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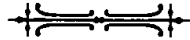
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### 3

## Genetics of Metapopulations: Aspects of a Comprehensive Perspective



*Philip W. Hedrick*

Conservation biology has been the major focus of extensive research and interest in recent years. Much of the reason for this emphasis is the critical situation of many endangered species and an effort to understand the factors that lead to their extinction. In documenting the factors that can result in extinction, Shaffer (1981, 1987) suggested that they can be divided into four major categories. (See Lande 1993 for a theoretical update of the nongenetic factors.) Two of these factors are extrinsic to the species: environmental uncertainty (such as variation in the influence of other species like pathogens or predators) and catastrophe (such as the effects of floods, fires, or droughts). The other two, demographic stochasticity and genetic deterioration, are intrinsic to the species.

The approach to determine the impact of the two intrinsic factors was termed the "small population paradigm" in conservation biology by Caughley (1994), who contrasted it to the "declining population paradigm" generally used by wildlife biologists. (See Hedrick et al. 1996 for a perspective.) According to Caughley, one of the weaknesses of the small population approach is that it is not obvious how often intrinsic factors have been involved in the extinction of a species. Indeed, he finds it much easier to document that extrinsic factors, such as introduced predators, may be important in causing the extinction of particular species.

For basic scientific researchers, the application of genetic or evolutionary principles to conservation biology, as in the small population paradigm, is particularly appealing because a number of theoretically based approaches have been developed. Even so, their application is somewhat controversial and their apparent exactitude may be misleading. (See the discussion in

Lande and Barrowclough 1987 and Hedrick and Miller 1996.) For example, the general suggestion that a population should have an effective population size of 500 to maintain standing genetic variation has recently been revised to approximately 5000 based on data demonstrating that many mutant variants that have an effect of increasing the genetic variance also have an overall detrimental effect on fitness (Lande 1995). Another important concept, based on ecological and evolutionary principles, is that of metapopulation analysis. This approach assumes that a population is divided into patches and that these subpopulations may themselves go extinct or become recolonized—dynamics that influence the probability of extinction of the whole metapopulation. It remains to be seen how important metapopulation dynamics are to the genetic constitution of endangered species, but it is presently a topic of great research interest. (See Hastings and Harrison 1994 and the references cited there for a comprehensive coverage.)

In leading up to an analysis of some of the genetic implications of metapopulation dynamics, I will first give some examples that concern the genetic influence on the long-term survival of a small population. These and other recent studies add significantly to our understanding of the small population paradigm in conservation biology. I begin by briefly discussing types of genetic variation and the association (or lack thereof) of allozyme heterozygosity and fitness in Scots pine. I then summarize the factors that can influence the extent of genetic variation with emphasis on genetic bottlenecks, give an example of the estimation of the effective population size in winter-run chinook salmon, and discuss an experiment in which the detailed effects of inbreeding depression were estimated in *Drosophila melanogaster*. Finally, I consider some of the effects that metapopulation dynamics may have on effective population size and, consequently, maintenance of genetic variation. Because the genetic implications of metapopulation dynamics are quite complicated, a thorough comprehension of the knowledge (or lack of it) on the population genetics of small populations is an essential perspective. In the following pages, I discuss a variety of topics, mainly from recent research on topics related to the small population paradigm, that are fundamental to a full understanding of genetics of metapopulations.

### Measuring Genetic Variation

A great deal of information has been accumulated about the extent of genetic variation within a number of endangered species for certain molecular markers, including allozymes and mitochondrial DNA, and more recently DNA fingerprints, microsatellites, and nuclear DNA sequences (for example,

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Hedrick and Miller 1992; Avise 1994; Smith and Wayne 1996). (Statistical techniques for analysis of molecular data are well developed (as in Weir 1990) and software to analyze these data is readily available.)

Molecular studies have often given invaluable insights into the population structure or phylogenetic relationships of endangered species. For example, molecular research has shown that although the Florida panther (*Felis concolor coryi*) has low genetic variation, part of the population has genetic variation that appears to be from an introduction that included South American ancestry (O'Brien et al. 1990; Roelke et al. 1993). A microsatellite survey of the certified Mexican wolf population (*Canis lupus baileyi*) and a comparison to two other putative Mexican wolf captive lineages has demonstrated that none of these three groups appears to have ancestry from dogs or coyotes and that they are close to each other genetically (García-Moreno et al. 1996; Hedrick 1995a).

Such molecular studies are making important contributions to the understanding of the genetics of endangered species. I should caution, however, that most of this molecular variation is probably not adaptive—although it is valuable for determining relationships between groups, past gene flow, and so on or may become adaptive in the future—and that other loci that may or may not show similar patterns are the ones of adaptive significance. One set of loci that may be of important adaptive significance is that involved in the major histocompatibility complex, which is thought to be essential for pathogen resistance. (For a review see Hedrick 1994.) Furthermore, the genes determining most adaptively important quantitative traits are not known, and it would be probably be a rare situation if a molecular marker was such a gene or was associated with an adaptive gene. For example, there are a number of cases from forestry provenance trials in which samples that show little or no differentiation among populations for allozymes have large genetic differences in adaptively important quantitative traits. Some of these differences are so dramatic that, for example, samples of Scots pine (*Pinus sylvestris*) transplanted to other areas cannot survive or reproduce in the transplant area (Muona 1990 and the references cited there).

