex × Population	5.20	0.023
Sex × Age × Population	3.36	0.068

Like wing length, wing pointedness changed in relation to population and age: migratory Blackcaps had more pointed wings than sedentary ones and juveniles had more rounded wings than adults. However, the variation with age in wing pointedness was dependent on sex. There was a significant interaction between sex and population, and a nearly significant interaction among sex, population and age (Table 4). An *a posteriori* comparison of means showed that sedentary Blackcaps had a low and homogeneous wing pointedness. In migrants, on the other hand, females showed the predicted increase in wing pointedness with age, while adult and juvenile males had a similar wing shape (Fig. 2).

Inevitably, a few incorrect classifications could have contributed to the observed variation between migratory and sedentary Blackcaps, since we rely on both wing length and wing pointedness to distinguish between the two populations. However, the differences in the two traits were much larger than those among the Iberian populations from which our discriminant function was developed (Tellería and Carbonell 1999, Pérez-Tris et al. 1999), suggesting that the bias is insignificant. More importantly, these misclassifications cannot have biased the differences between age classes and should have made the interaction between age and population harder to detect. Thus, possible errors in population assignment should not have confounded our results.

Discussion

Our comparisons of sedentary and migratory populations support the hypothesis that selection pressures related to migration are necessary to explain age-related differences in wing shape of Blackcaps. This means that a higher predation rate on juveniles as a consequence of their inexperience alone cannot drive the increase in wing length and wing pointedness after the first complete moult. Rather, predation could be a counter-selective force to pressures that favour longer and more pointed wings, such as those related to migration.

When comparing age-related variation in migratory and sedentary Blackcaps, we obtained different results for wing length and wing pointedness. Wing length changed in the predicted way, with juveniles having shorter wings than adults in migratory but not in sedentary Blackcaps. However, the change in wing pointedness with age was less pronounced in migrants and only occurred in females. The smaller variation with age in wing pointedness compared to wing length could be due to a stronger importance of the former for migration performance. In fact, several comparative studies have shown that wing pointedness predicts distance of migration in passerines better than wing length (Winkler and Leisler 1992, Mönkkönen 1995). If wing pointedness is subjected to a stronger selection in relation to migration performance than wing length, other selective forces, such as those related to predator avoidance early in life, could have less impact on shaping variations with age. It is more difficult, however, to explain why age-related variation in wing pointedness of migratory Blackcaps was more accentuated in females than in males. One possible reason for this unexpected result could be differential migration with respect to sex. In partially migratory Blackcap populations, males are less migratory than females, especially in adulthood (Berthold 1996). Since migratory behaviour and wing morphology are correlated in this species (Berthold and Querner 1982, Berthold 1996), different degrees of migration in relation to age and sex could explain both the similar wing pointedness of juveniles of each sex and the more pronounced increase with age in the more migratory females.

Notwithstanding these differences between traits, age-related variation in wing shape of Blackcaps occurs in migrants but not in residents, thus supporting the predictions posed by the trade-off between optimal migration and juvenile survival. One way in which migration could account for age-related differences would be selection against short and round-winged juveniles during the first migratory journey, which would favour the survival of individuals with long and pointed wings. However, a number of studies in which the same individuals were measured before and after the first complete moult have found age-related differences at the individual level (Leverton 1989, Harper 1999). Therefore, although mortality of short- and round-winged individuals during the first migration could contribute to explaining the longer and more pointed wings of adult Blackcaps, age-related variation is more likely to reflect ontogenetic changes.

Apart from the trade-off between migration and survival, other possible causes for age-related variation in wing shape have been proposed. For example, nutritional constraints during development could prevent juveniles from attaining the definitive feather length (van Balen 1967, Slagsvold 1983). However, this cannot explain our results for two reasons. First, Blackcaps experimentally raised on a poor diet did not differ in final feather length from Blackcaps raised under normal conditions (Berthold 1976). Second, should nutritional constraints have some effect, this would be stronger for sedentary Blackcaps than for migratory Blackcaps because of the summer drought in southern Spain. This is clearly evidenced by fledgling Robins *Erithacus rubecula* in our study area, which show a lighter body mass and a slower feather growth than those fledged in northern and central Spain (Pérez-Tris et al. 2000). An alternative to this hypothesis suggests that leaving the nest with a shorter wing reduces the nesting period, and hence the probability of nest predation (Nielsen 1993). This could well cause adaptive ontogenetic variation in wing shape, yet it should occur both in migratory and sedentary populations. Although the shorter breeding season at northern latitudes could somewhat increase the urge to fledge in migratory populations, Blackcaps wintering in the Mediterranean migrate at least two months after fledging (with a peak passage in October; Cramp 1992) and sedentary populations are also pressed to avoid extending the breeding season into the drought period.

