

S18-1 Rapid evolutionary divergence of environment-dependent sexual traits in speciation: a paradox?

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Abstract Expression of sexual displays is often closely linked to individual performance in a particular environment, i.e., male condition. Female preference for environment- and condition- dependent sexual displays in males evolves because of benefits of male condition to female fitness. Variation in these benefits can lead to divergence in female preferences that eventuate in speciation. To indicate condition reliably, sexual displays should have a significant environmental component in their development. Furthermore, mate preference favors a greater dependence on organismal functions in the development of ornaments (i.e., greater condition-dependence). Both environment- and condition-dependence might constrain evolutionary elaboration of the sexual trait as well as its effectiveness in achieving post-mating genetic isolation among divergent populations. Here we discuss an apparent paradox between the prevalent role of environment- and condition- dependent sexual displays in producing population divergence, and their expected slow rate of evolution.

Key words Integration, Modularity, Ontogeny, Sexual ornaments, Speciation

1 Introduction

Sexual ornaments and displays play an important role in establishing and maintaining reproductive isolation between divergent populations (Mayr, 1939; Dobzhansky, 1940; Schluter, 2000). There are several reasons for this. First, sexual traits are often highly sensitive to local environment and thus can reflect an organism's performance and local adaptation in a particular environment (reviewed in Andersson, 1994). For example, the expression of diet-dependent carotenoid ornamentation in male birds can express ability in finding sources of dietary carotenoids and so enable evolution of female preference that is locally adaptive (Endler, 1983). Secondly, selection for higher detectability in a particular environment favors greater dependency of sexual trait expression on environmental variation (Endler, 1992; Schluter and Price, 1993). For example, components of bird song differ in susceptibility to habitat structure, and female preference for the most detectable song features will enable locally adaptive female choice (reviewed in Slabbekoorn and Smith, 2002). Thirdly, sexual ornaments and displays can facilitate mate recognition and prevent interbreeding by imprinting or cultural inheritance of the local expression of sexual ornaments (Grant and Grant, 1996a; Irwin and Price, 1999). Ultimately, population divergence in the coevolution of trait expression and female preference will lead pre-mating isolation to eventuate in the genetic isolation of divergent populations (Grant and Grant, 1996b, 1997a).

Implicit in these explanations is the assumption of rapid evolutionary change, especially compared to non-

sexual traits. Moreover, rapid gain and loss of sexual ornaments is especially important for reproductive isolation when there is a spatial or temporal lag between female preference and ornament expression (Payne and Krakauer, 1997; Price, 1998; Brooks and Coullidge, 1999; Day, 2001), as is often the case with environment- and condition- dependent ornaments (Hill, 1994; Irwin and Price, 1999). The prediction of rapid evolution in sexual displays is well supported — it is commonly observed that sexual traits have high evolutionary lability, and closely related species differ more in sexual ornaments than nonsexual traits (e.g., Civetta and Singh, 1998). However, the mechanisms underlying rapid evolutionary change of sexual ornaments are not well understood.

Moreover, what is known about sexual ornaments is that their evolution — especially in those determined environmentally — is likely to be slow (Badyaev, 2003). First, the expression of sexual traits, such as elongated tail feathers or carotenoid-based pigmentation, is a complex summary of many organismal processes (Andersson, 1994). Because of this, sexual traits are probably involved in many organismal functions (Wedekind, 1992, 1994), and such involvement should constrain evolutionary change (Cheverud, 1996). Secondly, to indicate individual performance reliably in a local environment, the expression of sexual ornaments must incorporate a substantial amount of environmental variation during development (Andersson, 1994). If environmentally-dependent sexual traits are likely to respond rapidly to environmental change, they are less likely to facilitate genetic isolation between divergent

populations, especially in the absence of post-mating reproductive barriers. Thirdly, the expression of sexual displays and the preference for them are often specific to the social and ecological environment of breeding (Tregenza and Wedell, 2000; Qvarnström, 2001; Badyaev and Qvarnström, 2002). Although context-dependency in ornament expression or sexual imprinting on the phenotype of relatives or locally born individuals may enable locally adaptive female choice, it might also prevent the directional change in both trait expression and trait preference necessary for speciation.