### *Association of Heterozygosity and Fitness in Scots Pine*

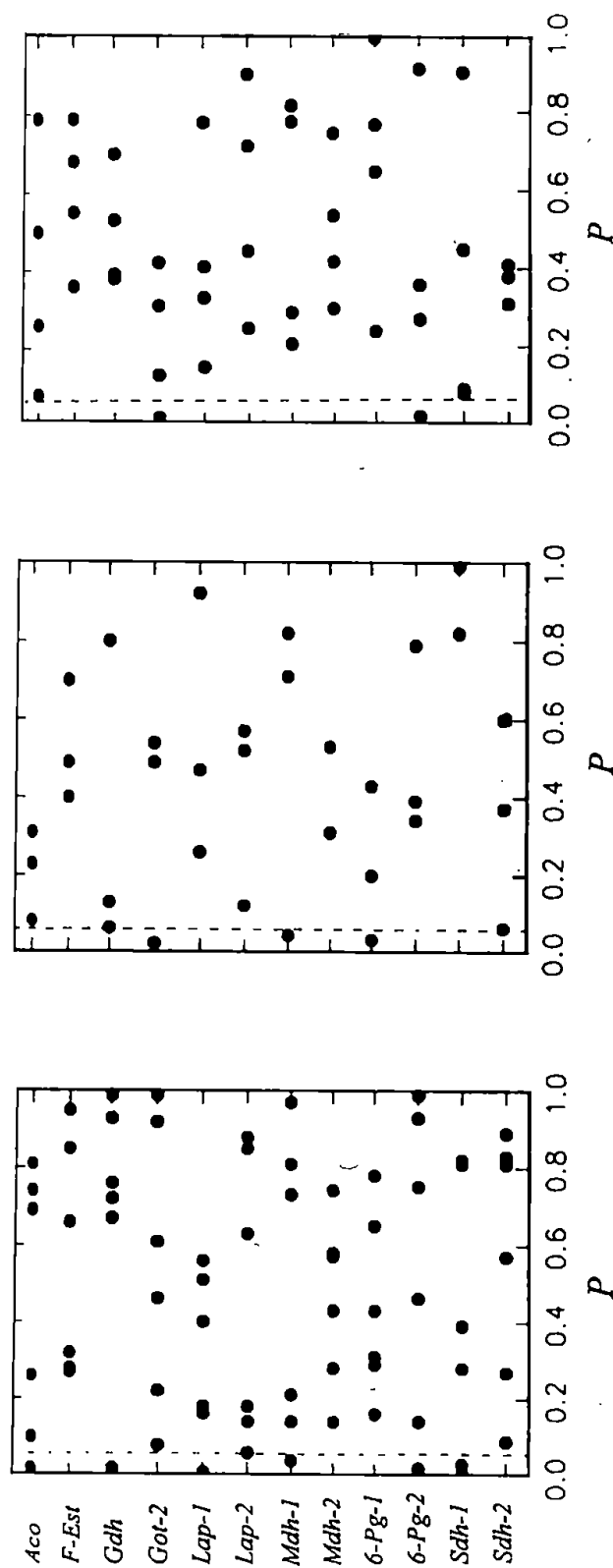
At one time it was hoped that a simple measure of overall molecular genetic variation, such as allozyme heterozygosity, would be useful in predicting the fitness of a population or individuals in a population—that is, high-fitness individuals would have high allozyme heterozygosity (for example, Mitton and Grant 1984). These optimistic suggestions have been cooled by a realistic evaluation of the situation (for example, Hedrick et al. 1986), however, and by the fact that a number of studies do not report such a positive association.

Of course, this lack of an association is not surprising when one realizes that most vertebrates have 20,000 or more genes and that the typical allozyme study surveys 50 or fewer loci, many of which are not polymorphic in a given species (Chakraborty 1981). It appears that with larger numbers of highly variable molecular markers, as from microsatellites, that a molecular approach can allow, for example, identification of highly inbred individuals in a generally random-mating population. On a population level, there are several examples of species that have rebounded from very low numbers and appear to have good fitness levels—such as the northern elephant seal (*Mirounga angustirostris*; Hoelzel et al. 1993) and the beaver (*Castor fiber*; Ellegren et al. 1992) in Sweden—but have very low genetic variation as measured by molecular techniques.

In a detailed study of Scots pine in Finland, Savolainen and Hedrick (1995) have measured the genetic variation at 12 polymorphic allozyme loci and six different quantitative traits related to fitness in three different populations. One of these populations was from above the Arctic Circle, a harsh climate even for Scots pine, and the other two were from southern Finland grown as clones from a limited number of genotypes, making the estimate of the actual genotype effect influencing the quantitative traits more accurate than in a natural population. Scots pine has extensive gene flow, as measured both by genetic and direct indicators, and an extremely large population size. As a result, if an association between heterozygotes and fitness was found, it would likely be due to an intrinsic heterozygote advantage effect at the loci being examined and not from other factors such as a statistical association with other genes resulting from a small population size or inbreeding.

Of 156 comparisons of heterozygotes and homozygotes possible in our study, approximately 8 percent were significant at the 5 percent level, but only half of these showed a positive association while the other half showed a negative association. A useful way to illustrate these results is given in Figure 3.1, where the level of significance is given for the three populations and 12 different loci using ANOVA. If there were a tendency for a statistically significant association, then the values would pile up on the left near or below the broken line that indicates 5 percent statistical significance. Obviously there is no pattern for these results (except a more or less random one), suggesting that there is no advantage for heterozygotes overall or at particular loci.

