
Modeling Factors Affecting the Severity of Outbreeding Depression

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Abstract: Hybridization between populations may cause either increased fitness (“hybrid vigor”) or decreased fitness (“outbreeding depression”). Translocation between populations may therefore in some cases be a successful means of combating genetic erosion and preserving evolutionary potential, whereas in other cases it may make the situation worse by inducing outbreeding depression. Because genetic distance alone is a poor predictor of the success or failure of hybridization, we developed a computer model (ELAB) to explore other factors affecting the consequences of hybridization. Our model simulates diploid, unisexual populations following Mendelian rules, and in this study we used it to test the effect of a variety of parameters on both the magnitude and duration of outbreeding depression. We focused our simulations on the effects of (1) divergence between populations, (2) the genetic basis of outbreeding depression (disruption of local adaptation vs. intrinsic coadaptation), (3) population parameters such as mutation rate and recombination rate, and (4) alternative management schemes (50:50 mixture vs. one migrant per generation). The magnitude of outbreeding depression increased linearly with genetic distance, whereas the duration of outbreeding depression showed a more complex curvilinear relationship. With genetic distance held constant, magnitude increased with larger population size, lower mutation rate, cross-fertilization, and higher recombination rate, whereas duration increased with larger population size and partial self-fertilization. Fitness problems caused by disruption of local adaptation were stronger but more transient than those caused by a disruption of intrinsic coadaptation. Finally, simulations showed that, depending on the genetic basis of outcrossing problems, recurrent transfer of only one migrant per generation into a population of 100 individuals could cause as much or more damage as a one-time 50:50 mixture.

Factores de Modelaje que Afectan la Severidad de la Depresión Exogámica

Resumen: La hibridación entre poblaciones puede causar mayor adaptabilidad (“vigor híbrido”) o menor adaptabilidad (depresión exogámica). Por lo tanto, en algunos casos la translocación entre poblaciones puede ser un medio exitoso para combatir la erosión genética y preservar el potencial evolutivo, mientras que en otros casos puede empeorar la situación al inducir la depresión exogámica. Debido a que la distancia genética por sí sola es un predictor pobre del éxito o del fracaso de la hibridación, desarrollamos un modelo de computadora (ELAB) para explorar otros factores que afectan las consecuencias de la hibridación. Nuestro modelo simula poblaciones unisexuales, diploides que siguen las reglas Mendelianas, y en este estudio lo utilizamos para probar el efecto de una variedad de parámetros sobre la magnitud y duración de la depresión exogámica. Enfocamos nuestras simulaciones sobre los efectos de (1) la divergencia entre poblaciones, (2) las bases genéticas de la depresión exogámica (disrupción de adaptación local vs. coadaptación intrínseca), (3) los parámetros poblacionales tales como tasas de mutación y de recombinación y (4) los esquemas alternativos de manejo (mezcla 50:50 comparado con un migrante por generación). La magnitud de la depresión exogámica aumentó linealmente con la distancia genética, mientras que la duración de la depresión exogámica mostró una relación curvilínea más compleja. Con la distancia genética constante, la magnitud incrementó a mayor tamaño poblacional, menor tasa de mutación, fecundación cruzada y mayor tasa de recombinación, mientras que la duración aumentó a mayor tamaño poblacional y fecundación

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cruzada parcial. Los problemas de adaptabilidad causados por la disrupción de la adaptación local fueron más pronunciados pero más efímeros que los provocados por la disrupción de la coadaptación intrínseca. Finalmente, las simulaciones mostraron que, dependiendo de las bases genéticas de los problemas de exogamia, la transferencia recurrente de solo un migrante por generación a una población de 100 individuos podría causar tanto o más daño como una mezcla única de 50:50.

Introduction

Human actions are increasing the frequency of hybridization between previously allopatric taxa. Accidental intercrosses occur, for example, when fish stray from hatcheries and mate with native populations (Quinn 1993; Lynch 1997) or when crop plants exchange genes with their wild relatives (Ellstrand et al. 1999). In other cases, gene flow between populations or species is an intentional consequence of management schemes such as corridors between reserves, translocation programs, or augmentation of wild populations with cultivated populations. Such strategies may be necessary to bolster dwindling population size, combat genetic erosion, and cure inbreeding depression (Hedrick 1995; Mills & Allendorf 1996; Land & Lacy 2000).

