S27-2　Trait evolution, morphological integration and functional complexes

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Abstract　A salient feature of bird morphology is the design of adaptive functional complexes. These complexes have evolved as a response to selection for function, which has led to integration of sets of traits that act evolutionarily as one coherent unit rather than as independent parts. For understanding the ecological importance and the evolution of these functional complexes, research needs to focus on three areas of analysis. At the basic level, it must unravel the quantitative genetics of trait complexes to understand the potential for evolutionary change. It can be shown that the magnitude of genetic correlations determines to a large extent the evolutionary trajectory of a population, almost irrespective of selection. So far, little is known about this in birds. Secondly, the ontogenetic basis of trait complexes needs appreciation, together with the variation in ontogenies in populations. This area is tightly linked to understanding the basic morphological interactions among parts in order to learn which parts constitute a functional complex. The ontogeny of birds is also poorly known. Thirdly, patterns of selection acting on the complexes need to be understood, in addition to the selection on means and variances. For the future, it is of importance to learn how many parts can be involved optimally in a functional complex, and how separate complexes evolve. This will have a profound impact on our understanding of avian evolution: how new complexes and new taxa evolve.

Key words　Genetic variance-covariance matrix, Size, Growth trajectories, Selection, Optimal integration, Carduelid finches

1　Introduction

In birds, most morphological variation among species within a genus, or among genera within a family, is confined to size (Björklund, 1991, 1994a). Differences in shape are usually minor such that species are commonly larger or smaller copies of one another on a common line of allometry. Thus, of all the theoretically possible phenotypes, only a few actually exist. Functional complexes are one of the reasons for this pattern, producing, for example, the different bills in cardueline and nectar-feeding birds, without which such birds cannot function properly in their environment. These complexes have evolved in response to strong selection for function, and, as a result, sets of traits have evolved to function as a single unit rather than a number of independent parts. For understanding the ecological importance and the evolution of functional complexes, research needs to focus on three areas of analysis and to integrate them into a common framework based on basic evolutionary principles. Those three areas — genetic, ontogenetic and functional (ecological) — are evaluated here. I also discuss briefly recent theoretical attempts to understand the evolution of integration by means of neural networks.

2　Genetics

One way to analyze genetic patterns of integration is through the genetic variance-covariance matrix (**G**), which describes the genetic variance for each trait and the genetic covariance (correlation) among traits. This matrix can provide vital information concerning the future paths of evolution because **G** appears in the standard equation for evolution, dz = ß**G**, where dz is the change in trait means and ß is the selection gradient vector (Lande, 1979). One way of analyzing the possible paths of evolution is through the eigenvalues of the **G**-matrix. A matrix with high correlations among traits has one eigenvalue that is much greater than the rest, producing a large variance in eigenvalues (Wagner, 1984). A matrix with low correlations has eigenvalues of about equal magnitude, and thus low variance. Vectors shed light here. Each eigenvalue corresponds to an eigenvector, and these have directions as do all vectors. The eigenvalue is a measure of the length of the associated eigenvector.

In biological terms, the eigenvalue measures the amount of variation that is associated with each combination of traits. If the correlations are high and positive, then the eigenvector associated with the largest eigenvalue can be interpreted as a size vector, and the magnitude of the eigenvalue represents a measure of the variation in size in the population. The importance of knowing the structure of **G** can be illustrated by the fact that the response to selection is determined by the length and the direction of the eigenvectors of **G** (Björklund, 1996a). In other words, the **G**-matrix biases the future evolutionary paths of a population. Biologically, this means that if the largest eigenvalue is very

large, almost all variation in the population is confined to a certain dimension. Since selection can only act on the variation that is available, this will direct the response to it. It can be shown that if the leading eigenvector is very long, indicating considerable variation, then the response is almost always in the direction of the eigenvector rather than the selection vector. Thus, if the largest vector is one of overall size, almost all selection for shape will nevertheless result in a response in size (Björklund, 1996a).

