NATURAL HYBRIDIZATION: HOW LOW CAN YOU GO AND STILL BE IMPORTANT?

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Abstract. This paper examines two assumptions that have formed the basis for much of the past and present work on hybrid zones. These assumptions derive from the observation that crosses between genetically divergent individuals (e.g., from different subspecies, species, etc.) often give rise to genotypes that are less fertile or less viable than those produced from crosses between genetically similar individuals. The first assumption is that natural hybridization will not affect the evolutionary history of the hybridizing forms because there is a low probability of producing novel genotypes with higher relative fitness. The second viewpoint is more extreme in that it assumes that all hybrid genotypes will be less fit. Even if rare gene flow does occur it will thus not contribute to patterns of diversification or adaptation because the hybrids will always be selected against. Examples from both plant and animal hybridization are discussed that are not consistent with these assumptions. Numerous instances of natural hybridization are used to demonstrate that extremely low fertility or viability of early-generation hybrids (e.g., F_1, F_2, B_1) does not necessarily prevent extensive gene flow and the establishment of new evolutionary lineages. In addition, it is demonstrated that various hybrid genotypes have equivalent or higher fitness than their parents in certain habitats.

Key words: adaptation; evolutionary innovations; hybrid fitness; hybrid zones; natural hybridization; natural selection.

INTRODUCTION

The subtitle of this manuscript draws attention to the basis of a common assumption concerning the process of natural hybridization. "How low can you go" refers to the observation that crosses in nature between genetically divergent individuals may only rarely produce fully viable and fertile individuals. In addition, most (but not necessarily all) recombinant genotypes may be less fit than their parents regardless of habitat. These observations have led many evolutionary biologists, particularly zoologists, to assume that natural hybridization is evolutionarily unimportant. Darwin (1859: 246) reflected this view by stating, "Pure species have of course their organs of reproduction in a perfect condition, yet when intercrossed they produce either few or no offspring. Hybrids, on the other hand, have their reproductive organs functionally impotent. . . ." Mayr (1963:133) extended this description in the following way, ". . . The majority of . . . hybrids are totally sterile. . . . Even those hybrids that produce normal gametes in one or both sexes are nevertheless unsuccessful in most cases and do not participate in reproduction . . . when they do backcross to the parental species, they normally produce genotypes of inferior viability that are eliminated by natural selection. Suc-

cessful hybridization is indeed a rare phenomenon among animals."

Earlier in this century and indeed extending through the modern synthesis, some authors argued for an important role for natural hybridization in the evolution of species complexes (e.g., Anderson and Stebbins 1954). However, the emphasis placed on the genetic integrity of species and evolutionary diversification resulted in the conclusion that natural hybridization had little if any effect on the evolution within groups of organisms—except to violate species boundaries and thus potentially arrest the process of divergence (see Arnold 1997 for a discussion). Although plants were often cited as potential examples of the influence of natural hybridization on organismal evolution (Lotsy 1916, 1931, Anderson 1948, 1949, Heiser 1949, Stebbins 1950, 1959, Grant 1963), this conclusion was subsequently disavowed or left in question by numerous authors (e.g., Wagner 1969, 1970, Heiser 1973). Indeed, Mayr (1992) has recently extended his view of the evolutionary unimportance of natural hybridization to encompass plants, "To be sure, the occasional production of an interspecific hybrid occurs frequently in plants. However, most of these hybrids seem to be sterile, or do not backcross with the parent species for other reasons."

Our goal for this paper is to illustrate the potential for natural hybridization to lead to adaptive evolution and evolutionary diversification. To achieve this goal we will address the following questions: (1) Can hy-

bridization events found evolutionary lineages, even if early generations (e.g., F_1, F_2, B_1) have much lower fitness than their parents? In the context of this review "evolutionary lineages" can be new taxa or new assemblages of populations with novel genotypic (hybrid) structure that have existed for extended periods of time. (2) Is it correct that all hybrids have lower fitness than their parents in all or most habitats? We address these two questions by reviewing estimates of hybrid and parental fitness, associations between genotypes and habitats, patterns of introgression in contemporary and ancient populations and phylogenetic analyses of species complexes where hybrid speciation has been inferred. Our conclusion is that hybrid genotypes can have high fitness compared to parental genotypes and that even if hybrids demonstrate low fitness, they can still act as the starting point for new evolutionary lineages. These conclusions rely on the same class of event that is the basis for descent with modification. Thus, the rare hybrid genotype that possesses increased fitness in a certain environment is analogous to a rare mutation that conveys a selective advantage to its carrier. Both should increase in frequency and possibly act as the starting point for further evolutionary diversification.

EVOLUTIONARY CONSEQUENCES OF UNFIT HYBRIDS

Hybridization is routinely represented as a process that leads to organisms with lowered fitness; these organisms can be either the parents that made the wrong "choice" in mating partner thus producing fewer or less fertile offspring or alternatively be the less viable/fertile offspring themselves (Dobzhansky 1940, Mayr 1963, Wilson 1965, Barton and Hewitt 1985). In the next section we will consider whether hybrids are always less fit than their parents. The present discussion is designed to demonstrate that the production of mainly less fertile or less viable hybrid offspring does not mean that natural hybridization will play a limited (or no) role in the evolution of a particular species complex (Arnold 1997).