As another approach to examine the association of heterozygosity and the various quantitative traits related to fitness, the association of the number of heterozygous loci in individual trees and value of the six different quantitative traits in the three populations was examined using multiple regression. Out of 16 combinations of traits and populations, none was significant at the 5 percent level. The combination of highest significance was diameter size in



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B. Vilhelminmäki

C. Yllästunturi

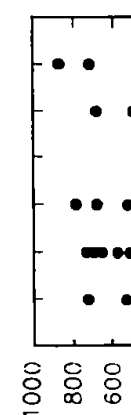
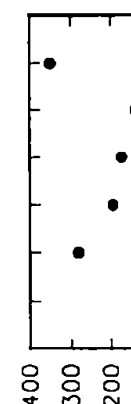
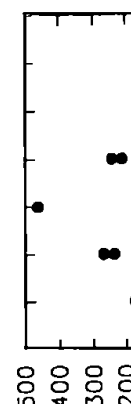
Figure 3.1. The probability of significance level ( $P$ ) for a difference between heterozygotes and homozygotes from ANOVA for the 12 polymorphic loci in three different populations of Scots pine. The individual points are the probability level for a given quantitative trait and allozyme locus. From Savolainen and Hedrick (1995).

one of the southern populations, which explained about 7 percent of the variance. In this case, however, there was a negative association of the trait and heterozygosity—that is, the most heterozygous individuals had the lowest values for the trait. As a graphic way to illustrate these results, Figure 3.2 gives for different numbers of heterozygous loci the mean values of three traits: pollen production, cone production, and height for the three different populations. Obviously there is no apparent positive association in which one would expect low values for these traits to have low heterozygosity and high values to have high heterozygosity. In fact, there appears to be a general lack of pattern between these traits (and the other traits that are not shown here) and individual heterozygosity.

A number of previous studies have searched for a relationship between individual heterozygosity and traits related to fitness. (For reviews see Mitton and Grant 1984; Houle 1989; and Pogson and Zouros 1994.) Of the published reports, a reasonable number have not shown such an association, a rather surprising finding given the difficulty in getting negative results published. In addition, many of the positive findings have been published by a few research groups, suggesting that there may be some bias from them in reporting results that only show a positive association between heterozygosity and traits related to fitness. Overall, it seems that one should not depend on a measure such as allozyme heterozygosity to determine fitness. More direct indicators of fitness should be used.

### Factors Influencing Genetic Variation

The factors that influence the extent and pattern of genetic variation in a population are traditionally defined as selection, gene flow (population structure), mutation, inbreeding, and genetic drift (for example, Hedrick 1985; Hartl and Clark 1989). Particularly important in endangered species is genetic drift, which may have an influence on the extent of genetic variation because of a long-term small population size, bottlenecks (constrictions of population size in time), or small founding numbers for a population (for example, Hedrick and Miller 1992; Chapter 16 in this volume). All of these factors may be important in metapopulations, but the major impact is probably that of the small effective population size, through either founding events or small numbers of individuals in the different patches. Of course, when there is a small population size, the rate of inbreeding will be higher because of the lack of mates that are not relatives. Also important in metapopulations are the rate and pattern of movement between patches as well as the rate and cause of extinction within the patches.



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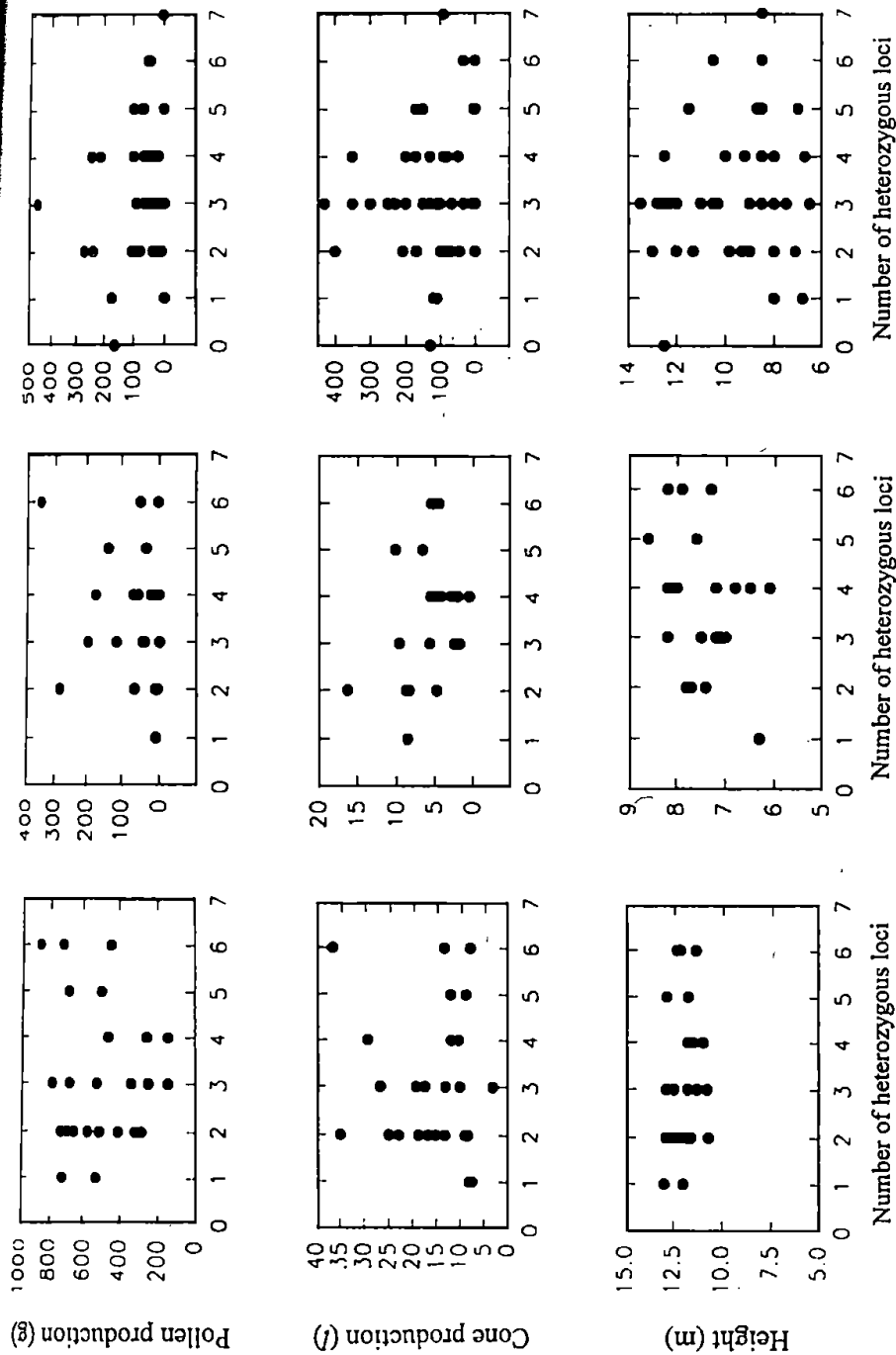