However, intermixing can cause a variety of problems. Migrants can introduce disease (Langdon 1990; Hess 1994), disrupt social behaviors (Bright & Morris 1994), outcompete natives, or breed with natives, sometimes resulting in reduced fitness in hybrids, a phenomenon known as outbreeding depression. Concern over the potential for outbreeding depression is increasing as the rate of anthropogenically induced hybridizations increases (Rhymer & Simberloff 1996; Storfer 1999; Johnson 2000; Allendorf et al. 2001). Predicting which crosses will be successful has proven difficult, prompting the belief that hybridization is a "hit or miss proposition" (Tave 1992).

One cause of the difficulty in predicting consequences of outbreeding is the conflicting gene interactions that can occur in hybrids (Templeton 1986; Lynch 1991; Turelli & Orr 2000). Hybridization can create beneficial gene interactions, including both overdominance (heterozygote advantage) and dominance (the masking of deleterious recessives). However, hybridization can simultaneously create detrimental gene interactions, including underdominance (heterozygote disadvantage), disruption of beneficial interactions between loci (intrinsic coadaptation or "coadapted gene complexes"), and disruption of beneficial interactions between genes and the environment (extrinsic or local adaptation). Hybridization can therefore create both within-locus (dominance) interactions, which are largely positive, and between-locus (epistatic) interactions, which are largely negative.

Another complicating factor is that the consequences of hybridization can change between generations (Endler 1977; Lynch 1991; Fenster & Galloway 2000a). In some cases, fitness reductions occur in first-generation (F_1) hybrids, where they can be attributed to disruptions in local adaptation, underdominance, or epistatic interactions. In many cases, however, fitness declines are delayed until the second (F_2) or later generations, in which recombination disrupts the original parental gene combinations and exposes incompatibilities involving recessive alleles. This may disrupt adaptation to specific environments (local adaptation) and internal gene interactions that are independent of the environment (intrinsic coadaptation).

One of the simplest potential indicators of the success or failure of hybridization is the distance (genetic or geographic) between parental populations or species (reviewed by Edmands 2002). The few groups that have been studied generally show a rough correspondence between parental divergence and reproductive compatibility. Some show optimal fitness at intermediate levels of divergence (Waser 1993; Trame et al. 1995), whereas many show optimal fitness at the lowest levels of divergence (Grosberg 1987; Coyne & Orr 1997; Sasa et al. 1998; Edmands 1999). These studies span a vast range of genetic and geographic distances, however, and they do not provide easy yardsticks by which to forecast safe divergence levels in other taxa. For example, mammals typically lose the capacity for hybridization after only 8 million years of divergence, whereas birds and frogs typically maintain compatibility for up to 55 or 60 million years (Prager & Wilson 1975; Zeh & Zeh 2000). Similar discrepancies occur even within closely related taxa. For example, some pairs of *Drosophila* species exhibit reduced F_1 viability or fertility as early as about 0.35 million years (assuming an allozyme divergence rate of $0.2D$ /million years, where D is genetic distance; Coyne & Orr 1989), whereas other *Drosophila* pairs up to 3–4.3 million years apart show F_2 fecundity heterosis (assuming a mtDNA divergence rate of 2%/million years; Rand 1994; Hercus & Hoffmann 1999; Kelemen & Moritz 1999).

By itself, divergence appears to be an unreliable predictor of the success or failure of hybridization. Further, we know little about what controls the duration of outbreeding depression. Although there are a few records of rapid recovery from hybrid breakdown (Templeton

1986; Rieseberg et al. 1996), the majority of studies that have systematically measured hybrid fitness have stopped at the F_1 generation, with a few extending to the F_2 or F_3 generations (Moll et al. 1965; Burton 1990; Edmands 1999; Fenster & Galloway 2000b). Beyond this, hybrid fitness might continue to decline as recombination further disrupts tight linkages, or it might increase and possibly surpass parental fitness as selection promotes beneficial gene combinations. To explore factors that may be important in determining both the magnitude and duration of outbreeding depression, we conducted computer simulations of the fitness consequences of combining differentiated populations.