Notropis cornutus and N. chrysocephalus

Dowling and his colleagues have examined the evolutionary effects of natural hybridization between species of fish. In one set of analyses they analyzed the pattern of genetic and morphological variation associated with two closely related cyprinid species, *Notropis cornutus* and *N. chrysocephalus*. One of their earliest studies examined the pattern of morphological and allozyme variation in natural populations. They concluded that there was extremely strong selection acting against hybrid individuals (Dowling and Moore 1985). It was estimated that selection was eliminating recombinant genotypes at the rate of 9.2% per annum. A subsequent study (Dowling et al. 1989) collected and compared allozyme and mtDNA data within the zone of overlap between these species. This study yielded non-concordant patterns of allozyme and mtDNA introgression. However, the findings were consistent with the previous conclusion that a major factor determining genotype and haplotype distributions was selection against hybrid fish (Dowling et al. 1989).

The *Notropis* studies support the hypothesis that at least some hybrid genotypes possess reduced fitness. A conclusion that could be (and often is) drawn from such findings is that genetic and evolutionary effects from hybridization episodes will be prevented by negative selection. For example, introgression of genetic material from one species into another would seem unlikely. In contrast to this prediction, Dowling and Hoeh (1991) found extensive introgression to the south of the present-day *Notropis* contact zone. This was inferred from the presence of *N. cornutus* mtDNA haplotypes and esterase (*Est-A*) alleles in populations that are morphologically identical to *N. chrysocephalus*. The populations that were furthest from the present-day hybrid zone actually demonstrated the highest frequencies of the introgressed mtDNA haplotypes (Dowling and Hoeh 1991).

Dowling and Hoeh (1991) concluded that the introgression to the south of the current hybrid zone was probably due to the zone moving from south to north during the glacial recession. The intriguing finding is that the most distant populations, relative to the current region of overlap, demonstrate the highest frequency of mtDNA from the alternate species. These authors considered and rejected the explanation that *N. cornutus* mtDNA was favored in the nuclear background of *N. chrysocephalus* (Dowling and Hoeh 1991). Instead they concluded that population structure and patterns of hybridization were the causal factors resulting in the high frequency of the foreign haplotype. In contrast to this conclusion, a number of experiments involving species of *Drosophila* have documented the effect of positive selection on the frequency of mtDNA haplotypes in intraspecific (e.g., MacRae and Anderson 1988, Kilpatrick and Rand 1995) and interspecific (Van Valen 1963, Hutter and Rand 1995) crosses. For example, Hutter and Rand (1995) documented the equal or greater fitness of flies that possessed *Drosophila pseudoobscura* mtDNA on the background of a *D. persimilis* nuclear genotype, relative to flies that had *D. persimilis* mtDNA and nuclear elements. Notwithstanding the causal factors that determined the mtDNA introgression in *Notropis*, the patterns of introgression are not consistent with the expectation that strong selection against some hybrid genotypes will destroy any possibility of a long-term effect on the genetic structure and evolution of the hybridizing taxa (Arnold and Hodges 1995, Arnold 1997).

Caledia captiva

Two decades ago Shaw described extensive chromosome variation in the Australian grasshopper genus *Caledia* (Shaw 1976). Since this description, Shaw and
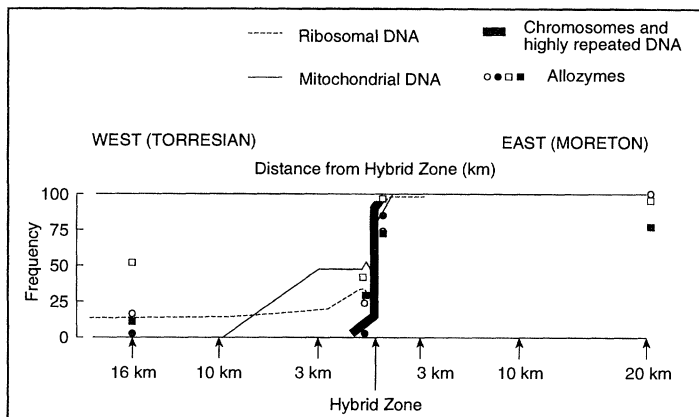
FIG. 1. Frequency of Moreton rDNA, mtDNA, chromosomal/highly repeated DNA, and allozyme markers across the present-day hybrid zone between the *Caledia captiva* taxa, Moreton and Torresian (from Shaw et al. 1990, with permission from the *Canadian Journal of Zoology*).

his colleagues have completed numerous experimental and field analyses on the determinants of reproductive isolation and the evolution of hybrid zones between two of the chromosomal races (i.e., "Moreton" and "Torresian"; Shaw et al. 1980). One of the consistent findings has been extremely narrow hybrid zones, as defined by chromosome markers. For example, in one zone the karyotype changes from a metacentric Moreton form to the acrocentric Torresian form over a distance of only 200 m (Fig. 1; Shaw et al. 1979, 1985).