Figure 3.2. The phenotypic values of three quantitative traits—height, cone production, and pollen production—for three populations of Scots pine (left to right, Viitaselkä, Vihelminmäki, and Ylästunturi) with different numbers of heterozygous loci. From Savolainen and Hedrick (1995).



Often several different factors may simultaneously influence the extent of genetic variation or the level of fitness in a population, and the guidelines that have been generally recommended for avoiding extinction in endangered species are based on such principles. For example, the guideline that at least 50 individuals should be used to form the initial basis of a population and that 50 is the minimum effective number to avoid inbreeding depression is the result of practical experience with livestock. (See Franklin 1980; but see Lande and Barrowclough 1987 and Hedrick and Miller 1992 for discussions.) The guideline of 500 to maintain genetic variation in a finite population is the result of the combination of the input of mutation and the loss of variation due to genetic drift. (See Lande 1995 for a revision of this number.) The guideline of one migrant per generation ( $Nm = 1$ ; for example, Lacy 1987) is based on the combination of the rate of gene flow,  $m$ , and the effective population size,  $N$ . Although these guidelines make general sense in a population genetics context, they should be used judiciously, case by case, and other information about the habitat, population ecology, or other factors should be given strong consideration.

### *Population Bottlenecks*

Population bottlenecks are common occurrences in endangered species, even if the species are able to rebound in number and not go extinct. The population bottleneck in the northern elephant seal, for example, was documented to some extent because these animals were hunted to near extinction in the late nineteenth century (for example, Hoelzel et al. 1993). After they were protected, a remnant population of a very few individuals was discovered on Guadalupe Island off the coast of Baja California in 1892. (Eight were found, and seven of these were killed.) From the few other animals that were not discovered, the population expanded to over 120,000 in 1980. This bottleneck and the low population numbers in those generations (and the immediate generations following it when the population began increasing) appear to have resulted in a great reduction in genetic variation—that is, much less mitochondrial DNA (mtDNA) and allozyme variation than the related southern elephant seal. Using either a detailed demographic model (Hoelzel et al. 1993) or a simple population genetics model (Hedrick 1995b), the low observed mtDNA variation is explainable by a bottleneck of approximately one generation with an effective population size of 10 to 20. But the complete lack of allozyme variation at 55 loci (Hoelzel et al. 1993) is not explainable by such a bottleneck (Hedrick 1995b), suggesting either that the northern elephant seal already had less variation than the southern elephant seal before the human-induced bottleneck or that some other unknown factor was important in reducing genetic variation.

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Presently, the Florida panther, a subspecies of the mountain lion, is undergoing a bottleneck and exists in only a small area of southern Florida with an estimated population size between 30 and 50. This population appears to have lower genetic variation than other mountain lion subspecies (O'Brien et al. 1990; Roelke et al. 1993) and appears to have low fitness (Roelke et al. 1993; Barone et al. 1994) because of its long isolation from other mountain lions and its small effective population size. As a result, a panel of scientists and panther workers has recommended that mountain lions from Texas be translocated to Florida (for example, Seal 1994). The level of gene flow recommended, 0.2 in the first generation and about 0.02 to 0.04 per generation thereafter, will in theory result in a restoration in fitness, restoration of genetic variation, and retention of adaptive Florida panther traits (Hedrick 1995c).