A number of researchers have simulated hybridization and its consequences. For example, Emlen (1991) predicted future fitness of a hybrid population based on the distance between parental populations (defined as the drop in fitness experienced by one stock reared at the site to which the other is locally adapted). This model mimics disruption of local adaptation driven by a series of epistatically interacting loci, and Emlen applies the model to a number of scenarios involving coho salmon (*Oncorhynchus gorbuscha*). McKenna (2000) took a different approach to simulating fish-stocking scenarios, creating a logistic-competition model in which pure stocks and hybrid stocks have different fitness levels. Huxel (1999) used a single-locus, two-allele model to look at how displacement of one species by another is affected by immigration rate, selection differential, extent of interbreeding, and degree of dominance. Wolf et al. (2001) also modeled extinction through hybridization, with individuals assigned to three classes based on parentage. They used realistic values based on naturally hybridizing plant taxa and focused on parameters such as selfing rate, population size, and hybrid fitness. Our model takes a different approach to assessing some of these same risk factors, as well as others (e.g., mutation rate, recombination rate), with individual fitness determined by an explicitly genetic, multilocus method that can mimic alternative causes of outbreeding depression (disruption of intrinsic coadaptation vs. local adaptation). Using conditions that result in outbreeding depression as a starting point, we assessed the qualitative effects of altering one parameter at a time.

The Model

We modeled hybridizations using ELAB (Evolutionary Laboratory), a highly flexible simulation program available from the authors upon request. In our simulations, each virtual organism had a genome made up of 10 pairs of interacting loci. For baseline simulations there was a single pair of chromosomes, and interacting loci were immediate neighbors. Therefore, all 20 loci were physically linked. Each pair of interacting loci had a fitness

value determined by its homozygous or heterozygous state (Fig. 1). To understand the fitness values, imagine a cross between an *AABB* population and an *aabb* population. The baseline fitness matrix (Fig. 1a) was de-

(a)

	bb	bB	BB
aa	0.220	0.195	0.190
aA	0.195	0.240	0.195
AA	0.190	0.195	0.220

(b)

	bb	bB	BB
aa	0.229	0.195	0.178
aA	0.195	0.230	0.195
AA	0.178	0.195	0.229

(c)

	bb	bB	BB
aa	0.210	0.195	0.190
aA	0.195	0.250	0.195
AA	0.190	0.195	0.210

(d)

	bb	bB	BB
aa	0.280	0.260	0.240
aA	0.260	0.240	0.220
AA	0.240	0.220	0.200

(e)

	bb	bB	BB
aa	0.200	0.220	0.240
aA	0.220	0.240	0.260
AA	0.240	0.260	0.280

Figure 1. Fitness matrices used in simulated hybridizations. For simulations of intrinsic coadaptation (a-c), the same matrix was used regardless of environment. Baseline simulations used matrix (a). Matrix (b) was used to simulate stronger deleterious epistasis, and matrix (c) was used to simulate stronger beneficial dominance. For simulations of local adaptation (d & e), in the first environment all 10 two-locus pairs utilized matrix (d), whereas in the second environment, one two-locus pair utilized matrix (e) and the remaining nine pairs utilized matrix (d).

signed to mimic intrinsic coadaptation in which fitness does not change between environments. Here, the most-fit genotype was the double heterozygote (*AaBb*), and the least-fit genotypes were homozygous for one parental type at one locus and the other parental type at the other locus (*AAbb* or *aaBB*). This fitness function is based on situations such as those in the copepod *Tigriopus californicus*, for which dominance interactions are beneficial and epistatic interactions are detrimental (Edmands 1999).

In addition to the baseline fitness function, we also modeled intrinsic coadaptation by using a fitness matrix in which the ratio of epistatic variance to dominance variance was doubled (Fig. 1b). Here the deleterious effects of epistasis are stronger and the beneficial effects of dominance are weaker. Conversely, we tested the effects of stronger beneficial dominance by using a fitness function in which this same ratio was halved (Fig. 1c). To mimic local adaptation, we used different fitness matrices (Figs. 1d & 1e) in different environments. For populations in the first environment, all loci evolved according to the same fitness matrix (Fig. 1d). Meanwhile, in the second environment one of the two-locus pairs evolved according to a matrix (Fig. 1e) in which fitness values were reversed so that the best genotype in the first environment (*aabb*) was the worst genotype in the second environment (and vice versa). All variance here was additive, and the maximum total genetic variance was the same as in the baseline intrinsic coadaptation example (Fig. 1a).

