HYBRIDS AND IRIS

Hybridization, hybrid fitness and the evolution of adaptations

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Abstract

This review focuses on two related outcomes of hybridization sensu lato (i.e. findings from both natural and experimental hybrids are discussed): (1) the production of hybrid genotypes with various fitnesses, and (2) the origin/transfer of adaptations in the Louisiana Iris species complex. Since effects on fitness, and the origin or transfer of adaptations, are of fundamental evolutionary importance, the examples discussed in this review reflect some of the most significant phenomena deriving from the transfer of genetic material via natural hybridization.

Key words: Adaptation, hybridization, genetic exchange, reticulate evolution

Introduction

With regard to the topic of this review, Arnold (2006) discussed examples encompassing viruses, bacteria, plants and animals—all of which reflected the acquisition of novel adaptations through genetic exchange events. Significantly, these acquisitions apparently increased the fitness of certain hybrid genotypes, allowing them to occupy novel environments. Adaptive genetic exchange can be inferred in multiple ways. First, inferences can be constructed through the examination of genetic markers across natural hybrid zones, either alone or in concert with data concerning the habitat associations of various parental and hybrid genotypes (see Moore, 1971; Endler, 1977; Arnold, 1997, 2006 for discussions and additional references). These types of analyses test for (1) the expected and observed frequencies of parental and hybrid genotypes across contact zones to test for a significantly increased frequency of introgressed markers, and/or (2) significant associations between certain genotypes and microhabitats. Either class of observation is consistent with a hypothesis of adaptive trait evolution. Thus, if specific genomic regions introgress at a significantly greater frequency than predicted, or are associated preferentially with certain novel habitats, they are identified as possible adaptive trait loci.

Another type of evidence that facilitates inferences concerning the relative fitness of hybrid genotypes and the role of adaptive trait origin or transfer derives from experimental analyses (e.g. Rhode & Cruzan, 2005). In this case, an array of hybrid and parental genotypes are placed into the same environmental setting (e.g. see Bolnick & Near, 2005 for a review of hybrid embryo viability in crosses between centrarchid fish taxa). Fitness estimates are obtained and the hybrid and parental genotypes ranked relative to one another. The fitness estimates may then be used to infer which hybrid genotypes demonstrate the acquisition of adaptive traits from one parent (i.e. adaptive trait transfer) or from a combination of genes from more than one parental taxon (i.e. the evolution of novel adaptive traits). Experimental investigations of hybrid fitness and adaptive trait origin/transfer have demonstrated a large variability in the number and category of fitness components examined. For example, Burke et al. (1998a) collected data for both asexual and sexual fitness components for Iris fulva Ker Gawl., Iris hexagona Walter, and their F1 hybrids. In a separate analysis, Burke et al. (1998b) estimated the fitness of F2 hybrids formed in crosses between I. fulva and Iris brevicaulis Raf. by examining the genotypes of the F2 progeny. In the latter study, fitness estimates were determined from the survivorship of only hybrid
genotypes, rather than from data for both hybrids and parental individuals (as in Burke et al., 1998a). However, both studies detected higher fitness for some hybrid genotypes in the controlled greenhouse environment. This concordant finding supported the hypothesis that some genotypes had gained adaptive traits that allowed an increase in their fitness—relative to other hybrid and parental genotypes—in this environmental setting.

In the following sections we will discuss a series of studies that define the role of introgressive hybridization in the plant group known as the Louisiana Irises. In particular, we will illustrate how introgression has apparently led to hybrid genotypes with increased fitness and the transfer and/or origin of adaptations to novel habitats.

**Louisiana Irises—A paradigm for studies of introgressive hybridization**

Edgar Anderson published his classic treatise, *Introgressive Hybridization*, in 1949. In the first chapter of his book, Anderson used the morphological variation found in naturally occurring parental and hybrid populations of the plants known as Louisiana Irises (as reported by Riley, 1938) to illustrate the process of introgressive hybridization (i.e. “introgression”); Anderson & Hubricht, 1938). Anderson had earlier (1948) utilized this same species complex to exemplify the effect of human-mediated, ecological disturbances on introgression. In both his paper and book, Anderson indicated the primary significance of natural hybridization in the evolutionary history of Louisiana Iris species. Specifically, he concluded that natural hybridization had resulted in genetic exchange in the form of introgression. Furthermore, Anderson held that the fundamentally important role of introgression lay in its ability to greatly increase the “variation in the participating species . . .” and thus “far outweigh the immediate effects of gene mutation” (Anderson, 1949: 61–62).