As with *Notropis,* the structuring of the present-day hybrid zones in *Caledia* has been largely attributed to selection against hybrids. In laboratory crosses F_1 individuals were found to be fully fertile and viable relative to progeny from control (i.e., parental) matings. In contrast, the F_2 generation is totally inviable and F_1 × Parental crosses (with either parent) produce only 50% viable B_1 offspring (Shaw and Wilkinson 1980). This F_2 and B_1 hybrid breakdown is explained by (1) the disruption of gene complexes through abnormal chiasma positioning in the F_1 individuals and (2) resulting inviable admixtures of the genetic backgrounds from the two subspecies (Coates and Shaw 1982, 1984, Shaw et al. 1982). This degree of hybrid unfitness could also lead to the prediction of little if any long-term genetic/evolutionary effects (Mayr 1963).

Though the changeover in chromosome marker frequency across *Caledia* hybrid zones is rapid, it has been shown that zone width is actually greater than expected (Barton 1981). There are two apparent explanations for a wider than expected zone: (1) selection does not disfavor all hybrid genotypes or (2) the dispersal distances used to predict zone width were underestimates. More recent studies within the *Caledia* hybrid zones have supported earlier estimates of limited dispersal distances (Kohlmann, 1996). It therefore seems more probable that selection against hybrid genotypes is not uniform across all genotypes. Shaw et al. (1983) have detected certain recombinant types at increased frequencies both in the hybrid zone and in laboratory crosses. This would be expected if certain hybrid genotypes were under positive selection. Indeed, Shaw et al. (1980) argued that positive selection was one cause of introgression across hybrid zones between the Moreton and Torresian forms. The experimental crossing results indicate that positive selection would be favoring some of the B_1 genotypes.

Another demonstration of the evolutionary effectiveness of those rare, viable hybrid individuals produced in crosses between Moreton and Torresian grasshoppers is reflected in the pattern of genetic variation in contemporary populations far from the present-day region of overlap. Shaw et al. (1990) summarized the findings from studies of chromosome, allozyme, mtDNA, rDNA, and highly repeated DNA variation across a hybrid zone. Moreton allozyme, rDNA, and mtDNA markers are found at low frequencies 10 to >16 km from the present-day contact zone (Fig. 1; Shaw et al. 1990). In contrast to this limited introgression near the zone of contact, an 800-km transect extending north from the present-day hybrid zone discovered much higher frequencies of Moreton mtDNA and rDNA markers. Thus, the Moreton mitochondrial markers are fixed in Torresian populations 200 km north of the present-day hybrid zone (Fig. 2; Marchant 1988), and the Moreton rDNA is found in very high frequencies up to 400 km north of this zone (Figs. 1 and 3; Marchant et al. 1988). As with numerous other examples of cytoplasmic introgression (e.g., Ferris et al. 1983, Powell 1983, Spolsky and Uzzell 1984, Solignac and Monnerot 1986, Harrison et al. 1987, Tegelström 1987) the mtDNA findings for *Caledia* can be ascribed to chance fixation due to the smaller effective population size of this genome (Avise et al. 1984; but see Aubert and Solignac 1990). As discussed above, an additional factor might be positive selection.

The presence of Moreton rDNA (and mtDNA) in Torresian populations that are distant from the present-day hybrid zone are most likely the consequence of ancient gene exchange between these taxa (Marchant et al. 1988). The observation that the Moreton cytoplasmic and nuclear genes have not only remained in
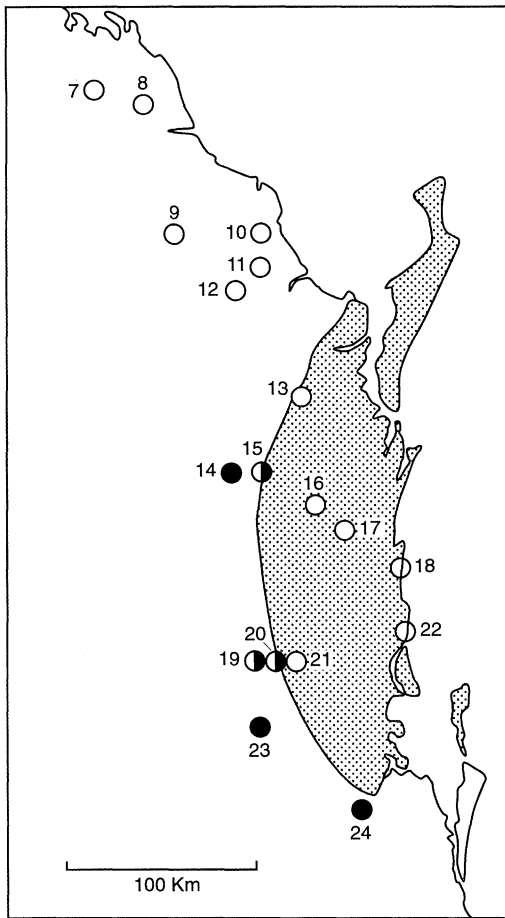
FIG. 2. Frequency of the Moreton (open portion of circles) and Torresian (filled portion of circles) mtDNA variants in populations of *Caledia captiva* in eastern Australia. The line associated with populations 13–24 indicates the hybrid zone between these two taxa. The shaded portion of the map indicates the distribution of chromosomally Moreton individuals (from Marchant 1988).

