S27-3　Interaction between morphological integration and ecological factors

Bernd LEISLER[1], Hans WINKLER[2]

1. Max-Planck-Research Centre for Ornithology, Schloßallee 2, D-78315 Radolfzell, Germany; leisler@vowa.ornithol.mpg.de
2. Konrad Lorenz Institut für Vergleichende Verhaltensforschung, Austrian Academy of Sciences, Savoyenstrasse 1a, A-1160 Vienna, Austria; H.Winkler@klivv.oeaw.ac.at

Abstract　Closely related species may have similar traits not because these traits are adaptive but because they are strongly intercorrelated and inherited from a common ancestor. We examined how intraspecific morphological integration (first principal component within each species) relates to the direction of interspecific divergence in species of two passerine genera (*Oenanthe*, *Ploceus*). We used thirteen traits to describe external morphology, more than have been analyzed in any previous study. Ecological data on migration distances, food type, habitat type and type of locomotion were used to interpret interspecific variation. For pairwise comparisons we used closely related species within the set of species studied. In all cases examined, interspecific differences affected several correlated characters at the same time. The direction of interspecific change did not coincide with the main direction of intraspecific variation described by common principal components. In another finding, the main axis of intraspecific variation was not determined solely by variation in size. We used data on six *Ploceus* species with resolved molecular phylogeny to examine the relationship between morphological integration, morphological differentiation, ecological differentiation and phylogeny. The main direction of morphological integration changed slowly over phylogenetic time and not as a response to immediate adaptive needs. Our main conclusion is that the three different domains of correlated variation (intraspecific, interspecific, ecological) are only loosely interdependent.

Key words　Ecomorphology, Line of least resistance, Multivariate evolution, Size, Shape

1　Introduction

The concept of morphological integration emphasizes the fact that characters co-vary. From such covariance, resistance to change in certain directions may ensue. Basically, two kinds of model of microevolutionary divergence have been put forward. One, the constraint model, stresses that selective forces can produce correlated responses only in the directions set by morphological integration. The other model type holds that inherited patterns of covariation are overridden easily in the course of adaptive divergence (Björklund and Merilä, 1993).

In our previous studies of integrated ecomorphology, we concentrated on the fit between morphology, environment and behavior among closely related species, involving interspecific comparisons (e.g., Leisler et al., 1989; Gamauf et al., 1998; Winkler and Preleuthner, 1999). In our comparisons, we used (1) species means, which were analyzed with respect to allometric shape rather than size, and (2) traits of known function and suspected ecological relevance. From this approach we found that subtle morphological differences among species in shape had profound ecological effects (Leisler and Winkler, 1985).

Here we examine how phenotypic patterns of covariation within and between species correspond to ecology in two song bird genera, *Oenanthe* and *Ploceus*.

2　Material and methods

2.1　The taxa

Wheatears (*Oenanthe*) are morphologically very uniform, and live year-round under extreme ecological conditions in which food (terrestrial insects) is scarce or not permanently available (Potapova and Panov, 1977). Molecular data indicate that the wheatear lineage, as currently understood, is monophyletic (A. Helbig, pers. comm.). The study species comprise three migrants (*O. oenanthe*, sample size = 30; *O. pleschanka*, 63; *O. isabellina*, 56) and two residents (*O. (lugens) lugubris*, 31; *O. pileata*, 18) that all coexist during the northern winter in Africa, where their ecology has been studied in detail (see below).

In contrast, the species of the genus *Ploceus* studied are members of a group that has undergone remarkable adaptive radiation, its members separately occupying a wide spectrum of habitats, feeding on a variety of food types and developing different modes of locomotion (Moreau, 1960). Although the species of *Ploceus* have acquired diverse life-styles, morphological differentiation is rather moderate.