Only when selection is collinear with other vectors will the variables respond according to those vectors. This pattern has been described by Schluter (1996) as "the trajectory of least resistance". It is an unfortunate label because it suggests freedom of movement when it is actually a brute force process of constraint. This finding has two important evolutionary implications: first, selection against the leading eigenvector is very ineffective, and thus the structure of the **G** matrix can act as a true constraint with a strength determined by the strength of the correlations among traits. Secondly, it can be shown that the response to selection in the direction of the leading eigenvector is much larger than if selection were to act on each trait independently, as would be the case if there were no correlations among traits (Björklund, 1994b, 1996a). In short, the pattern of integration can promote evolutionary change in some cases, but also constrain it in others.

Data bearing on these issues in natural populations of birds is limited, especially with respect to the same traits. I found six species — three of *Geospiza* (Grant, 1986), *Melospiza melodia* (Schluter and Smith, 1986), *Ficedula albicollis* (Merilä et al., 1994), and *Pyrenestes ostrinus* (Smith and Griman, 2000) — in which bill length, depth and width, tarsus length and wing length were all included. To describe the level of integration, I used the variance of the eigenvalues of the genetic correlation matrix and expressed that as a percentage of the maximum possible (equals the number of traits for correlation matrices). Integration varied between 85 % in *Geospiza fortis* to 36 % in *Melospiza melodia*. To analyze the pattern of variation, I compared the direction of the longest eigenvector to an isometric size vector. The correlation between these two vectors varied between 0.906 and 0.998 across species.

This reveals variation among species in the level of integration, from quite low to quite high, and that in all cases the variation involves size. Thus the response to selection is one of overall size change, even though selection may act on shape. The same pattern emerges from analysis of the three bill traits alone, only even more strongly, with level of integration at 53%–94 % and correlation with isometry vector at 0.985–1.0. It shows that the size-alone response to selection is the by far most likely outcome of selection on bill form in these species. Unfortunately, sample sizes were generally low, ranging from 12–84, with *Ficedula* an exception with 744. The most general conclusion that can be drawn from this analysis is that more data are needed from more species. Given the logistic problems inherit in these kinds of studies, this will take time.

3 Ontogeny

At the mechanistic level, any evolutionary change in morphology is rooted in change during ontogeny, particularly in timing and rate of growth (McKinney and McNamara, 1991). For example, an increase in size can arise through either prolonged growth or increased growth rate or both. Changes in shape will occur if timing and rate of growth change in one trait but not the other. Therefore, it is of fundamental importance to analyze the amount of variation in these growth parameters. Such variation may be of two kinds: variation in the elevation of growth curves which result almost exclusively in changes in size, and variation in the shape of growth curves which can lead to changes in shape. Studies of variation in elevation of growth curves abound, but those on the actual shape of growth curves are rare. There are almost always differences in growth curves among individuals in a population, and in some cases these can be substantial. Such variation not only has an environmental basis but also a genetic one, the extent of which, however, is unknown for most bird populations.

Thus, Björklund (1993) found very little variation in the shapes of growth trajectories among three species of cardueline finches. Variation was confined almost exclusively to elevation trajectories, representing size. Furthermore, correlations among the trajectories for the different traits were very strong, indicating that the only variation available for selection to act on is in size and so predicting evolutionary change only in size. This analysis was repeated for two species of tits, with the same result (Björklund, 1995, 1996b).

4 Selection

The analysis of patterns of multivariate selection gives considerable insight into the functional properties of phenotypes. For example, where selection acts consistently to stabilize a particular trait combination, then the correlations among the traits should become strengthened. The pattern of integration, i.e. the correlational structure, is itself the result of past selection, and may today be reinforced or broken down by current selection. Questions about current selection now emerge: is current selection concordant with the pattern of integration, or is it pressuring in other directions? An analysis of this will give answers to the more general question of whether the pattern of integration is acting to facilitate or constrain future evolution.

There are, however, few studies of multivariate selection on birds. There are a number of reasons for this, one of the most important being that very large sample sizes are needed if the statistical machinery of selection analyses is to be fully utilized. Another is that the literature and techniques in this area are not easy reading, and researchers may avoid more appropriate analyses for this simple but sad reason. It cannot be stressed strongly enough, however,

that, if the data are available, a full multivariate analysis of selection is worthwhile because information concerning the correspondence between phenotype and environment is of enormous value.