Using the baseline settings (Table 1), a simulation would proceed as follows. The ancestral population starts with 100 individuals with genotype *aabb* for each of the 10 pairs of loci. Both individuals and gametes are unisexual, and self-fertilization is allowed. Each individual produces a number of gametes equal to the sum of its two-locus fitness values (Fig. 1a). Noninteger values are treated in a probabilistic fashion. That is, an individual with a fitness value of 1.71 produces one gamete, with a 71% chance of producing a second gamete. Gamete production involves a mutation rate (from *A* to *a* or *B* to *b* and vice versa) of 0.001 per locus and a recombination rate of 0.05 between each pair of neighboring loci. Gametes are paired randomly to produce zygotes. If fewer than 100 zygotes are formed, all survive to reproduce. If more than 100 zygotes are formed, 100 are selected randomly. After 2000 generations, the ancestral population is split into two populations, and the maximum size of each population is maintained at 100. These two populations evolve independently. The genetic distance (*D*; Nei 1975) between the populations is assessed for each generation. The first time distance falls between a given *D* and *D* + 0.01, the two populations are merged. Fitness of the combined population is then assessed for each generation. This procedure is repeated 1000 times, and the average fitness of the combined

Table 1. Baseline settings for hybridization simulations.

Parameter	Baseline
Number of chromosomes	$2n = 2$
Number of loci	20
Number of alleles per locus	2 (<i>a/A</i> or <i>b/B</i>)
Maximum population size	100
Recombination rate (per locus per generation)	0.05
Mutation rate (per locus per generation)	0.001
Mating	random
Viability	random
Fitness	fecundity determined by intrinsic coadaptation matrix (Fig. 1a)
Hybridization event	50% population 1/50% population 2

population is calculated for each generation. To find the magnitude and duration of any outbreeding depression that occurs, the fitness of the combined population is compared with the average of the two parental populations immediately before the populations were combined (F_0). The magnitude is defined as the fitness difference between F_0 and the lowest point in the combined population. Duration is defined as the number of generations between F_0 and the return to F_0 fitness.

Results and Discussion

Effects of Genetic Distance

Using our baseline settings (Table 1), we assessed the magnitude and duration of outbreeding depression at genetic distances ranging from 0.05 to 0.6 (Fig. 2). Magnitude was roughly constant from 0.05 to 0.10 and then increased linearly from 0.1 to 0.6. Duration had a more complex curvilinear increase because distance affected the starting (F_0) fitness by constraining the distribution of genotypes, and this small effect was amplified during the gradual recovery. Below a genetic distance of 0.05, results were highly variable because there were no "adaptive peaks" separated by distances this small with our base fitness function. Above a genetic distance of 0.6, most simulations did not recover within 3000 generations. Mean fitness for each generation (Fig. 3) showed that increasing interpopulation distances amplified both the initial increase in fitness (a result of the benefits of heterozygosity) and the maximum decline in fitness (a result of the detriments of epistasis).

We chose 0.15 as our baseline distance because it produced clear outbreeding depression and because recovery occurred within a manageable amount of computer time, allowing all subsequent hybridizations to be run for just 1000 generations. This genetic distance is at the border between typical interpopulation and interspe-

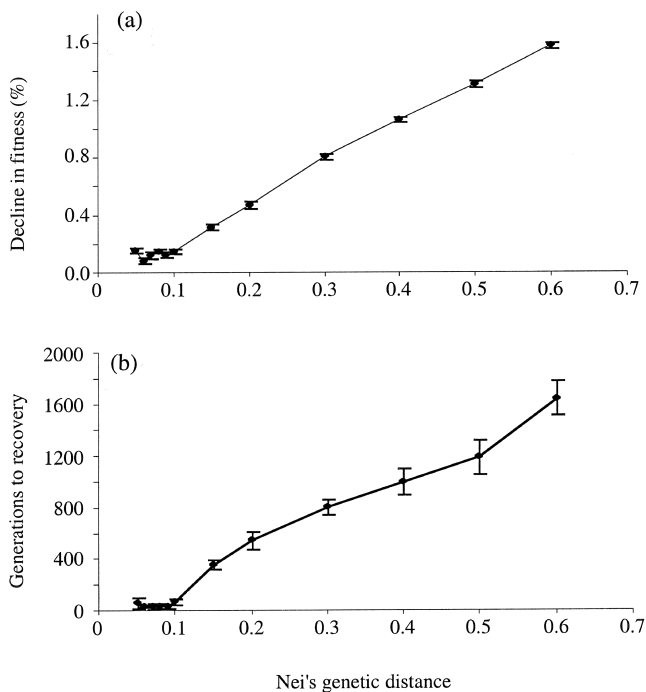


Figure 2. Effect of genetic distance (Nei 1975) on the (a) magnitude and (b) duration of outbreeding depression. Magnitude and duration were calculated from generation averages for 100 replications. This was repeated 10 times to determine mean and standard error.