Bryant et al. (1986) carried out some laboratory bottleneck experiments on the housefly and from their results suggested that bottlenecks may in fact increase the amount of additive genetic variation in a population and, therefore, the potential for future adaptation. But in their experiments and those of Lopez-Fanjul and Villaverde (1989), the value of traits related to fitness greatly declined as the result of the bottlenecks. In a later study, Bryant et al. (1990) found that over a series of bottlenecks, the initial fitness loss was ameliorated and the fitness returned to its prebottleneck level (see also Miller and Hedrick 1996). (I should note that the probability of extinction from demographic factors under such a series of bottlenecks would be quite high for most endangered species, which of course do not have the reproductive potential of houseflies.) Both Bryant et al. (1986) and Goodnight (1987) gave explanations of this observation based on the generation of additive genetic variation from epistatic variation, but Willis and Orr (1993) have shown that detrimental variants not having epistatic effects might be responsible.

O'Brien et al. (1983, 1985, 1987) have suggested that cheetahs underwent one or more bottlenecks that resulted in a low amount of genetic variation and low fitness. Pimm et al. (1989) and Gilpin (1991), however, have pointed out that the probability of extinction, given a bottleneck that would greatly reduce the amount of genetic variation, would be quite high. As an alternative explanation, Pimm et al. (1989) suggest that a metapopulation structure could result in the extensive loss of genetic variation apparently observed in cheetahs and also a low probability of extinction.

### *Effective Population Size in Winter-Run Chinook Salmon*

Winter-run chinook salmon from the Sacramento River, California, are listed as a federally endangered species (Hedrick 1994). The estimated annual run dropped from an average of 86,000 in the period from 1967 to 1969 to low numbers in the late 1980s and early 1990s with an extreme estimated low of

191 spawners in 1991. As a result, a program was started to capture adults, artificially spawn them, raise the young in Coleman National Fish Hatchery, and then directly release these progeny to augment the natural population.

There was concern, however, that these released hatchery fish could overwhelm the natural population and that the overall effective population size would be a reflection of the few number of breeders used at the hatchery. As a result, a breeding protocol was instituted as an attempt to equalize the contributions from the captured spawners and make the effective population size from the hatchery as large as possible (Hedrick et al. 1995). In this protocol, eggs from each female are divided into two lots and, when possible, fertilized with gametes from two different males. Furthermore, the gametes of each male are used to fertilize at least two different females. In this way, the contributions of fertile individuals are retained even if one of their mates is not fertile. Furthermore, this protocol will tend to equalize the contributions from different individuals, a factor that results in a larger effective population size (for example, Lande and Barrowclough 1987; Caballero 1994; Hedrick et al. 1995).

Hedrick et al. (1995) evaluated this program over its first 3 years. In the first year, 1991, there were only six females and nine males that were successfully combined in 12 matings. To have exactly equal contributions, each female should contribute 0.167 of the female gametes and each male 0.111 of the male gametes. However, the breeding protocol was not yet in place; and as a result of this and uneven maturation in the spawners, a high proportion of the gametes were contributed by one 4-year-old male (0.614 of the male gametes) and one 4-year-old female (0.411 of the female gametes). As a result of these unequal contributions, the effective population size from the hatchery was estimated to be only 7.02 individuals. (See Hedrick et al. 1995 for the estimation approach.)

In 1992, more spawners were captured and 13 males and 13 females contributed to 22 matings. Table 3.1 gives the number of progeny contributed from these parents and their proportionate contributions. For equal contributions from each parent, they should contribute 0.077 each. Notice that the largest value for any female was 0.138 and the largest for any male was 0.197, much closer to the equality goal than in the 1991 matings. The estimated effective population size from the hatchery in 1992 was significantly higher at 19.02.

In 1993, only 18 spawners were caught and there were only 12 matings among the surviving nine females and three males that produced smolts. Even with a number of problems encountered with these spawners, the distribution of progeny from these individuals was fairly even with the largest female contribution at 0.254 and largest male contribution at 0.509. (The

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TABLE 3.1.  
Number of progeny or gametes from the different  
female and male spawning winter-run chinook salmon  
in the 1992 brood year

Female (Age)	No. of progeny (proportion)	Male (Age)	No. of progeny (proportion)
A (3)	2890 (0.105)	1 (4)	2778 (0.101)
B (4)	3440 (0.125)	2 (3)	2220 (0.080)
C (4)	3429 (0.124)	3 (3)	5441 (0.197)
D (3)	2763 (0.100)	4 (3)	2992 (0.108)
F (3)	3897 (0.138)	5 (3)	2272 (0.082)
G (3)	290 (0.010)	7 (3)	1452 (0.053)
H (?)	1962 (0.071)	8 (3)	153 (0.006)
I (3)	1581 (0.057)	9 (3)	137 (0.005)
J (4)	268 (0.010)	10 (3)	867 (0.031)
K (3)	609 (0.022)	11 (3)	3479 (0.126)
L (3)	3167 (0.115)	13 (4)	1076 (0.039)
M (3)	867 (0.031)	14 (3)	3853 (0.140)
N (3)	2524 (0.092)	15 (3)	877 (0.032)
Mean	2123 (0.077)	Mean	2123 (0.077)

Source: Hedrick et al. (1995):

goals for females and males were 0.111 and 0.333, respectively.) The effective population size was only 7.74 in 1993, but this low number is primarily due to the unequal numbers of the two sexes (only 3 males out of 12 spawners) and not because of unequal contribution of different individuals within the two sexes.