Helianthus annuus and H. petiolaris

Arnold and Hodges (1995) used the case of natural hybridization between the annual sunflower species, *Helianthus annuus* and *H. petiolaris* as an example of strong selection against early hybrid generations, and important evolutionary consequences. Experimental crosses between these two species result in F_1 individuals with pollen fertilities of 0–30% (mean ~14%; Heiser 1947). Furthermore, crosses involving F_2 and first backcross generation individuals result in a maximum of 1% and 2% viable seed, respectively (Heiser et al. 1969). There is thus strong selection against hybrids at the F_1 generation and in subsequent generations.

Despite low fertility and viability in the initial generations, natural hybridization between *H. annuus* and *H. petiolaris* is ongoing and has resulted in numerous, widespread, contemporary hybrid populations (Heiser et al. 1969, Rieseberg 1991). In addition, the phylogenetic history of *Helianthus* reflects the hybrid origin of numerous species and races. Fig. 4 illustrates this pattern of reticulate evolution and indicates that at least three (and possibly five) species and one subspecies have arisen from natural hybridization (Rieseberg 1991). The semi-sterile and semi-viable F_1, F_2, and B_1 generations have apparently been the foundation for

the Torresian populations, but increased in frequency is suggestive of the deterministic effects of positive selection. A similar conclusion has been reached from an examination of fossil and extant species of the snail genus *Cerion* found on the island of Great Inagua (Goodfriend and Gould 1996). In one case, the existing population is derived from hybridization between a fossil species that went extinct ~13 000 years ago and an extant species found in areas near the hybrid population. In another instance of hybridization, a hybrid transition also endured for thousands of years after one of the parents went extinct (Goodfriend and Gould 1996). These authors concluded that long-term persistence of hybrids, after the loss of one of the parental forms, is not expected ". . . unless the mixed population evolves selected developmental and genetic uniqueness of its own, thus permitting the production of stable novelty by hybridization" (Goodfriend and Gould 1996).
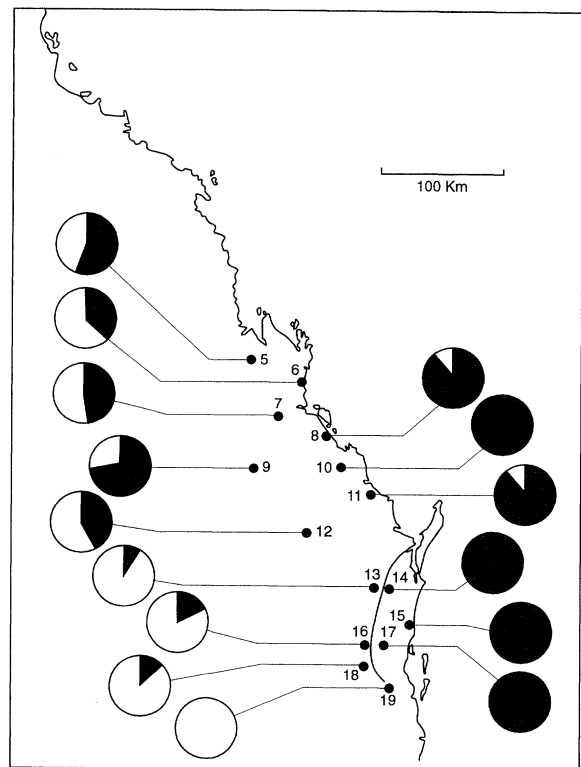

FIG. 3. Frequency of the Moreton (filled portion of circles) and Torresian (open portion of circles) rDNA variants in populations of *Caledia captiva* in eastern Australia. The line associated with populations 13–19 indicates the hybrid zone between these two taxa (from Marchant et al. 1988).
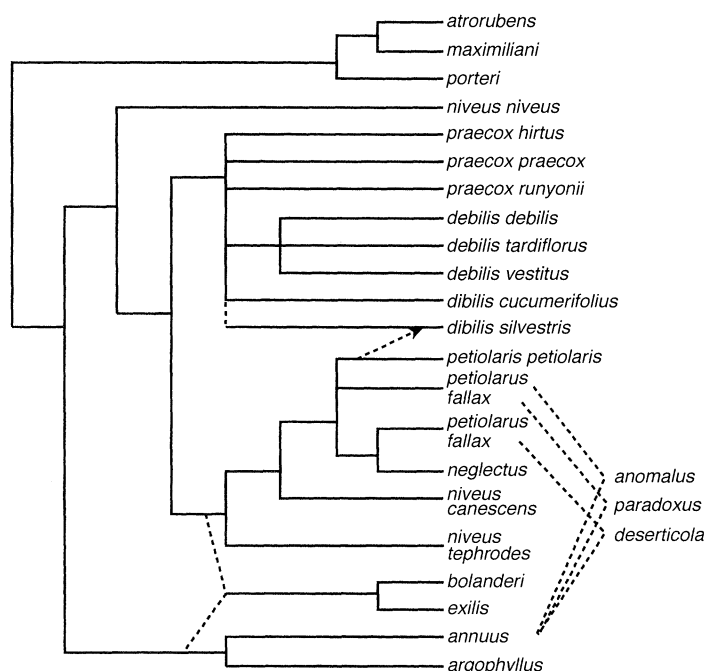
FIG. 4. Phylogeny for *Helianthus* (sect. *Helianthus*) species based upon rDNA and cpDNA restriction site and length data. All internodes had bootstrap values ≥50%. Reticulate events are indicated by dashed lines (from Rieseberg 1991).