However, juveniles have been found to have shorter wings in species considered to be mainly sedentary (such as the Bearded Tit *Panurus biarmicus*; Nielsen

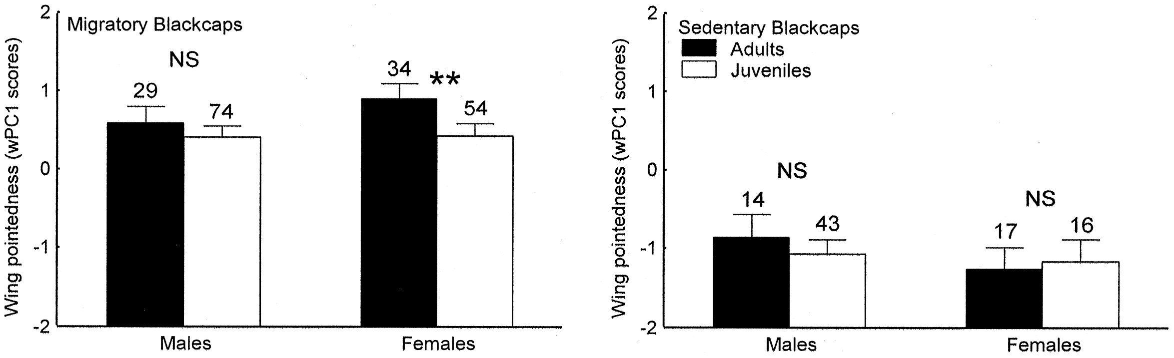

Fig. 2. Variation in wing pointedness in relation to sex and age in migratory and sedentary Blackcaps. Means, standard errors and sample sizes are shown. Results of Tukey's tests for differences between age classes are also given (NS: $P > 0.99$; ** $P = 0.003$).

1993), or in partial migrants in which the migratory fraction is chiefly composed of first-year birds (such as the *Parus* tit species; Alatalo et al. 1984 and references therein). In these species, assuming survival benefits accrued to juveniles because of their shorter wings, a selection pressure other than migration must be invoked for the longer wings of adults. This pressure could be related to winter movements, described in these species (Alatalo et al. 1984, Nielsen 1993). Evidence for selection for long and pointed wings in relation to other movements of less extent than migration was provided by Senar et al. (1994), who found winter-transient Siskins *Carduelis spinus* to have more pointed wings than winter-residents. Nevertheless, the possibility that other pressures not related to flight performance or predation rate, acting on adults or juveniles, lead to age-related variation in wing morphology should not be dismissed. Particularly, further studies are needed to disentangle the causes of age-related variation in completely sedentary species.

The costs and benefits of migration have important fitness consequences for birds, and this has led to the evolution of physiological, behavioural, and morphological responses that contribute to optimise migration performance (Greenberg 1980, Alerstam 1991, Berthold 1993). These include the increase in wing length and wing pointedness with increasing distance of migration (Leisler and Winkler 1985, Rayner 1988, Lockwood et al. 1998). As a consequence of their morphological adaptations, migratory birds likely reduce the costs of migration at the expense of manoeuvrability. In turn, the loss of manoeuvrability should constitute a mechanical constraint on the increase in wing length and wing pointedness since, once a given threshold is exceeded, further variation would impair flight performance beyond the affordable limits (Pennycuick 1989, Norberg 1990). This relationship between the costs of migration and the costs of impaired manoeuvrability predicts a negatively accelerated increase in wing length and wing pointedness with increasing distance of migration, which in fact is found in European Blackcaps, at least for wing length. Thus, short-distance migrants show a strong increase in wing length compared to sedentary populations, but trans-Saharan migrants only show a slight additional increase in wing length despite migrating about five times farther (Fig. 3).

Taking into account the shape of the relationship between distance of migration and wing length, our results suggest a possible mechanism that may account for the evolution of differences in wing shape between adult and juvenile migrant Blackcaps (Fig. 4). In sedentary populations, the costs of migration are absent and hence morphological adaptations to long-distance flights lack importance. In this situation, both adults and juveniles have a similar wing shape, formed by the requirements of habitat structure, feeding habits, and so on (Leisler and Winkler 1985, Winkler and Leisler 1985). In migratory populations, on the other hand, both adults and juveniles face additional selective pressures that force them to increase wing length and wing pointedness with increasing distance of migration (Winkler and Leisler 1992, Mönkkönen 1995, Lockwood et al. 1998). As discussed above, the costs of an impaired manoeuvrability will impose an upper limit to wing