cific divergence levels (Thorpe & Solé-Cava 1994), although distances between our simplified, virtual populations may not be comparable to real populations. Because distances in our model were based only on loci under selection, they likely exceed distances found in typical data sets (see McKay and Latta [2002] for a review of molecular vs. adaptive divergence). On average, isolated populations took 707.7 generations to reach a genetic distance of 0.15. After mixing, the hybrid population (Fig. 4) showed a brief increase in fitness, followed by a rapid decline and a slow recovery. In this baseline example the magnitude of outbreeding depression was 0.26% and the duration was 375 generations. Like most of the simulations in our study, fitness in this baseline hybridization eventually rose above the F_0 . This is because restricting genetic distance to a specific value constrained diverging populations to evolve to suboptimal fitness peaks.

Effect of the Fitness Function

The consequences of hybridization were entirely dependent on the fitness function. We tested the effect of stronger intrinsic coadaptation by using a fitness matrix (Fig. 1b) in which the ratio of epistatic variance to dom-

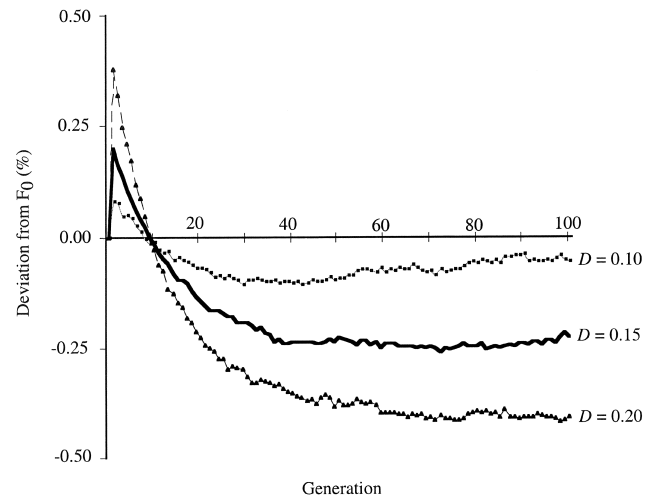


Figure 3. Fitness over time in a mixed population relative to the mean of the parents (F_0), averaged for each generation over 1000 replications. Shown are the first 100 generations after hybridization between populations at Nei's (1975) genetic distances (D) of 0.10, 0.15, and 0.20.

inance variance was doubled. This made the deleterious effects of breaking up coadaptation stronger and the beneficial effects of increasing heterozygosity weaker. This change slowed the rate of population divergence and increased the magnitude of outbreeding depression (Table 2; Fig. 4a). Less predictably, it slightly decreased the duration, apparently because selection is more efficient when hybridity is unambiguously deleterious. To test the effects of stronger beneficial dominance, we used a fitness matrix (Fig. 1c) in which the ratio of epistatic variance to dominance variance was cut in half. This resulted in more-rapid population divergence and no outbreeding depression whatsoever (Table 2; Fig. 4a).

The fitness matrices in Fig. 1d and 1e were used to mimic local or extrinsic adaptation, an alternative mechanism for outbreeding depression. These two matrices were reversed so that that the best genotype in Fig. 1d would be the worst genotype in Fig. 1e. All variance here was additive, and the maximum total genetic variance was the same as in the earlier example of intrinsic coadaptation. For these simulations the initial population evolved according to the fitness matrix in Fig. 1d. After 2000 generations the population was split in two. One subpopulation continued to utilize fitness values in Fig. 1d, and one pair of loci in the other subpopulation utilized Fig. 1e. Once the subpopulations reached a genetic distance of 0.15, they were mixed back together and monitored for 1000 generations with fitness determined by Fig. 1d. Relative to the baseline intrinsic coadaptation simulations, disruption of this local adaptation caused a more rapid and larger decline in fitness because the e-adapted individuals were unfit in the d envi-