genetic and evolutionary diversification. This suggests that the earliest *Helianthus* hybrid generations have simultaneously been a bottleneck to the formation of further generations of hybrids and a bridge for the production of advanced hybrid generations that possess relatively fit genotypes.

Rieseberg et al. (1996) discovered evidence that certain *Helianthus* hybrid genotypes possessed increased fitness. The evidence comes from genomic mapping of independently derived experimental hybrid lineages and the comparison of their genotypic composition with naturally occurring hybrid species. Experimental hybrid (i.e., backcross) progeny possessed little recombined genetic information (~2.4%) from regions in which *H. annuus* and *H. petiolaris* demonstrated chromosomal structural changes. However, 40% of the genome from collinear linkage groups introgressed (Rieseberg et al. 1995). The absence of recombination in the remaining 60% of collinear genomic regions was attributed to selection against certain hybrid genotypes (Rieseberg et al. 1995). This conclusion is supported by the high levels of similarity between the genotypes of a natural hybrid species, *H. anomalus,* and the three experimental hybrid lineages (Rieseberg et al. 1996). However, there was also evidence of positive selection for certain hybrid genotypes. This evidence came from the observation that similar genotypes were reconstructed independently from each of the three experimental hybrid lineages and in the naturally occurring hybrid species. This led Rieseberg et al. (1996) to conclude that "... a small percentage of alien genes do appear to interact favorably in hybrids."

Pinus contorta and P. banksiana

Natural hybridization between the pine species *P. contorta* (lodgepole pine) and *P. banksiana* (jack pine) has been documented by Critchfield and others (e.g., Critchfield 1980, 1984, 1985, Wagner et al. 1987, Wheeler and Guries 1987). Examinations of fossil and contemporary populations using morphological, biochemical, and molecular markers have indicated that both contemporary and ancient hybridization have affected the distribution of genetic variation and possibly the ecological and taxonomic diversity within these species (Critchfield 1984).

Hybridization between lodgepole pine and jack pine results in relatively unfit individuals in the earliest generations. Thus, Critchfield (1984) has related the narrowness of the zone of present-day hybridization to the fact that crosses between these species result in "... a high incidence of reproductive breakdown ..." and hybrids that demonstrate "... a moderately high percentage of aborted pollen." Crosses to form the F_1 generation are unsuccessful 69% of the time relative to control crosses (Critchfield 1980). In addition, F_1 individuals possess 0–50% aborted pollen and F_2 and F_3 individuals demonstrate 0–42% pollen abortion (Critchfield 1980). Although the strength of the barrier that impedes the formation of initial hybrid generations is consistent with the relative narrowness of contemporary hybrid zones, it is not predictive of the distribution of genetic and morphological variation seen in these two species. For example, introgression from jack pine into lodgepole pine is limited near the hybrid zone.

There are, however, lodgepole pine populations separated from the present-day hybrid zone by long distances that contain introgressed genes from jack pine (Critchfield 1984). These latter populations are hypothesized to have resulted from ancient contact and hybridization. Critchfield (1985) thus concluded that introgression from jack pine into lodgepole pine is ". . . the result of genetic contacts long before the last glacial period."

GENOTYPIC DIVERSITY AND HYBRID FITNESS

One outcome of the modern synthesis was an emphasis on the concept of reproductive isolation as the basis for evolutionary diversification (Dobzhansky 1937, Mayr 1942). Following from this was the viewpoint that natural hybridization and gene exchange was bad (especially between recognized species) because it represented a violation of "species boundaries" that maintained the "integrity of species." Furthermore, it was assumed that recombination between differently co-adapted genomes gave rise to uniformly unfit arrays of genotypes (e.g., Mayr 1963, Wagner 1970).

The assumption of consistent hybrid unfitness, regardless of genotype or environment, has been adopted into the hybridization and speciation literature. In particular, this assumption lies at the base of the most widely applied model that predicts the evolution of hybrid zones. This model has been alternately referred to as the Tension Zone or Dynamic-Equilibrium model (Key 1968, Barton and Hewitt 1985). The Tension Zone model assumes that the stability of hybrid zones reflects a balance between selection against hybrid individuals (independent of environment) and continual dispersal of parental genotypes into the zone of overlap (Barton and Hewitt 1985). A more recent model also incorporates the view that hybrids are less fit than parents in all environments, but the distribution of the parental genotypes into a "mosaic" pattern in nature is assumed to reflect habitat selection that favors one parent over the other in different niches (i.e., Mosaic model; Howard 1982, 1986, Harrison 1986). Alternative models have been produced that assume environment-dependent selection with parents *and* hybrids selected for or against depending on habitat (e.g., May et al. 1975, Endler 1973, 1977, Moore 1977). These latter models, however, are rarely used as a basis for predicting the evolutionary consequences of hybridization (Arnold 1997).