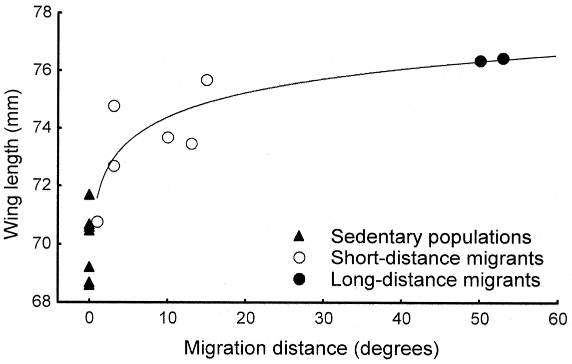

Fig. 3. The relationship between distance of migration and wing length in 15 European Blackcap populations reviewed by Cramp (1992). Distance of migration has been measured as the difference in degrees of latitude between breeding and wintering areas. Wintering latitude is the same as breeding latitude in sedentary populations; 40°N (the average latitude of Blackcaps' Mediterranean wintering areas) in short-distance migrants; and 10°N (the average latitude of sub-Saharan wintering areas) in long-distance migrants. The logarithm of distance of migration plus one explains 83.9% of the variation in wing length among these populations ($F_{1,13} = 67.89$, $P < 0.0001$).

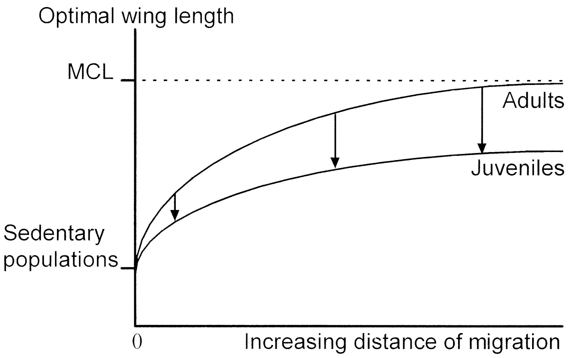

Fig. 4. Graphical description of how the interaction between migration pattern and juvenile inexperience might cause age-related differences in wing shape of Blackcaps (here illustrated for wing length). Wing length increases with distance of migration, but this increase is negatively accelerated due to the costs of impaired manoeuvrability, which in turn will set an upper limit to wing modification (a mechanical constraint limit, MCL). In addition, juveniles incur further costs of wing modification in relation to their higher vulnerability to predators (arrows), which make them benefit from having shorter wings than adults at a given distance of migration. In sedentary populations, however, manoeuvrability will be maximised and hence adults and juveniles will have the same optimal wing length (see text for further details).

modification. Age-related differences in wing shape could then appear if these costs were larger in juveniles than in adults. Above some threshold juveniles' higher vulnerability to predators would impair survival. In this situation, an optimal performance during the first migration is traded against improved manoeuvrability early in life, which may result in a different optimal wing shape for juveniles and adults.

Acknowledgements – We thank A. Ramírez for his help during the fieldwork, and L. M. Carrascal, J. A. Díaz, J. C. Senar and three anonymous referees for their valuable comments on the manuscript. The Consejería de Medio Ambiente (Junta de Andalucía) kindly authorised us to capture and measure Blackcaps. This paper was funded by the Ministerio Español de Educación y Cultura (Project PB97-0325) and a FPI Grant from the Universidad Complutense de Madrid (to J.P-T.).

References

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

Alerstam, T. 1991. Bird Migration. – Cambridge University Press, Cambridge.

Alerstam, T. and Lindström, Å. 1990. Optimal bird migration: the relative importance of time, energy and safety. – In: Gwinner, E. (ed). Bird Migration: the Physiology and Ecophysiology. Springer, Berlin Heidelberg New York, pp. 331–351.

Bednekoff, P. A. 1996. Translating mass dependent flight performance into predation risk: an extension of Metcalfe & Ure. – Proc. R. Soc. Lond. B 263: 887–889.

Berthold, P. 1976. Über der Einfluss der Nestlingsnahrung auf die Jugendentwicklung, insbesondere auf das Flügelwachstum, bei der Mönchsgrasmüche (*Sylvia atricapilla*). – Vogelwarte 28: 257–263.

Berthold, P. 1993. Bird Migration. A general survey. – Oxford University Press, Oxford.

Berthold, P. 1996. Control of Bird Migration. – Chapman & Hall, London.

Berthold, P. and Querner, U. 1982. Genetic basis of moult, wing length, and body weight in a migratory bird species, *Sylvia atricapilla*. – Experientia 38: 801–802.

Boag, P. T. and van Noordwijk, A. J. 1987. Quantitative genetics. – In: Cook, F. and Buckley, P. A. (eds). Avian Genetics. Academic Press, London, pp. 45–78.

Chandler, C. R. and Mulvihill, R. S. 1988. The use of wing shape indices: an evaluation. – Ornis Scand. 19: 212–216.

Cramp, S. (ed). 1992. The Birds of the Western Palearctic. Vol. VI. – Oxford University Press, Oxford.