The bounds of the effective population size of the natural run in the 3 years were also estimated based on a lower bound of 0.1 and an upper bound of 0.333 of the run estimate (after Bartley et al. 1992; R. Waples, National Marine Fisheries Service, personal communication). In 1992, for example, the run was fairly strong and these lower and upper bounds were 115.1 and 383.6, respectively. Ryman and Laikre (1991) have shown how the hatchery and natural run estimates of the effective population size can be combined to give the overall effective population size. Figure 3.3 gives these estimates as a function of the contribution that the captive (hatchery) progeny makes to the population. At one extreme, if the captive proportion is 1.0 and there is no survival from the natural run, then the overall effective population size is 19.02. The estimated contribution from the hatchery in 1992 was 0.061, so that the bounds on the overall effective population size using this value were

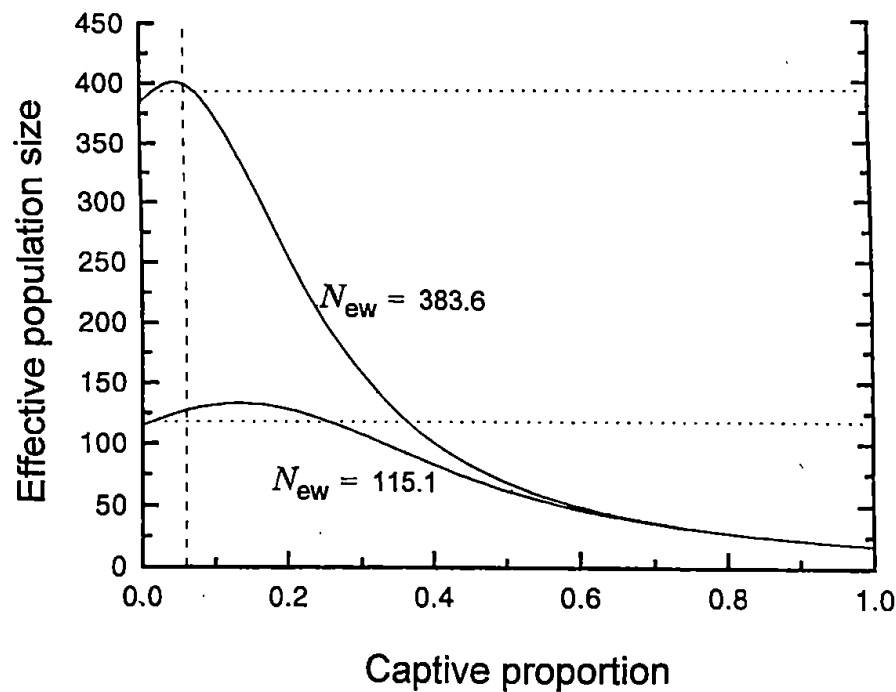


Figure 3.3. The estimated effective population size for the 1992 run of the winter-run chinook salmon using the estimated effective population size from the hatchery stock and a high and a low estimate of the effective population size of the natural run ( $N_{ew}$ ). The vertical broken line indicates the estimated captive proportion; the horizontal dotted lines indicate the estimated population sizes if no salmon were removed for artificial spawning. From Hedrick et al. (1995).

between 127.3 and 401.0. In other words, the hatchery program does not seem to have reduced the overall effective population size in 1992 and may have slightly increased it. (In the other years, there was a slight increase at the lower bound and a slight decrease at the upper bound; see Hedrick et al. 1995.)

Winter-run chinook salmon, like other anadromous salmon, exist in year classes that tend to mate within the year class, making a given run a metapopulation existing in time rather than space. One of the main concerns is that if one of the year classes goes extinct, then recolonization from other year classes may be difficult. If year classes do go extinct and are subsequently recolonized, then such dynamics may greatly reduce the overall effective population size. (See the discussion of spatial metapopulations in the next section.)

### Inbreeding

In an effort to understand the genetic consequences of captive breeding, Murray (1995) has carried out a study of *Drosophila melanogaster*. There is a need to investigate the influence of captive breeding on the genetic diversity of wild populations. Murray (1995) has shown that captive breeding can lead to a loss of genetic diversity, which can be detrimental to the survival of the population. This is because captive breeding often involves a small number of individuals, which can lead to a loss of genetic variation. This loss of variation can be detrimental to the survival of the population, as it reduces the ability to adapt to changing environmental conditions. Murray (1995) has shown that captive breeding can lead to a loss of genetic diversity, which can be detrimental to the survival of the population. This is because captive breeding often involves a small number of individuals, which can lead to a loss of genetic variation. This loss of variation can be detrimental to the survival of the population, as it reduces the ability to adapt to changing environmental conditions.

We have seen that captive breeding can lead to a loss of genetic diversity, which can be detrimental to the survival of the population. This is because captive breeding often involves a small number of individuals, which can lead to a loss of genetic variation. This loss of variation can be detrimental to the survival of the population, as it reduces the ability to adapt to changing environmental conditions. Murray (1995) has shown that captive breeding can lead to a loss of genetic diversity, which can be detrimental to the survival of the population. This is because captive breeding often involves a small number of individuals, which can lead to a loss of genetic variation. This loss of variation can be detrimental to the survival of the population, as it reduces the ability to adapt to changing environmental conditions.