The following species were used in our comparisons:

P. baglafecht, 52; *P. bertrandi*, 15; *P. pelzelni*, 44; *P. ocularis*, 38; *P. nigricollis*, 40; *P. alienus*, 42; *P. subaureus*, 28; *P. xanthops*, 45; *P. aurantius*, 25; *P. castanops*, 15; *P. nigerrimus*, 63; *P. weynsi*, 32; *P. jacksoni*, 37; *P. rubiginosus*, 42; *P. tricolor*, 31; *P. philippinus*, 24; *P. hypoxanthus*, 17; *P. bicolor*, 40; *P. insignis*, 33.

2.2 Ecological data

To describe the ecological requirements of the five *Oenanthe* species, we used fifteen characteristics of diet, foraging and migratory behavior (Leisler, 1990; Flinks and Leisler, unpubl.): prey size (four categories), food type (percentage of ants, beetles, Isoptera, others), foraging speed, percentage of time spent on perches vs. ground, number of ground-stays per minute, distance covered by running vs. flying, number of runs per minute, number of sallies per minute and distance of migration. Information for the species of *Ploceus* was drawn from Leisler et al. (1997) and unpublished data, and uses four categories of food type on a gradient from granivory to insectivory, four habitat type categories from open savannah to forest, and four types of locomotion on a gradient from ground-hopping to climbing with frequent upside-down hanging.

2.3 Morphometric analysis

We used thirteen morphometric characters to describe external morphology: wing length, tail length, tarsus length, bill length, bill width, bill height, hind toe, middle toe, hind claw, middle claw, tarsus diameter in *Ploceus*, plus primary projection, notch length, rictal bristle length in *Oenanthe*.

2.4 Data analysis

From these data, which were not corrected for size but log-transformed, we computed covariances. To determine major axes of morphological variation within the lineages, we used principal component analysis (PCA). We determined the ecological relevance of the trait combinations from interspecific comparison, and assumed that they held for species at intraspecific level. To describe relationships of within- and between- species covariation, we used canonical discriminant analysis (DA), and combined those analyses with common principal component analysis (CPCA; Flury, 1988). The discriminant analysis was used to represent morphological divergence between species in correspondence with the model of multivariate evolution of adaptive change (Lande, 1979; Schluter, 2000). The common principal components reflect best the ideas put forward in models of constraint evolution by morphological integration. This statistical model assumes that two populations share common components of variation (eigenvectors) which, however, may differ in their relative contribution (eigenvalues) to total variation (Steppan et al., 2002).

3 Results

3.1 Interaction in wheatears, *Oenanthe*

Our first example deals with the species of *Oenanthe*.

PCA of the external morphological variables resulted in two axes that together explained 97% of the total interspecific variance. The first factor (54%) was not a pure size factor, since characters of the flight apparatus were not correlated with this factor. The second component (43%) represented a contrast between wing length, primary projection and tarsus length (positively correlated), and tail length and rictal bristle length (negatively correlated). Both components were correlated with ecological factors. Migration distance and the second component explained 98% of the variation in the first component (*F*-value = 52.106, *P* < 0.02, *df* = 2.2).

This may seem surprising because principal components are, by definition, not correlated with one another. In a multivariate context that includes other predictors, however, such a result does make sense. The second component acts as a suppressor variable and suppresses irrelevant variation in the other predictor (Tabachnick and Fidell, 2001). Almost 100% of the second component was explained by the proportion of 5–8 mm food size items in the diet, and percent distance covered by running vs. flying during foraging. These results show that one can relate morphological integration at the interspecific level to ecological factors.

In the next step, pairwise comparisons were made between species according to the following procedure. First a DA of the morphological variables was run. Then we ascertained that the differences found corresponded to ecological differences. The same morphological data were also used for a CPCA. The subsequent analyses were based on species pairs presumed to be recently diverged. According to the predictions of the constraint model, morphological differences associated with ecological divergence should be highly correlated with the main component of intraspecific variation. This component is furthermore thought to represent mainly variation in allometric size (Björklund, 1994). In terms of our analyses, scores along the major common principal component would be highly correlated with the individual scores along the discriminant axis under the constraint model. These correlations could be either negative or positive as the vector of "least resistance" represents a line rather than a directed ray (Björklund and Merilä, 1993). Under a pure adaptive model such correlation should occur only accidentally and hence be rare.