Cresswell, W. 1996. Surprise as a winter hunting strategy in sparrowhawks *Accipiter nisus*, peregrines *Falco peregrinus* and merlins *F. columbarius*. – Ibis 138: 684–692.

Greenberg, R. 1980. Demographic aspects of long-distance migration. – In: Keast, A. and Morton, E. S. (eds). Migrant Birds in the Neotropics. Smithsonian Institution Press, Washington, DC, pp. 493–504.

Harper, D. G. C. 1999. Feather mites, pectoral muscle condition, wing length and plumage coloration of passerines. – Anim. Behav. 58: 553–562.

Jenni, L. and Winkler, R. 1994. Moult and Ageing of European Passerines. – Academic Press, London.

Kullberg, C., Fransson, T. and Jakobsson, S. 1996. Impaired predator evasion in fat blackcaps. – Proc. R. Soc. Lond. B 263: 1671–1675.

Kullberg, C., Jakobsson, S. and Fransson, T. 1998. Predator-induced take-off strategy in great tits (*Parus major*). – Proc. R. Soc. Lond. B 265: 1659–1664.

Lee, S. J., Witter, M. S., Cuthill, I. C. and Goldsmith, A. R. 1996. Reduction in escape performance as a cost of reproduction in gravid starlings *Sturnus vulgaris*. – Proc. R. Soc. Lond. B 263: 619–624.

Leisler, B. and Winkler, H. 1985. Ecomorphology. – Curr. Ornithol. 2: 155–186.

Leverton, R. 1989. Wing length changes in individually-marked Blackbirds *Turdus merula* following moult. – Ring. Migr. 10: 17–25.

Lind, J., Fransson, T., Jakobsson, S. and Kullberg, C. 1999. Reduced take-off ability in robins (*Erithacus rubecula*) due to migratory fuel load. – Behav. Ecol. Sociobiol. 46: 65–70.

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

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

Newton, I. 1986. The Sparrowhawk. – T & AD Poyser, Carlton.

Newton, I. 1989. Lifetime Reproduction in Birds. – Academic Press, London.

Nielsen, B. 1993. Age dependent variation in wing length of Bearded Tits *Panurus biarmicus*. – Ornis Svecica 3: 117–124.

Norberg, U. M. 1990. Vertebrate Flight: Mechanics, Physiology, Morphology, Ecology and Evolution. – Springer, Berlin Heidelberg New York.

Norberg, U. M. 1995. How a long tail and changes in mass and wing shape affect the costs for flight in animals. – Funct. Ecol. 9: 48–54.

Norman, S. C. 1997. Juvenile wing shape, wing moult and weight in the family Sylviidae. – Ibis 139: 617–630.

Opdam, P. 1978. Feeding ecology of a Sparrowhawk population (*Accipiter nisus*). – Ardea 66: 137–155.

Pennycuick, C. J. 1989. Bird Flight Performance: a practical calculation manual. – Oxford University Press, Oxford.

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

Pérez-Tris, J., Carbonell, R. and Tellería, J. L. 2000. Abundance distribution, morphological variation, and juvenile condition of Robins *Erithacus rubecula* (L.) in their Mediterranean range boundary. – J. Biogeogr. 27: 879–888.

Rayner, J. M. V. 1988. Form and function in avian flight. – Curr. Ornithol. 5: 1–66.

Rising, J. D. and Somers, K. M. 1989. The measurement of overall body size in birds. – Auk 106: 666–674.

Rudebeck, G. 1950. The choice of prey and modes of hunting of predatory birds with special reference to their selective effect. – Oikos 2: 65–88.

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

Slagsvold, T. 1983. Morphology of the Hooded Crow *Corvus corone cornix* in relation to age, sex and latitude. – J. Zool. Lond. 199: 325–344.

Solonen, T. 1997. Effect of Sparrowhawk predation on forest birds in southern Finland. – Ornis Fenn. 74: 1–14.

Svensson, L. 1992. Identification Guide to European Passerines. – British Trust for Ornithology, Tring.

Tellería, J. L. and Carbonell, R. 1999. Morphometric variation of five Iberian Blackcap *Sylvia atricapilla* populations. – J. Avian Biol. 30: 63–71.

van Balen, J. H. 1967. The significance of variations in body weight and wing length in the Great Tit, *Parus major*. – Ardea 55: 1–59.

Winkler, H. and Leisler, B. 1985. Morphological aspects of habitat selection in birds. – In: Cody, M. L. (ed.). Habitat Selection in Birds. Academic Press, New York, pp. 435–444.

Winkler, H. and Leisler, B. 1992. On the ecomorphology of migrants. – Ibis 134 (suppl. 1): 21–28.

(*Received 25 April 2000, revised 7 December 2000, accepted 4 January 2001.*)