In spite of the potential for genetic exchange to affect evolutionary change, Anderson and Hubricht (1938) discussed the difficulty in detecting introgression when using quantitative (e.g. morphological) traits such as those utilized by Riley (1938) and Anderson (1949). Although such transfer might result in evolutionarily novel and important genotypes (e.g. see Anderson & Hubricht, 1938; Anderson, 1949; Anderson & Stebbins, 1954; Lewontin & Birch, 1966; Arnold, 1997, 2006; Chiba, 2005), the “wider spread of a few genes . . . might well be imperceptible” (Anderson, 1949: 102) when quantitative traits were the markers for gene transfer. In Louisiana Irises, as in taxa as diverse as protozoans, plants and animals, rigorous tests for introgressive hybridization awaited the availability of discrete, molecular markers (see Arnold, 2006 for a discussion). The development of the genetic markers necessary to test for (1) introgressive hybridization in nature, (2) the effect of such introgression on the fitness of various hybrid genotypes, and (3) the origin and/or transfer of adaptations through introgression began in the early 1990s. The first of these analyses supported Anderson’s contention (Anderson, 1948, 1949) that the evolution of the Louisiana Iris species had been influenced by introgression. Specifically, some populations of *I. fulva*, *I. brevicaulis* and *I. hexagona* possessed genetic markers from the alternate species (Arnold et al., 1990a,b; Nason et al., 1992).

The initial molecular analyses confirmed the occurrence of introgressive hybridization as an evolutionary force in the Louisiana Iris species complex. Recent studies have further clarified the role of introgression in determining the fitness and ecological adaptations demonstrated by hybrid individuals. In particular, various investigators have come to the conclusion that genetic exchange has resulted in the transfer of loci that affect the fitness of hybrid genotypes across habitats. For example, Cruzan and Arnold (1993) and Johnston et al. (2001) defined microhabitat associations within natural hybrid zones between *I. fulva*, *I. brevicaulis* and *I. hexagona*. Results from these analyses reflected diagnostic, environmental associations for some of the parental and hybrid genotypic classes. Significantly, one hybrid class was found to occur in a novel habitat relative to the parental individuals and other hybrid genotypic classes as well (Cruzan & Arnold, 1993). This observation was consistent with the hypothesis that adaptations to novel microhabitats could evolve through the combining of parental, genomic regions in hybrid progeny.

**Louisiana Irises and the origin/transfer of adaptations**

More recent analyses of the spatial distribution of genotypes and paternity in natural hybrid zones along with linkage and QTL (quantitative trait locus) mapping of fitness components have added further support to the conclusions of Anderson (1949), Cruzan and Arnold (1993) and Johnston et al. (2001). For example, Cornman et al. (2004) determined the spatial distribution of different hybrid clones in a naturally occurring hybrid zone between *I. fulva*, *I. brevicaulis* and *I. hexagona*. In addition, they determined the contribution to paternity by various genotypes within the hybrid zone and by plants outside the study area. Their findings—of significant spatial genetic structure and recruitment favoring certain hybrid genotypes—were consistent with the
Figure 1. Frequencies of introgressed alleles segregating in (A) *I. brevicaulis* Raf. and (B) *I. fulva* Ker Gawl. BC$_1$ hybrids. Each linkage group (i.e. "1 – 22") is represented by a graph and genetic distances are given on the x-axis in Kosambi centimorgans. A scale of the frequencies of the introgressed alleles is given on the y-axis (expected value is 0.50). Frequencies greater than 0.50 indicate an overrepresentation of the introgressed alleles. Frequencies less than 0.50 reflect an underrepresentation of the introgressed alleles. Marker transmission ratio distortion as evaluated by $\chi^2$ tests is indicated by an open circle (nonsignificant), $\times$ ($p < 0.05$), and a solid circle ($p < 0.01$). For instances where two or more contiguous markers demonstrated significant transmission ratio distortion, the Bayesian posterior probability of a transmission ratio distorting locus (i.e. TRDL) is given in italics and the posterior distribution of the TRDL location is shown as an accompanying histogram (Bouck et al., 2005).
hypothesis of hybrid genotypes having a higher fitness due to acquired adaptations (Cornman et al., 2004). Indeed, these authors argued that selection for certain hybrid genotypes and against other hybrid progeny could lead to “the establishment of recombinant lineages that are more fit than the parental types in some habitats” (Cornman et al., 2004).