Analyses of selection involve three steps: selection on trait means, selection on trait variances, and selection on trait covariances. Completing all three steps allows multivariate fitness surfaces to be estimated (Phillips and Arnold, 1989; Schluter and Nychka, 1994; Arnold et al., 2001), providing much important information. The first two steps have been employed in a large number of studies. Kingsolver et al. (2001) list more than a dozen; and there are more as they confined their meta-analysis to studies published in general journals without searching the ornithological literature.

For example, in an analysis of survival in the serin (*Serinus serinus*), Björklund and Senar (2001) found that probability of survival increased with increasing wing and tail length in males. There was, however, significant selection against the correlation between tail and wing, leading to a fitness surface with a valley between two peaks and most individuals in the valley. The reason for this might be a consequence of both traits developing in the same way — energy allocated to wing growth going to the tail as well, hence the correlation of 0.69 in males. If energy is insufficient to increase both tail and wing length, then the consequent compromise is likely to be medium-sized birds with a suboptimal fitness. Another example taken from the same study showed a distinct difference in fitness surface between males and females in bill traits: whereas males were close to an adaptive peak, females were positioned on a slope well away from theirs. Such inferences could not have been reached without detailed multivariate analysis, using sample sizes in the hundreds; simple univariate analysis would have even been misleading.

5   Optimal integration

At a general theoretical level in functional trait evolution, one must ask the following questions: how many elements should be integrated? Under what ecological conditions are large complexes favored? And under which conditions are small complexes favored? These questions relate closely to an issue addressed in theoretical physics: the stability-flexibility dilemma. It observes, in short, that large complexes, networks or organizations are able to perform many tasks but are slow and costly to maintain, whereas small complexes are fast and cheap but cannot perform many tasks. Thus, depending on the demands imposed by the environment, different organisms may evolve different levels of integration or networks.

To test this, Repsilber et al. (unpublished) used neural networks of different size to compete in a genetic algorithm under a wide variety of ecological conditions. A neural network is a general construction where "something" is put in, and the construct is trained to handle the input in such a way that a certain output is delivered. This is a very

general and flexible model that can handle all levels of organization, from the strictly molecular to ecosystems. In this context, the network or complex can be thought of as an individual that is given a certain amount of resources and which uses the energy from the resources in a way to maximize reproductive output (or Darwinian fitness). Thus, complex networks correspond to individuals with a high level of integration (many parts, strong correlations), while small networks correspond to individuals with a low level of integration.

In the study of Respilber et al., the ecological environments comprised between three and eight different habitats each with different resources. Networks of sizes three to ten were then allowed to compete within these environments. The results were clear, and show that in the short run, smaller networks out-compete (have higher fitness) than larger ones, but that in the long run, after hundreds of generations, the larger ones won. A correlation was also found between the size of the optimal ("winning") network and the degree of environmental heterogeneity such that larger networks were more successful in more heterogenous environments. Thus, at a given level of heterogeneity, a certain size of network is the most successful, and larger and smaller networks at a disadvantage.

The biological conclusions to be drawn from this study are that smaller networks are favored in unpredictable environments, and larger networks in predictable ones. Thus, the levels of integration can be predicted to vary according to the long-term properties of the habitat in which each species has evolved. In this context, the model relates both to the number of traits that should optimally be included in each module of integration, and to the number of different modules that would be optimal.

6   Conclusions

The main conclusions of this paper are that, first, more data are needed on the structure of the genetic variance-covariance matrix in natural bird populations for understanding and predicting future evolutionary change, and to learn how and when patterns of integration aid or constrain that change. Secondly, more data are needed to assess natural variation in the shape of growth trajectories, since this is the raw material for selection at different levels of integration. Thirdly, more data are needed concerning the pattern of selection on integration itself, in addition to selection on trait means and variances. Needless to say, the basis for all this is a firm understanding of the actual patterns of morphological integration and functional complexes of birds, knowledge of which is still rudimentary today.

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