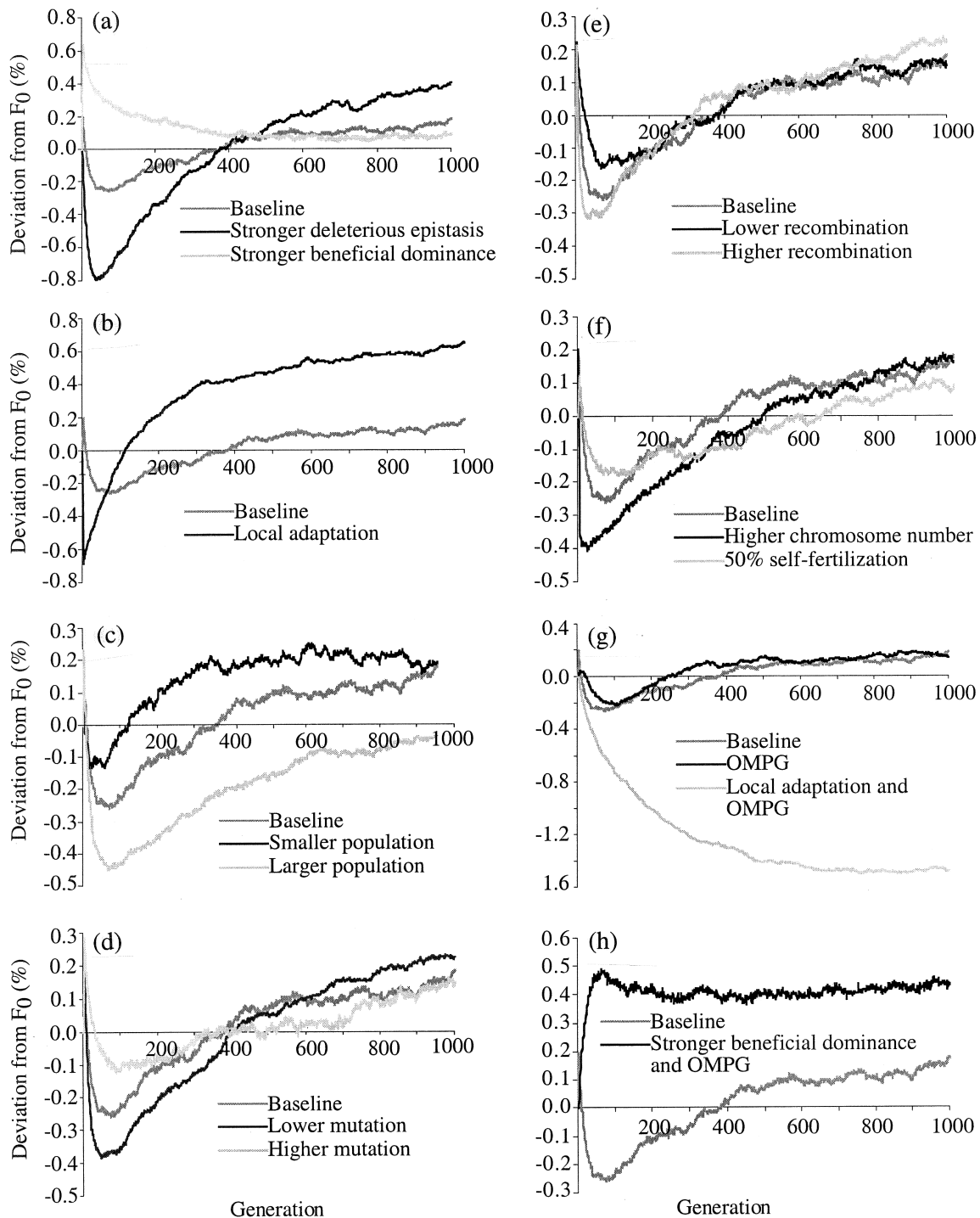


Figure 4. Fitness over time in a mixed population relative to the mean of the parents (F_0), averaged over 1000 replications. Baseline settings are shown in Table 1, and the genetic distance (Nei 1975) between populations is 0.15. Shown here are examples of the effects of (a–b) fitness function, (c) population size, (d) mutation rate, (e) recombination rate, (f) chromosome number and self-fertilization, and (g–h) management strategy. Abbreviation: OMPG, one migrant per generation.

Table 2. Effects of altering baseline settings in simulated hybridizations.*

<i>Parameter altered</i>	<i>Effect on divergence time (%)</i>	<i>Effect on magnitude of OBD (%)</i>	<i>Effect on duration of OBD (%)</i>
Fitness function			
stronger intrinsic coadaptation (Fig. 1b)	+206.4	+205.8	-2.7
stronger beneficial dominance (Fig. 1c)	-60.1	-100.0	-100.0
local adaptation (Fig. 1d and e)	+14.6	+165.9	-70.1
Population parameters			
larger population size (200)	+65.6	+69.6	+128.8
smaller population size (50)	-47.6	-49.0	-65.9
higher mutation rate (0.002)	-65.1	-51.3	-14.1
lower mutation rate (0.0005)	+238.5	+47.6	+4.8
higher recombination rate (0.10)	+1.7	+23.1	-3.5
lower recombination rate (0.025)	-5.9	-38.5	-1.1
higher chromosome number ($2n = 4$)	+8.5	+56.4	+30.4
50% self-fertilization	-17.0	-30.8	+52.8
Management scheme			
OMPG	na	-15.2	-36.3
local adaptation + OMPG	na	+478.0	(no recovery within 1000 generations)
stronger beneficial dominance + OMPG	na	-100.0	-100.0