A recent series of genetic mapping analyses have also underlined the importance of introgressive hybridization in the origin and evolution of adaptations to various environments. Figure 1 illustrates results from a study by Bouck et al. (2005). Their study defined genomic regions, in both *I. brevicaulis* and *I. fulva* backcross (*BC1*) individuals, which were characterized by either significantly lower- or higher-than-expected levels of introgression. In regard to the current discussion, the observation of a significantly increased frequency of introgression likely reflects positive selection for regions that contributed to increased survivorship in the greenhouse environment. Similarly, Martin et al. (2005) defined QTLs that were significantly associated with, and thus inferred to have affected, long-term survivorship in the greenhouse environment (Figure 2). Although the Louisiana Iris plants propagated in the greenhouse were watered regularly, this environment reflects a water-limited setting for some of the genotypes. In particular, although *I. brevicaulis* is often found in dryer, greenhouse-like, natural environments, wild populations of *I. fulva* most often occur in water-saturated soils (Viosca, 1935; Cruzan & Arnold, 1993; Johnston et al., 2001). One expectation derived from the observations of habitat associations in the natural populations of these species is that alleles from *I. brevicaulis* (i.e. the “dry-adapted” species) should increase survivorship in the relatively dry greenhouse environment.

Consistent with the above prediction, differences in mortality were found between the two backcross (*BC1*) hybrid classes (originally studied by Bouck et al., 2005), with *I. fulva* backcrosses demonstrating twice the frequency of mortality as *I. brevicaulis* backcross plants. Furthermore, mapping analyses detected four QTLs in the *I. fulva* hybrids that were significantly associated with survivorship (Martin et al., 2005). As expected, introgressed *I. brevicaulis* DNA increased survivorship at three of the four QTLs. Surprisingly, the fourth QTL indicated that such introgression was associated with decreased survivorship. In this latter case, the presence of two

![Figure 2](image-url)
copies of the *I. fulva* genomic region increased survivorship (Martin et al., 2005). Although unexpected, this result indicates the adaptive potential that derives from combining genomic elements from different evolutionary lineages, in hybrid individuals.

In light of their results, Martin et al. (2005) concluded the following:

The present findings have important implications for the evolutionary dynamics of naturally occurring hybrid zones. Regions of the genome that increase survivorship when in a heterozygous (i.e., hybrid) state should have an increased likelihood of passing across species boundaries, whereas those that decrease survivorship will be less likely to introgress.

A subsequent investigation strengthened this conclusion. In this latter study, Martin et al. (2006) again utilized genomic surveys including QTL mapping. However, unlike either Bouck et al. (2005) or Martin et al. (2005), their analyses involved genotypes grown under natural conditions. Furthermore, in contrast to the relatively dry greenhouse setting of the first two experiments, the genotypes in the Martin et al. (2006) analysis were exposed to a flood event. The following observations were made from this latter study:

1. *I. fulva* individuals survived at significantly higher frequencies than *I. brevicaulis* plants;
2. *I. fulva* backcrosses had a significantly higher frequency of survivorship than the reciprocal backcross toward *I. brevicaulis*;
3. survivorship of the *I. brevicaulis* BC1 hybrids was influenced by the presence of introgressed *I. fulva* alleles located throughout the genome; and
4. survivorship in the *I. fulva* BC1 hybrids was significantly affected by two epistatically acting QTL of opposite effects (Martin et al., 2006).

With regard to point (4), it is intriguing that the two QTLs that affected survivorship in the natural setting were on two of the linkage groups that contained QTLs that also impacted survivorship in the dry greenhouse environment. However, the effects were in opposite directions—i.e. the introgressed QTLs in one setting lowered survivorship while in the other setting they increased survivorship (Martin et al., 2006).

Taken together, the above studies indicate broadly based support for Anderson’s (1949) conclusion that introgression has affected the evolutionary trajectory of the Louisiana Iris species complex. In general, these findings “demonstrate the potential for adaptive trait introgression between these two species and may help to explain patterns of genetic variation observed in naturally occurring hybrid zones” (Martin et al., 2006).

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**References**

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