For the pairwise comparisons, we begin with *O. isabellina* vs. *O. oenanthe*. Both are closely related but represent an old divergence (A. Helbig, pers. comm.). Both are long-distance migrants and highly terrestrial, but *isabellina* feeds on larger insects, flies more and hunts more by sitting-and-waiting. These differences correspond to a longer tarsus, larger bill and greater overall size in *isabellina* (Fig. 1a). The same morphological data for individuals were used in a CPCA. There was no correlation between the first principal component and scores of the DA in either species (Fig. 1a). Both species, however, showed significant correlation between CPC5 (explaining 6.2% variance in *Oenanthe* and 4.4% variance in *isabellina*, and comprising mainly

variation in bill length and height) and the discriminant axis (Fig. 1b). Thus these two species did not diverge along the line of least resistance.

Other tested species pairs showing no correlation between DA and CPC scores were *O. isabellina* vs.*O. pileata* and *O. pileata* vs. *O. pleschanka*. A different pattern was found in the resident *O. lugubris* and long-distance migrant *O. oenanthe*. They differ little in diet but substantially in foraging behavior, the latter running more and perching less. Accordingly, the discriminant axis represents differences in wing length, primary projection, rictal bristle length and tail length, with *O. oenanthe* being the species with the longer and more pointed wings, short tail and short rictal bristles. First inspection of the CPCs showed that two axes had high loadings in these variables. The DA and two most important CPCs were correlated in *O. oenanthe* but not in *lugubris*.

3.2 Interaction in weaver finches, *Ploceus*

PC analysis of the external morphological variables of the 19 species of *Ploceus* produced two axes. The first factor was a size factor and all characters correlated positively with it. However, it also contained shape information, as correlations varied from 0.56 (claw 1) to 0.88 (thickness of tarsus, wing length), and from 0.49 to 0.77 for respective traits when the very small *P. pelzelni* was omitted. The second component was correlated with measurements of the hind limb (long claws and middle toe, thin tarsus). Principal component 1 was only weakly related to ecology, namely type of habitat (one-way ANOVA, $P < 0.05$), whereas component 2 was significantly associated with habitat ($P < 0.001$) and locomotion ($P < 0.05$).

In pair-wise comparisons, we begin with a pair of very closely related species, *P. nigricollis* vs. *P. ocularis* (Moreau, 1960). *P. nigricollis* forages in higher strata in

forests, and *ocularis* more on the edge and lower in bushes. The DA axis represents differences in bill width, primary projection and wing length, more arboreal *nigricollis* having a wider bill, longer, more pointed wings and smaller feet. Multiple regressions with the CPCs show that the DA axis is not related to them, as expected. The relationship is significant, but the contribution of the CPCs becomes more important as their contribution to the within-species variation falls. As in the case of *Oenanthe lugubris* vs. *O. oenanthe*, such significant relationships were found only in one species, namely *Ploceus ocularis*.

In the pair *P. aurantius* vs. *P. castanops* (subgenus *Textor*, Moreau, 1960), the latter occurs in reed-like vegetation, is insectivorous to a substantial extent, and clings frequently on vertical structures; *P. aurantius* is less specialized. In this pair, *castanops* has larger and rounder wings, and has longer legs and larger feet. The DA and CPC scores were not correlated.