*Abbreviations: OBD, outbreeding depression; na, not applicable; OMPG, one migrant per generation.

ronment (Table 2; Fig. 4b). We also saw a faster recovery, however, because selection could act more efficiently on purely additive variance.

What do these results imply for conservation? Local adaptation, which is driven by selection in differing habitats, might be expected to evolve more rapidly than intrinsic coadaptation, which is driven by genetic drift and indirect selection (Hendry et al. 2000; Waser & Williams 2001). It has therefore been suggested that local adaptation may be more important in a conservation context, where we are most often concerned about intraspecific hybridization (Allendorf et al. 2001). The relative effects of intrinsic and extrinsic mechanisms are difficult to assess because they can act simultaneously, and clean partitioning of these effects awaits careful studies of multiple cohorts in both parental environments (Rundle & Whitlock 2001). Nevertheless, outbreeding depression is commonly thought to stem from purely extrinsic mechanisms (Allendorf et al. 2001). Our simulations suggest that these disruptions of local adaptation will be more severe than disruptions of intrinsic coadaptation. If a population can survive the initial decline, however, recovery might be expected to be rapid.

Effects of Population Parameters

Doubling the population size slowed population divergence by reducing the effect of drift (Table 2; Fig. 4c). These larger populations suffered from a higher magnitude and duration of outbreeding depression because larger populations started at a higher fitness and had further to fall and further to recover. The absolute fitness of

these larger populations was always higher than the baseline or that of small populations, however, so hybridization might not be expected to endanger population persistence. Doubling the mutation rate (Table 2; Fig. 4d) sped divergence by reducing the efficiency of selection. Similarly, it decreased both magnitude and duration, apparently because reduced selection efficiency caused the parental populations to start with lower fitness. Doubling the recombination rate (Table 2; Fig. 4e) slightly increased divergence time and increased magnitude because recombination creates unfit genotypes. There was no clear effect on duration, however, apparently because recombination created both favorable and unfavorable gene combinations and therefore increased the efficiency of selection. Maximal recombination was modeled with two pairs of chromosomes, with interacting loci on separate chromosomes (Table 1; Fig. 4f). This change increased divergence time, magnitude, and duration. Finally, going from 100% random mating to 50% self fertilization/50% random mating (Table 2; Fig. 4f) slightly increased the rate of divergence by increasing drift. Because individuals outcrossed only half the time, outbreeding depression took longer to appear, the magnitude was smaller, and the duration longer.

Can any practical conclusions be gleaned from the effects of these parameters? The higher degree of outbreeding depression in large populations is of limited concern because relatively high absolute fitness was maintained even after hybridization. Indeed, translocations are typically proposed for small populations which, like our simulated small populations, are already suffering from low absolute fitness. As for the implica-

tions of mutation, knowledge of actual rates is limited to a few model species, but evidence is mounting for substantial variation among taxa in per-generation mutation rates (Lynch et al. 1999). If real organisms behaved as our simple model did, those with higher mutation rates such as fruitflies would suffer milder and briefer outbreeding depression than those with lower mutation rates such as plants and nematodes.

One of the most interesting patterns was the effect of recombination. The result of increased magnitude with higher recombination was consistent with empirical studies going back as far as Brncic's work on *Drosophila* (Brncic 1961). This is somewhat counterintuitive, however, because high recombination should prevent coadapted gene complexes from developing in the first place. Indeed, some of the strongest examples of hybrid inferiority come from animals with restricted recombination—*Drosophila* spp. (Templeton 1986) and the copepod *Tigriopus californicus* (Burton et al. 1981; Burton 1986; Edmands 1999). We might reconcile this finding with our results by noting that our baseline fitness function forced the evolution and maintenance of coadaptation even in the face of high recombination. Little is known about recombination rates in the majority of taxa facing conservation decisions, but we do know that recombination rates are subject to selection (Otto & Barton 2001), and we are beginning to learn about recombination distances between coadapted loci (Wu & Palopoli 1994; Rieseberg et al. 1996). Our results suggest that disruption of loosely linked complexes will cause the greatest damage.