### *Inbreeding Depression in Drosophila melanogaster*

In an effort to document the overall effects of inbreeding on fitness, we have carried out a series of laboratory experiments in wild-caught *Drosophila melanogaster* (Miller and Hedrick 1993; Miller et al. 1993; Miller 1994). There is a long history of using *Drosophila* as an experimental organism to investigate various aspects of evolutionary genetics (for example, Hedrick and Murray 1983) and recently in conservation genetics (for example, Frankham 1995) because of its short generation time, ease of culture, and our vast knowledge of its genetics. It is important to note, however, that some factors influencing extinction under the small population paradigm are not addressed in experimental studies using *Drosophila* because of its high reproductive value compared to most endangered species.

We determined in detail the effects, on the main components of fitness, survival, female fecundity, and male mating success, of a single chromosome that constitutes about 40 percent of the *Drosophila melanogaster* genome when it was made completely homozygous in a single generation (Miller and Hedrick 1993). The impact of inbreeding on the different fitness components for six individual wild chromosomes is given in Table 3.2. Male mating ability and female fecundity were not evaluated for line 7 because of the very low homozygote viability in that line. Only two of the six chromosomes showed significantly lower viability as homozygotes (lines 7 and 16), and only one of the lines showed significantly lower female fecundity (line 17). On the other hand, all five of the lines when made homozygous had a greatly reduced ability for male mating success. In line 17, the worst mating line, only 2 out

TABLE 3.2.  
Fitness component estimates for six experimental  
lines of *Drosophila melanogaster*

Line	Viability	Male mating ability	Female fecundity
4	1.260 (0.053)*	0.061 (0.133)*	1.116 (0.202)
7	0.198 (0.012)*	—	—
8	1.063 (0.043)	0.297 (0.103)*	1.202 (0.202)
16	0.800 (0.084)	0.212 (0.062)*	1.325 (0.225)
17	0.999 (0.051)	0.023 (0.017)*	0.554 (0.110)*
21	1.041 (0.040)	0.237 (0.071)*	0.878 (0.179)
Mean	0.894 (0.371)	0.275 (0.212)*	1.015 (0.305)

Source: Miller and Hedrick (1993).

Note: Values indicate the fitness component of the chromosomal homozygote relative to that of the heterozygote.

\* Significantly different from 1.



pared to most other large cat species (for example, O'Brien et al. 1983, 1985, 1987; Yukhi and O'Brien 1990). (It should be noted that a number of other species also have low amounts of genetic variation as noted by Caughley 1994 and that cheetahs do have genetic variation at two allozyme loci, for minisatellites, and for mitochondrial DNA; see Menotti-Raymond and O'Brien 1993). As a result, O'Brien et al. (1983) have hypothesized that cheetahs went through a bottleneck about 10,000 years ago and at that time lost most of their genetic variation. But Pimm et al. (1989) suggest that a bottleneck small enough and long enough to result in this loss of genetic variation would have also resulted in a very high probability of extinction due to demographic considerations (see Hedrick 1996). As an alternative explanation, they suggest that a metapopulation structure and the resulting dynamics may have resulted in loss of genetic variation without a high probability of extinction. (Menotti-Raymond and O'Brien acknowledge indirectly that the suggestion of Pimm et al. is a valid alternative explanation.)

Gilpin (1991) has illustrated how the total population (census) number could be fairly large but the loss of genetic variation because of a small effective population size could still be substantial. Figure 3.4 gives a diagrammatic representation of this theoretical situation in which there are three patches in a metapopulation. Initially all patches or subpopulations have high heterozygosity, and each has an effective (and census) population size of 500. The important sequence of events starts in generation 48 when patch 2 goes extinct and is subsequently recolonized from patch 3 with a consequent reduction in heterozygosity. Next patch 1 is colonized from patch 2 with a founder population having no genetic variation. When patch 2 goes extinct in generation 71, the metapopulation has no variation, although there are still 500 individuals in patch 1. All of these individuals can be traced back to some individuals in patch 3 before generation 51. In other words, there is, in Gilpin's terminology, a rapid coalescence of ancestry to a few individuals in the metapopulation.

The general effect of extinction and recolonization dynamics on the effective population size can be estimated by measuring the rate of loss of heterozygosity. Hedrick and Gilpin (1996) have developed a computer simulation to determine the influence of the different parameters in a metapopulation model on the effective population size. The impact of metapopulations dynamics is illustrated in Table 3.3, for example, where there are ten patches of size  $K$  and the per-generation rate of colonization is 0.2 (when all patches are occupied) and the per-generation rate of extinction is 0.05. In this case, the probability of metapopulation extinction is very low, about 0.2 percent over the first 50 generations. The estimated overall effective population size of the metapopulation ( $N_{e(T)}$ ) is given in the third column; it is apparent that it does not increase very much as the