3.3 Interaction among morphology, ecology and phylogeny

We also used data on six *Ploceus* species with resolved phylogeny (*pelzelni, ocularis, castanops, jacksoni, rubiginosus, bicolor*) to examine the relationship between morphological integration, morphological differentiation, ecological differentiation, and phylogeny. Morphological integration was represented by the first PC within each species. The corresponding differences between species were calculated as $1-\cos\theta$, with θ representing the angle between the PCs. Morphological differentiation was based on the Mahalanobis-distance, which bears close relationship to discriminant analysis. Ecological differentiation was recorded by Euclidean distances between species with the scores of the habitat, food and locomotion discriminant axes as variables. Phylogenetic distances were based on Kimura distances of cytochrom-*b* data.
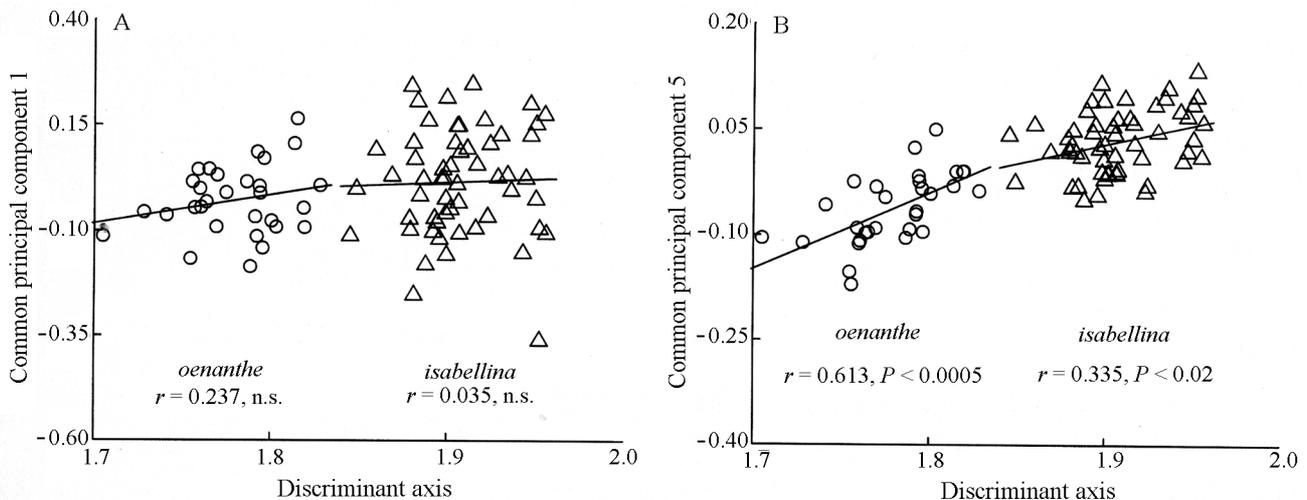

Fig. 1 Correlation between scores of a discriminant and a common principal component analysis of morphological traits in two species of wheatears, *Oenanthe*

O. oenanthe = circles, *O. isabellina* = triangles. The discriminant axis represents differences in tarsus length, bill dimension and overall size that pertain to ecological differences. A = correlation with CPC1, B = correlation with CPC5.

We then tried to unravel the interactions between these four domains of differentiation in the fifteen possible combinations. Unexpectedly, morphological distances and ecological distances were not correlated (0.17), which may be due to the rather unspecific ecological information. Morphological distances and genetic distances were correlated (0.62). Morphological distances and divergence of PCs were only weakly correlated (0.48). This correlation may be mediated by the common relationship to phylogeny. Genetic distances and divergence of PCs were highly correlated (0.75) as shown in Fig. 2.

4 Discussion

The main objective of this study was to examine how intraspecific morphological integration relates to interspecific adaptive radiation. The prediction of the constraint hypothesis is that both should be closely correlated. In our examples, we found very little evidence for this notion. Even in closely related species, adaptive changes affected several characters at the same time. These correlated changes, however, did not take place along the so-called line of least resistance. Rather, the main direction of morphological integration changes slowly with phylogenetic time. Thus morphological integration appears to be subject to phylogenetic inertia. Such inertia was not found in our analysis of interspecific variation.