Here we discuss the apparent paradox between the expectations of low evolutionary lability of environment-dependent sexual ornaments and their widespread role in speciation, and offer possible explanations.

2 Speciation by sexual selection: models and evidence

Correlated evolution of ornament expression and mate preference can strongly facilitate speciation (Lande, 1982). In allopatry, different environments or gene pool compositions can lead to elaboration of different sexual ornaments and thus population divergence (Lande, 1980; West-Eberhard, 1983; Lande and Arnold, 1985; Price, 1998). Unstable equilibria in ornament expression and preference is expected to result in repeated cycles of ornament elaboration and exaggeration of different sexual traits (Pomiankowski and Iwasa, 1998; Iwasa and Pomiankowski, 1999). Sympatric speciation by sexual selection may occur through similar mechanisms (Wu, 1985; Payne and Krakauer, 1997; Day, 2000) or the splitting of an existing trait or preference into two extremes (Turner and Burrows, 1995; Higashi et al., 1999; Takimoto et al., 2000); but see Turelli et al. (2001) for a discussion of assumptions.

Three lines of evidence suggest that sexual selection strongly facilitates speciation (Price, 1998). First, in many avian taxa, intensity of sexual selection, often measured as the degree of sexual dimorphism, is correlated with species diversity (Barraclough et al., 1995; Mitra et al., 1996; Prum, 1997; Moller and Cuervo, 1998; Owens et al., 1999). Secondly, sexually-selected traits within species are often those used in species recognition, suggesting that a mate-recognition system evolved as a by-product of divergent sexual selection (Wiernasz and Kingsolver, 1992; Ryan and Rand, 1993; Gray and Cade, 2000; McKinnon and Rundle, 2002). Moreover, in taxa where speciation is incomplete, an evolutionary lag between the extent of trait expression and preference for it often leads to preference for traits of heterospecific males, resulting in hybridization (e.g., Collins and Luddem, 2002; Price, 2002). Thirdly, speciation can occur rapidly through divergence in sexually-selected traits prior to divergence in ecology or onset of genetic incompatibility (Deutsch, 1997; Masta and Maddison, 2002; Price, 2002). Thus, sexual selection can facilitate pre-zygotic isolation through genetic change in ornament expression and female preference (Hollocher et al., 1997; Ting et al., 2001).

3 Mechanisms of sexual selection and the development of sexual traits

That sexual displays differ in genetic and environmental determination has important consequences for both the mechanism of mate choice and the effectiveness of speciation by sexual selection. Theory suggests that sexual displays which reflect indirect benefits should have a high genetic component, whereas those that reflect direct phenotypic benefits should have a high environmental component (Andersson, 1994), and, potentially, higher genetic integration with many of the organismal functions that produce them. Because speciation is more effective when it involves sexual traits with a greater genetic component, the rate of genetic divergence should depend on the mechanism of sexual selection.

4 The paradox: environment- and condition- dependent sexual traits play an important role in speciation

Sexual selection may facilitate speciation in birds (Barraclough et al., 1995; Mitra et al., 1996; Grant and Grant, 1997b; Moller and Cuervo, 1998; Badyaev and Hill, 1999; Uy and Borgia, 2000). Given that sexual ornaments with a considerable genetic component are expected to diverge more rapidly and thus facilitate speciation, their displays should be the most common. Yet, empirical studies suggest that most sexual displays are condition- or environment-dependent (Veiga and Puetra, 1996; Badyaev and Hill, 1999; Qvarnström, 1999; Hill, 2000; Kotiaho et al., 2001). Furthermore, phenotypic effects of male condition that affect female survival and fecundity directly generate much stronger selection in female preference than do indirect effects (Kirkpatrick, 1985; Kirkpatrick and Barton, 1997; Møller and Jennions 2001), and thus should be more effective in speciation. How do can the importance of sexual traits of greater genetic component be reconciled with the apparent prevalence of condition- and environment-dependent sexual displays in the speciation process?