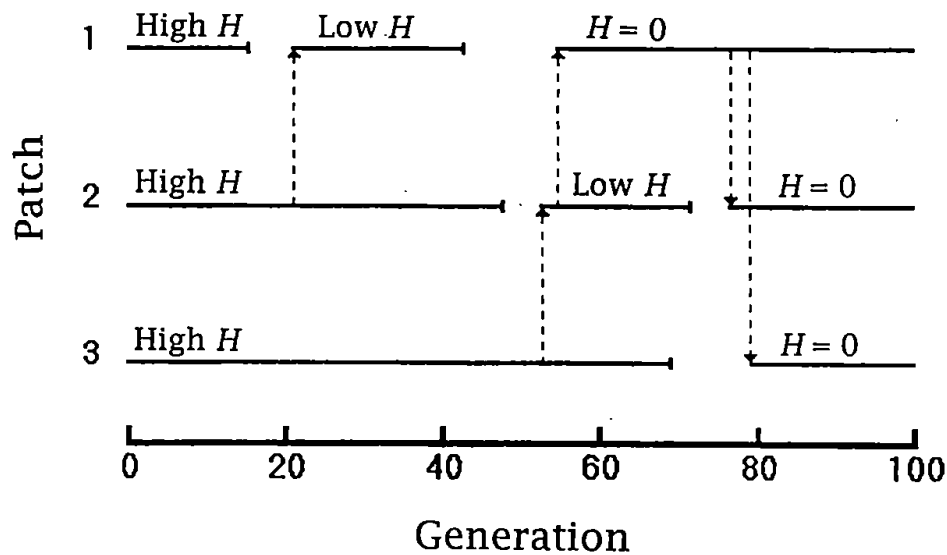


Figure 3.4. The level of heterozygosity ( $H$ ) over time in a simulation of a population existing in three patches. The short vertical bars on the right-hand end of horizontal lines indicate extinctions in a patch; the arrows indicate recolonization. After Gilpin (1991).

number of individuals in a patch ( $K$ ) increases or the actual observed (census) number of the metapopulation ( $N$ ) increases. As a result, the ratio of the effective population number to the observed number declines to a very low value as  $K$  increases. The effective size within a patch ( $N_{e(S)}$ ) given in column 2 also remains small but becomes a larger proportion of the overall effective size as the value of the carrying capacity increases.

The primary basis for the low effective population size of the metapopulation is the assumption that each recolonization event is by one fertilized female, or the genomes of two founder individuals. Because it is assumed that the patch increases to its  $K$  value in one generation, the small founder number is the factor that greatly reduces the heterozygosity in the patch. With a series of extinction and recolonization events, the whole metapopulation becomes genetically connected, the metapopulation heterozygosity is markedly reduced, and this results in the low effective population for the metapopulation.

The impact of other parameters varies from the highly predictable to the surprising (Hedrick and Gilpin 1996). Increasing the number of founders, for example, increases the effective population size as expected, and increasing the turnover rate, the rate of extinction and subsequent recolonization, greatly reduces the effective population size. But adding gene flow ( $m$ ) to each generation among the patches increases the effective population size (Table 3.4)—a finding that is somewhat counterintuitive given the previous findings on substructured populations (for example, Lacy 1987; Lande and Barrowclough 1987). In other population-structure models, the lowest

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amount of gene flow leads to high differentiation among patches (as it does here as indicated by the high value of  $F_{ST}$ , a statistic to measure the level of between-patch diversity) and therefore retention of overall genetic variation. In the basic metapopulation model presented earlier, there is no gene flow between patches: thus a patch that once had no genetic variation can have restored nonzero heterozygosity only if there was an extinction and a recolonization. Gene flow allows restoration of heterozygosity without such a series of events. Because the effective population size is measured by loss of heterozygosity, adding gene flow results in a higher effective population size.

In discussing the impact of population structure on the retention of genetic variation, it has been suggested that more genetic variation in the total population could be retained with a low amount of gene flow because different subpopulations could become fixed for different alleles (for ex-

TABLE 3.3.  
Estimated effective population sizes for different local carrying capacities ( $K$ ) when the colonization and extinction rates are 0.2 and 0.05 per generation, respectively, and there are ten patches

$K$	$N_{e(S)}$	$N_{e(T)}$	$N$	$N_{e(T)} / N$
25	16.4	38.2	174.4	0.219
50	22.4	46.6	345.9	0.134
100	30.4	64.2	690.2	0.093
200	36.0	66.7	1392.9	0.048
$\infty$	40.7	76.6	$\infty$	0.000

Source: Hedrick and Gilpin (1996).

TABLE 3.4.  
Estimated effective population size for different levels of gene flow between patches when the number in a patch is infinite, the colonization and extinction rates are 0.2 and 0.05 per generation, respectively, and there are ten patches

$m$	$N_{e(S)}$	$N_{e(T)}$	$N_{e(S)} / N_{e(T)}$	$F_{ST}$
0.00	40.7	76.6	0.531	0.312
0.00125	66.5	95.1	0.699	0.224
0.0025	88.9	115.7	0.769	0.167
0.005	125.8	140.1	0.898	0.114
0.01	156.7	172.4	0.909	0.069
0.02	217.7	219.7	0.991	0.040

Source: Hedrick and Gilpin (1996).

ample, Lacy 1987; Lande and Barrowclough 1987). But this retention of overall variation occurs only if there is no metapopulation dynamics—that is, there is no population extinction and recolonization from other patches that causes the coalescence of ancestry demonstrated above.

## Lessons

Many endangered species appear to have some of the characteristics of a metapopulation—that is, subdivision into small isolated populations and subsequent extinction of local populations. Because of extreme isolation, however, the recolonization of extinct patches may not readily occur and may have to rely on human translocations. To understand the effects of metapopulation dynamics on the extent and pattern of genetic variation entails understanding and documenting a number of basic population genetic parameters, such as the effective population size, level of inbreeding depression, and type of selection. As Caughley (1994) suggests, there is a distinct lack of information on many of these factors, but the examples given here as well as those from other recent studies (see the citations in Frankham 1995) are adding to our collective knowledge of the small population paradigm's parameters. The population structure of a metapopulation adds reality and complexity to the general picture, of course, but the fundamental aspects still need to be understood before we can determine the additional influence of metapopulation dynamics.

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