Another finding of the study is that the main axis of intraspecific variation is not solely attributable to variation in size. Likewise, adaptive changes are mainly changes in shape (Schluter, 2000). Thus we conclude that the three different domains of correlated variation (intraspecific, interspecific, ecological) are only loosely interdependent.

References

Björklund M, 1994. Processes generating macroevolutionary patterns of morphological variation in birds: a simulation study. J. Evol. Biol. 7: 727–742.

Björklund M, Merilä J, 1993. Morphological differentiation in *Carduelis* finches: Adaptive vs. constraint models. J. Evol. Biol. 6: 359–373.

Flury B, 1988. Common Principal Components and Related Multivariate Models. New York: John Wiley and Sons.

Gamauf A, Preleuthner M, Winkler H, 1998. Philippine birds of prey: interrelations among habitat, morphology, and behavior. Auk 115: 713–726.

Lande R, 1979. Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. Evolution 33: 402–416.

Leisler B, 1990. Selection and use of habitat of wintering migrants. In: Gwinner E ed. Bird Migration. Berlin, Heidelberg: Springer-Verlag, 156–174.

Leisler B, Winkler H, 1985. Ecomorphology. Current Ornithology 2: 155–186.

Leisler B, Winkler H, Siebenrock K-H, 1997. Ecomorphological analysis with weaverbirds (Ploceidae) and kingfishers (Alcedinidae). Mitt. Zool. Mus. Berl. 73(Suppl.): Ann. Ornithol. 21: 17–43.

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

Moreau RE, 1960. Conspectus and classification of the ploceine weaver-birds. Ibis 102: 298–321, 443–471.

Potapova EG, Panov EN, 1977. Structural patterns of jaw apparatus in wheatears of the genus *Oenanthe*, with special reference to the ways of decrease of food competition between closely related species. Zool. Zh. 56: 743–752 (in Russian).

Schluter D, 2000. The Ecology of Adaptive Radiation. Oxford: Oxford University Press.

Steppan SJ, Philips PC, Houle D, 2002. Comparative quantitative genetics: evolution of the G matrix. Trends Ecol. Evol 17: 320–327.

Tabachnick BG, Fidell LS, 2001. Using Multivariate Statistics, 4th edn. Boston: Allyn and Bacon.

Winkler H, Leisler B, 2004. To be a migrant: ecomorphological burdens and chances. In Greenberg RS, Marra PP ed. Birds of Two Worlds: the Ecology and Evolution of Migration. Washington: Smithsonian Institute Press, 79–86.

Winkler H, Preleuthner M, 1999. The ecomorphology of neotropical frugivores. Acta. Ornithol. 34: 141–148.
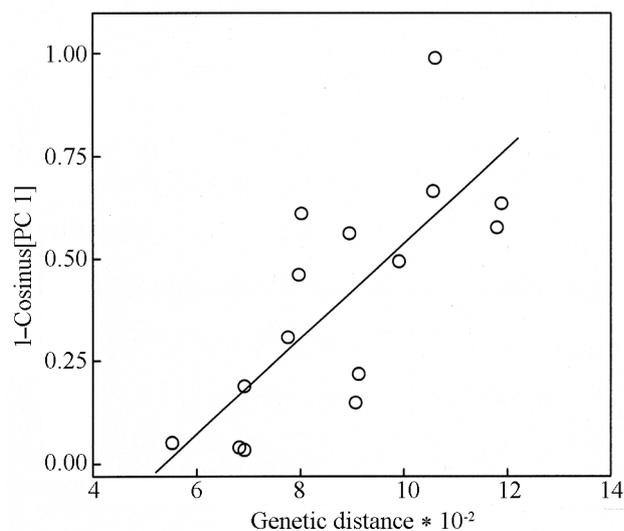

Fig. 2 Correlation between genetic distances (Kimura distances) and divergence of PCs (13 morphological characters) in 5 *Ploceus* species (15 possible combinations).