5 Resolution of the paradox

5.1 Environmental component of condition is genetically determined

Whereas the development of a sexual trait that indicates direct benefits may be determined largely by the environment, an individual's ability to acquire resources (e.g., behavior) can have a genotypic basis (Moore et al., 1997; Wolf et al., 1997, 1998). For example, ability to take and hold high quality territory or food may be determined genetically by aggression. Although the probability of inheriting a complete developmental program for expressing these complex behavioral traits may be low, its inheritance and modification might strongly facilitate genetic isolation (Badyaev, 2003).

5.2 Allocation of resources between an organism and sexual ornaments has a significant genetic component

Individual differences in acquisition and allocation of resources between nonsexual traits and a sexual display may have a genetic basis (Brooks, 2000; David et al., 2000; Kotiaho et al., 2001), and be subject to mate choice. Thus, whereas the proximate target of sexual selection might be the elaboration of sexual ornaments, the ultimate target is the underlying relationship between the expression of the ornament and condition of the organism, i.e., the developmental program of the ornament.

5.3 Allocation of resources among components of sexual ornaments has a significant genetic component

Mate preference for different condition-dependent benefits of ornament expression may favor the evolution of composite sexual ornaments, the components of which are linked to different organismal processes and thus reliably reflect condition across a wide range of environments (Badyaev, 2003). Although selection by female choice is expected to be stronger for components of sexual ornamentation that are more relevant locally, developmental cohesiveness and functional integration may still be needed to maintain stability in ornaments that are composite (Wedekind, 1994; Johnstone, 1995; reviewed in Badyaev, 2003).

For example, carotenoid-based ornamentation in house finches (*Carpodacus mexicanus*) requires a coordination of multiple processes associated with the consumption, digestion, transportation, and deposition of carotenoids (Badyaev et al., 2001). However, despite population variation in environment- and condition- dependence in each of these processes, and corresponding variation in female choice of different components in different environments, production of carotenoid-based sexual ornaments requires some degree of integration along these pathways, so maintaining developmental interdependency among ornament components (Badyaev et al., 2001). Mate preference for a particular component of a composite sexual ornament will result in acquisition of a complex developmental program that produces expression of this component in relation to the other parts, ultimately leading to genetic isolation (also Wu, 2002).

5.4 Greater environment- and condition- dependence in ornaments evolves after divergence

Over time, sexual display may be influenced by different mechanisms capitalizing on different aspects of the developmental program of the ornaments involved (Price et al., 1993; Kokko et al., 2002; Badyaev, 2003). Sexual ornaments may thus have different environmental and genetic determinants at different stages of population divergence. Divergent sexual selection on a sexual ornament of initially high genetic determination could, for example, facilitate speciation. As elaboration of the ornament progresses, the cost of ornament development and maintenance increases (Price et al., 1993), leading to an increase in condition-dependence (Nur and Hasson, 1984; Grafen, 1990). Accordingly, speciation by sexual selection could follow

divergence in sexual ornaments with a high genetic component, bearing in mind that these ornaments, in the course of their elaboration, may subsequently develop greater condition- and environment- dependence.

The paradox between the role of sexual traits in speciation and prevalence of condition- and environment-dependent ornaments turns on several crucial assumptions. First, it is assumed that the developmental program of sexual ornaments, in particular its genotypic and phenotypic components, remains constant over evolutionary time. This assumption is untested for sexual ornaments, but recent studies suggest that the lack of evolution in sexual ornaments under progressively stronger directional selection may be explained by an increasing environmental component in their developmental program (e.g., Merilä et al., 2001; Kruuk et al., 2002).

Secondly, it is not known whether an increase in the environmental component in the development of most sexual traits is associated with a reduction in their genetic component (Merila and Sheldon, 2001). Theoretical and empirical studies suggest that condition-dependent traits may have a significant genetic component (van Tienderen and de Jong, 1994; Rowe and Houle, 1996; Glazier, 2002), consistent with the results of recent empirical studies (David et al., 2000; Kotiaho et al., 2001). Investigating the assumptions underlying the paradox between prevailing condition-dependent sexual traits and their slow rate of evolution could provide crucial insights into speciation by sexual selection.

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