Moore and Price (1993) have highlighted the difficulty in testing the alternate predictions of the environment-dependent and environment-independent models. The difficulty (impossibility?) is due to the fact that even if it is possible to test for the magnitude of selection by examining zone width, etc. (Barton and Hewitt 1985), it is problematic to use these estimates to discern the form of selection (Moore and Price 1993, Emms and Arnold 1997). Thus, is the selection detected uniformly disfavoring hybrid genotypes or does it vary

TABLE 1. Fitness of 1987 cohorts of Darwin's Finches (over four years). The "Product" reflects the multiplication of recruitment, survivorship, and breeding success of individuals for each of the species and hybrid classes (Grant and Grant 1992).

Class	Product (recruitment/survival/breeding)
G. fuliginosa	0.300
G. fortis	0.844
G. scandens	0.780
G. fortis × *G. fuliginosa*	1.330
G. fortis × *G. scandens*	2.868
G. fortis × (*G. fortis* × *G. fuliginosa*)	1.669
G. fortis × (*G. fortis* × *G. scandens*)	1.148

depending on habitat? However, one way to rigorously test the models is to test their underlying assumptions concerning hybrid fitness (Arnold and Hodges 1995).

Individual organisms with different genotypes demonstrating varying fitnesses depending on environment is a fundamental concept of evolutionary theory (e.g., Lewontin 1974). However, this truism is not usually extended to cases where natural hybridization has occurred (see Arnold 1997 for a discussion). In this section we will discuss a number of studies that support the hypothesis that hybrid individuals can possess higher, equivalent, or lower fitness relative to their parents due to genotype × environment interactions.

Geospiza

For over two decades Peter and Rosemary Grant have examined the ecology and evolution of Darwin's finch species inhabiting the Galapagos islands (Grant et al. 1975, 1976). Most recently these authors have witnessed a change in the fitness of hybrid offspring between *Geospiza fuliginosa, G. fortis,* and *G. scandens* following a major transition in habitat (Grant and Grant 1992, 1993, 1994, 1996, 1997). The transition in habitat and change in the relative fitness of parental and hybrid individuals were attributable to an El Niño event. Before the El Niño, hybrid individuals were extremely rare and did not reproduce (Grant and Grant 1993). After this event, F_1 (*G. fortis* × *G. fuliginosa* and *G. fortis* × *G. scandens*) and backcross individuals (*G. fortis* × *fortis/fuliginosa* F_1 hybrids and *G. fortis* × *fortis/scandens* F_1 hybrids) demonstrated equivalent or higher fitness than their parental species (Table 1). These fitness estimates included measurements of survival, recruitment, and breeding (Grant and Grant 1992).

The change in the fitness of hybrids before and after the climatic perturbation was correlated with a change in the types of seeds available for food (Grant and Grant 1996). Hybrid individuals possessed novel beak morphologies that facilitated more efficient use of the new array of seeds, resulting in higher levels of reproduction (Grant and Grant 1996). Hybridization thus enhanced genetic variation (Grant and Grant 1994), giv-

ing rise to (hybrid) genotypes that were more fit in a novel habitat. The *Geospiza* studies support the hypothesis that certain hybrid genotypes can be more fit than parental genotypes in novel environments (e.g., Anderson and Stebbins 1954, Lewontin and Birch 1966).

Gambusia

A genetic and ecological survey of the genus *Gambusia* led to the conclusion that two forms previously identified as subspecies were instead genetically, ecologically, and morphologically well-differentiated species (Wooten et al. 1988). These two species of mosquitofish, *Gambusia affinis* and *G. holbrooki,* were subsequently used to test the effect of differences in life histories (e.g., population size, patterns of recruitment) on the population genetic structure and evolution of experimental and natural hybrid populations (Smith et al. 1989, Scribner 1993, Scribner and Avise 1993, 1994*a, b*). Scribner (1993) used laboratory crosses to define life history traits that were specific for these two species of mosquitofish and then examined the effect of these differences on the dynamics of experimental populations. He found that *G. holbrooki* offspring and F_1 progeny from crosses with *G. holbrooki* as the female parent were (1) larger at birth and at the end of development, (2) grew faster, and (3) obtained sexual maturity at younger ages than either *G. affinis* or those F_1 progeny with *G. affinis* mothers.

In regard to the present discussion, Scribner's (1993) results suggest that hybrids from *G. holbrooki* maternal lineages would be as fit as their maternal parent species and more fit than their paternal parent (i.e., *G. affinis*). This fitness hierarchy could result in the rapid displacement, via hybridization, of *G. affinis* by *G. holbrooki.* This would be due to the life history traits described above that lead to faster growth and higher carrying capacity of *G. holbrooki* populations (Scribner 1993). Indeed, Scribner (1993) and Scribner and Avise (1993, 1994*a, b*) have documented directional selection that favors *G. holbrooki* over *G. affinis,* resulting in the genetic swamping of the latter species by the former. Some patterns of genetic variation in natural populations are consistent with the predictions from these experiments while others are not (Scribner and Avise 1993). However, these experiments do indicate that the fitness of hybrid individuals can be as high or higher than both of their parents (Scribner 1993).