Self-fertilization sped divergence, reduced magnitude, and increased duration. Notably, many plants vulnerable to outbreeding depression are at least partially self-fertile, including *Chamaecrista fasciculata* (Fenster & Galloway 2000a), *Ipomopsis aggregata* (Waser et al. 2000), *Lotus scoparius* (Montalvo & Ellstrand 2001), and *Delphinium nuttallianum* (Waser & Williams 2001). Our results suggest that—all other things being equal—the outbreeding depression observed in these selfers will be more persistent than similar problems found in purely outcrossing species.

Effect of Management Schemes

In our baseline simulations we mixed 50 individuals from one population with 50 individuals from a second population. A more likely management tactic may be to augment an ailing population with small doses from a healthy population. In fact, it is often suggested that managers should promote the movement of one migrant per local population per generation (OMPG) to maintain connectivity among isolated populations (Franklin 1980; Frankel & Soulé 1981; Allendorf 1983; Newman & Tallmon 2001). This strategy is based on Sewall Wright's classic work showing that OMPG is sufficient to main-

tain polymorphism and moderate cohesion between subpopulations (Wright 1931). Because the OMPG rule relies on ideal populations and a host of other simplifying assumptions, it has been suggested that between 1 and 10 migrants per generation may be a more widely applicable rule of thumb (Mills & Allendorf 1996). To simulate the OMPG strategy, we let populations of 100 individuals each diverge until they reached a distance of $D = 0.15$. We then introduced one individual from population 1 into population 2 at each generation and monitored fitness in population 2 while maintaining both populations at a maximum of 100 individuals.

With our baseline intrinsic coadaptation fitness function, introducing only one migrant per generation caused a decline in fitness that was nearly as severe and long-lasting as that caused by combining 50 individuals from each population (Table 2; Fig. 4g). Using our local adaptation fitness function, the OMPG strategy was considerably more damaging than the 50:50 mix, and no recovery was found after 1000 generations (Table 2; Fig. 4g). This is because selection cannot battle the constant influx of maladapted genes in these simulations. Conversely, using our beneficial dominance fitness function, the OMPG strategy produced a strong and long-lasting increase in fitness (Table 2; Fig. 4h). These results reiterate the surprising power of small doses of migration first pointed out by Wright. Just as one migrant per generation can save compatible populations from fragmentation and drift, the same low level of migration between partially incompatible populations can have surprisingly deleterious effects, particularly when the basis for incompatibility is disruption of local adaptation. The fitness consequences of migration depend on the interplay between migration rates, selection coefficients, and drift, as can be shown with single-locus population genetic theory (e.g., Hedrick 1995). Future work with this or other multilocus models might focus on determining optimal levels of gene flow over a broader range of population sizes and modes of selection.

The finding that OMPG had both beneficial and detrimental effects in our simulations underscores the need for more work on the fitness effects of inbreeding versus outbreeding. Although inbreeding depression is generally thought to be more widespread than outbreeding depression (e.g., Lacy et al. 1993), the data on relative effects are few. A study of captive callimico by Lacy et al. (1993) found inbreeding depression an order of magnitude higher than outbreeding depression when both effects were tested within the same model. Conversely, Marshall and Spalton (2000) studied simultaneous inbreeding and outbreeding depression in Arabian oryx and found the effects approximately equal, leading them to argue that outbreeding depression may be more common in vertebrates than previously supposed. It is clear that more work should be done on comparing the relative risks of inbreeding and outbreeding.

Conclusions

Results of this highly simplified model cannot be easily translated into reliable management prescriptions. Instead, they are meant as a first step in exploring factors that may increase the risk of outbreeding depression. Our results suggest that, in addition to genetic distance, a number of other factors may be important. In our simulated hybridizations between fairly divergent populations ($D = 0.15$), magnitude of outbreeding depression (OBD) was aggravated by larger population size, lower mutation rate, cross-fertilization, and higher recombination rate. Duration of OBD increased with larger population size and partial self-fertilization. In addition, OBD driven by disruption of local adaptation followed a very different trajectory than that driven by a disruption of intrinsic coadaptation, with local adaptation causing a sharper but more transient decline. This is notable, because the mechanisms underlying OBD are virtually unknown. Finally, our simulations suggested that recurrent transfer of just one migrant per generation could have surprisingly strong benefits when hybrids have high fitness and could cause surprisingly strong damage when hybrids have low fitness.

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