Artemisia

Various fitness components have been measured for two subspecies of Big Sagebrush (i.e., Basin Big Sagebrush, *A. tridentata* ssp. *tridentata* and Mountain Big Sagebrush, *A. t.* ssp. *vaseyana*) and various hybrid classes (Freeman et al. 1995, Graham et al. 1995, Wang et al. 1997). Studies of developmental stability, herbivore damage, flowering, seed production, germination frequencies, and survivorship of parental and hybrid plants have generated fitness estimates for a large portion of their life history. These experiments detected higher, equivalent, or lower fitness for hybrid and parental individuals depending on the environment. The hybrid classes included both experimentally produced F_1 hybrids and natural hybrid individuals (Freeman et al. 1995, Graham et al. 1995, Wang et al. 1997).

Measures of fluctuating asymmetry have been used by numerous authors to infer the relative fitness of animal hybrids and their parents (e.g., Ross and Robertson 1990). The underlying assumption is that departures from bilateral symmetry are indicative of developmental instability and thus lowered fitness. A similar technique for measuring stability has also been developed for plants (Graham 1992). This technique was used to estimate the fitness of hybrid and parental genotypes of sagebrush (Freeman et al. 1995). The hybrids were not found to be developmentally less stable relative to the two parental subspecies. Instead, significantly higher estimates of instability were actually associated with Mountain Big Sagebrush (Freeman et al. 1995). Similarly, studies of herbivore damage, seed production, and germination frequencies, demonstrated that hybrids were equivalent to the subspecies with the highest estimated fitness (Graham et al. 1995).

Most recently D. C. Freeman and his colleagues reported results from a reciprocal transplant experiment in an area of overlap (Wang et al. 1997). Habitat characteristics, germination frequencies, seedling growth, and fecundity were examined during this study. Seeds were collected from the parental subspecies and from three hybrid classes. *A. t.* ssp. *tridentata* and *A. t.* ssp. *vaseyana* occur at low and high altitudes, respectively. Parental and hybrid seeds were collected from open pollinated plants within (hybrid seeds) or on either side (parental seeds) of the hybrid zone. These seeds were then transplanted into both of the parental and one of the hybrid habitats. Wang et al. (1997) found that individuals of the two subspecies did significantly better in their own habitat relative to either hybrid individuals or the other subspecies (Fig. 5). In contrast, the hybrid class demonstrated significantly greater fitness in the hybrid zone region relative to the two parents.

Iris

Cruzan and Arnold (1993) examined nuclear and cytoplasmic markers to determine the genetic structure and to assess possible genotype-environment associations in a hybrid zone between the Louisiana iris species *Iris fulva* and *I. brevicaulis.* These data were used to test whether different hybrid genotypes were associated with non-parental habitats. Such a finding would be consistent with the hypothesis that certain hybrid genotypes are adapted to novel environments (Anderson 1948). In this analysis, habitat associations were defined for four genotypic classes ("*I. brevicaulis,*" "*I. brevicaulis*-like," "*I. fulva,*" "*I. fulva*-like"). Each of the classes occurred throughout the hybrid zone
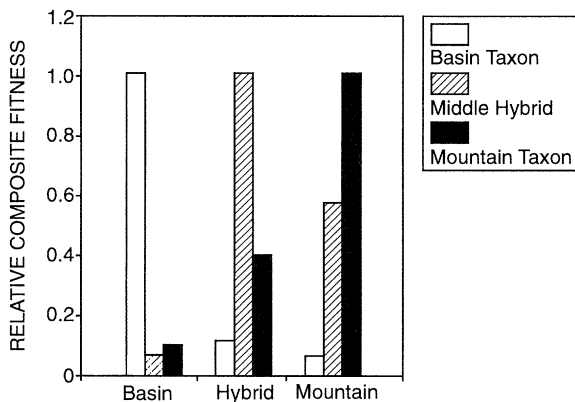
FIG. 5. The relative fitness of *Artemisia tridentata* ssp. *tridentata* ("Basin"), *A. tridentata* ssp. *vaseyana* ("Mountain"), and hybrid individuals in the Basin, Mountain, and Hybrid habitats (indicated on *x*-axis; from Wang et al. 1997).

at any site. These findings suggest that F_1 and F_2 hybrids possess equivalent or higher fitness than their parents in the parental and hybrid habitats. If this is true, natural hybridization between these species could lead to the replacement of parental forms by hybrid individuals. This prediction is consistent with the extensive introgression observed in southern Louisiana.

CONCLUSIONS

Natural hybridization may affect changes in the genetic diversity, population dynamics, and interactions between the hybridizing forms and other species. Furthermore, natural hybridization may have a significant effect on the genetic structure of rare taxa when they come into contact with a more numerous relative. Negative consequences (i.e., with regard to preservation of the rare form) from such contact include outcrossing depression or genetic assimilation (Ellstrand and Elam
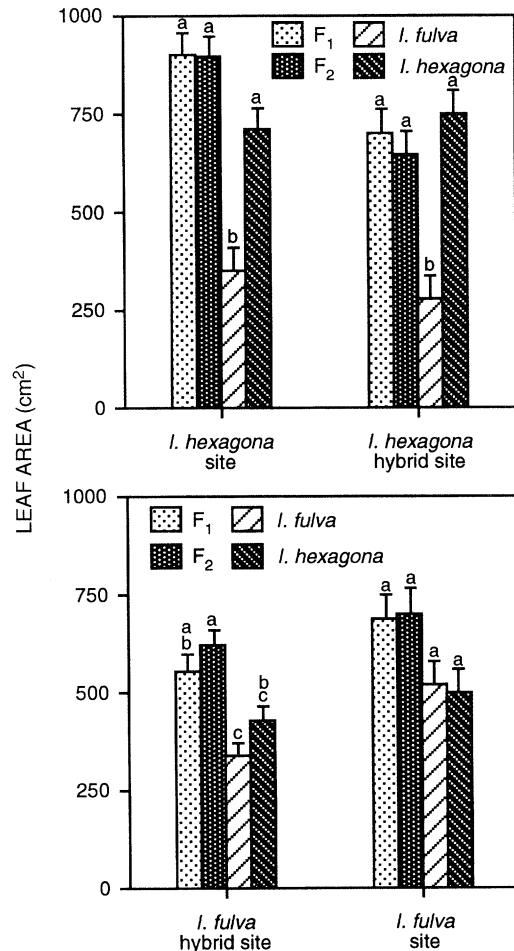
(Cruzan and Arnold 1993). However, the *I. brevicaulis, I. fulva,* and *I. fulva*-like genotypic classes were shown to occur in different environments. *I. brevicaulis*-like individuals occurred in habitats that were very similar to those containing *I. brevicaulis* plants (Cruzan and Arnold 1993). The *I. fulva*-like hybrid type occurs in a novel habitat relative to all of the other genotypes. This is consistent with the hypothesis that the *I. fulva*-like individuals are the most fit of the four genotypes in this novel habitat (Cruzan and Arnold 1993).

Emms and Arnold (1997) used a reciprocal transplant experiment to estimate the relative fitness of hybrid and parental classes of Louisiana irises in both hybrid and parental habitats. *I. fulva, I. hexagona,* and experimental F_1 and F_2 hybrids were transplanted into four natural populations in southeastern Louisiana. These populations had previously been assayed for species-specific nuclear and cytoplasmic markers (Arnold et al. 1991, Arnold and Bennett 1993). The four populations were defined by the presence of (1) *I. fulva* plants, (2) *I. fulva*-like plants with low frequencies of *I. hexagona* markers, (3) *I. hexagona*-like plants with low frequencies of *I. fulva* markers, or (4) *I. hexagona* plants. The four sites also differed significantly for a range of biotic and abiotic characters (Emms and Arnold 1997).

There were no significant differences in survivorship among the four classes at any site. In contrast, measurements of leaf production indicated that both hybrid classes performed significantly better than *I. fulva* in all but the *I. fulva* site, and that F_2 plants performed significantly better than *I. hexagona* at the *I. fulva* hybrid site (Fig. 6; Emms and Arnold 1997). F_1 rhizomes gained as much, or significantly more, mass than either parent after one year of growth. Rhizome growth reflects a form of clonal (asexual) reproduction that is significant in the life history of these organisms. Further, there is a correlation between numbers of rhizomes and flowering (Bennett 1989). There were no significant differences between F_2 rhizomes and either parent

FIG. 6. Amount of leaf growth achieved by *Iris fulva* and *I. hexagona,* F_1, and F_2 plants in four natural sites. Standard errors are indicated by the vertical bars. Shared letters on bars within a site indicate no significant difference. Different letters between bars within a site indicate significant differences (from Emms and Arnold 1997).

1993, Levin et al. 1996). A second, more positive, perspective assumes that hybridization may result in a genetic enrichment of the endangered form. Under this scenario the rare form may benefit from hybridization through the addition of genetic variability that facilitates habitat expansion.

The examples discussed in this paper are inconsistent with the hypothesis that natural hybridization in plants and animals is evolutionarily unimportant. Introgression continues to be identified for an increasing number of plant and animal taxa. In most cases the initial hybrid generations demonstrate lower fertility and/or viability. Yet, the ongoing effects from such crosses can be seen in literally hundreds or even thousands of examples throughout the plant and animal kingdoms (Arnold 1997). These effects include the formation of hybrid taxa. Furthermore, fitness estimates for some hybrid genotypes are equal to or greater than those of their parents suggesting a significant role for natural hybridization in adaptive evolution (Arnold and Hodges 1995). The consequences of natural hybridization in different taxonomic groups varies but, overall, it has played a part in the evolution of a large percentage of contemporary and extinct organisms (Arnold 1997).

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SPECIAL FEATURE