Migration

Migration, in an evolutionary sense, is the movement of alleles between populations. That is, migration involves the transfer of alleles from the gene pool of one population to the gene pool of another population. The actual amount of migration among populations in different species varies enormously, depending on how mobile individuals or propagules are at various stages of their life cycle.

1. **Adding Migration to the Hardy-Weinberg Analysis: the One-island Model**
    a. Imagine two populations: one on a continent, and the other on a small, offshore island. Because the island population is so small relative to the continental population, any migration from the island to the continent will be inconsequential for allele and genotype frequencies on the continent. So, gene flow is effectively one way, from the continent to the island. As usual, consider a single locus with two alleles, A_1 and A_2. Can migration from the continent to the island take the allele and genotype frequencies on the island away from Hardy-Weinberg equilibrium?
        i. Imagine that before migration, the frequency of A_1 on the island is 1.0 (i.e., A_1 is fixed in the island population). When gametes in a gene pool in which A1 is fixed combine at random to make zygotes, the genotype frequencies among the zygotes are 1.0 for A_1A_1, 0 for A_1A_2, and 0 for A_2A_2. Our calculations will be simpler if we give our population a fixed size, so imagine that there are 800 zygotes that we will let grow up to become adults.
        ii. Now suppose that the continental population is fixed for allele A_2 and that before the individuals on the island reach maturity 200 individuals migrate from the continent to the island. After migration, 80% of the island population is from the island and 20% is from the continent. The new genotype frequencies are 0.8 for A_1A_1, 0 for A_1A_2, and 0.2 for A_2A_2. When individuals on the island reproduce, their gene pool will have allele frequencies of 0.8 for A_1 and 0.2 for A_2.
        iii. Migration has changed the allele frequencies in the island population, violating Hardy-Weinberg conclusion 1. Before migration, the island frequency of A_1 was 1.0; after migration, the frequency of A_1 was 0.8. The island population has evolved as a result of migration. Migration has also produced genotype frequencies among the adults on the islands that are not consistent with Hardy-Weinberg conclusion 2. Under the Hardy-Weinberg equilibrium principle, a population with allele frequencies of 0.8 and 0.2 should have genotype frequencies of 0.64, 0.32, and 0.04. A single bout of random mating will, of course, put the population back into Hardy-Weinberg equilibrium for the genotype frequencies.

2. **Empirical Research on Migration as a Mechanism for Evolution**
    a. The water snakes of Lake Erie provide an empirical example of migration from a mainland population to an island population. These snakes (*Nerodia sipedon*) live on the mainland surrounding Lake Erie and on the islands in the lake. Individuals vary in appearance, ranging from strongly banded to unbanded. To a rough approximation, color pattern is determined by a single locus with two alleles with the banded allele dominant over the unbanded allele (King 1993a).

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b. On the mainland virtually all the water snakes are banded, whereas many of the snakes are unbanded on the islands. The difference in the composition of mainland versus island populations appears to be the result of natural selection caused by predators. On the islands, the snakes bask on limestone rocks at the water's edge. King (1993b) showed that among very young snakes unbanded individuals are more cryptic on island rocks than are banded individuals. The youngest and smallest snakes are presumably most vulnerable to predators. King (1993b) used mark-recapture studies, among other methods, to show that on the islands unbanded snakes indeed have higher rates of survival than banded snakes.

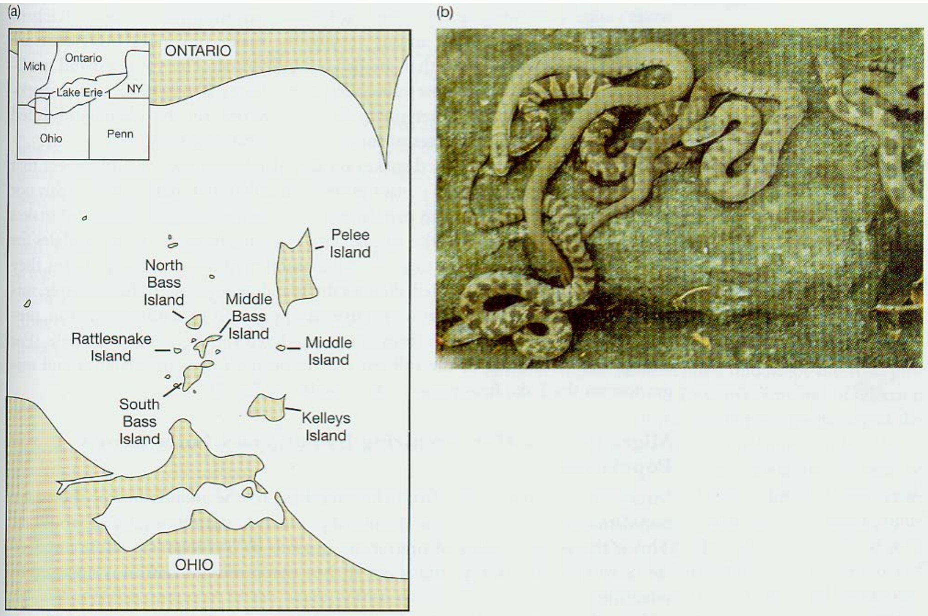

Figure 6.6 **Water snakes and where they live** The map in (a) shows the island and mainland areas in and around Lake Erie where Richard King and colleagues studied migration as a force of evolution in water snakes. From King and Lawson (1995). Copyright © 1995 Evolution. Reprinted by permission. The photo in (b) shows unbanded, banded, and intermediate forms of the Lake Erie water snake (*Nerodia sipedon*). (Richard B. King)

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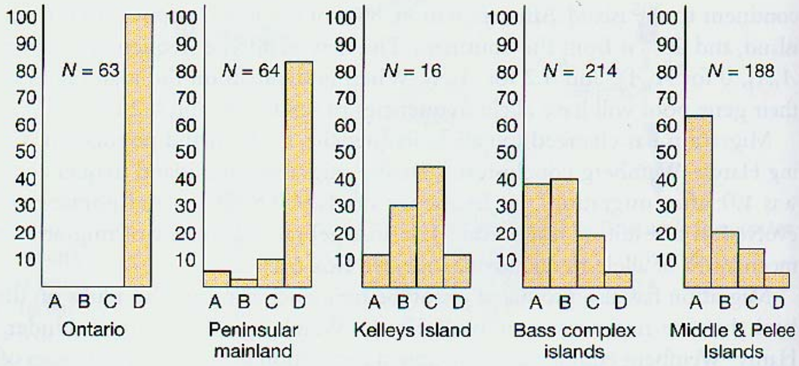
Figure 6.7 **Variation in color pattern within and between populations** These histograms show frequency of different color patterns in various populations. Category A snakes are unbanded; category B and C snakes are intermediate; category D snakes are strongly banded. Snakes on the mainland tend to be banded; snakes on the islands tend to be unbanded or intermediate. From Camin and Ehrlich (1958). Copyright © 1958 Evolution. Reprinted by permission.



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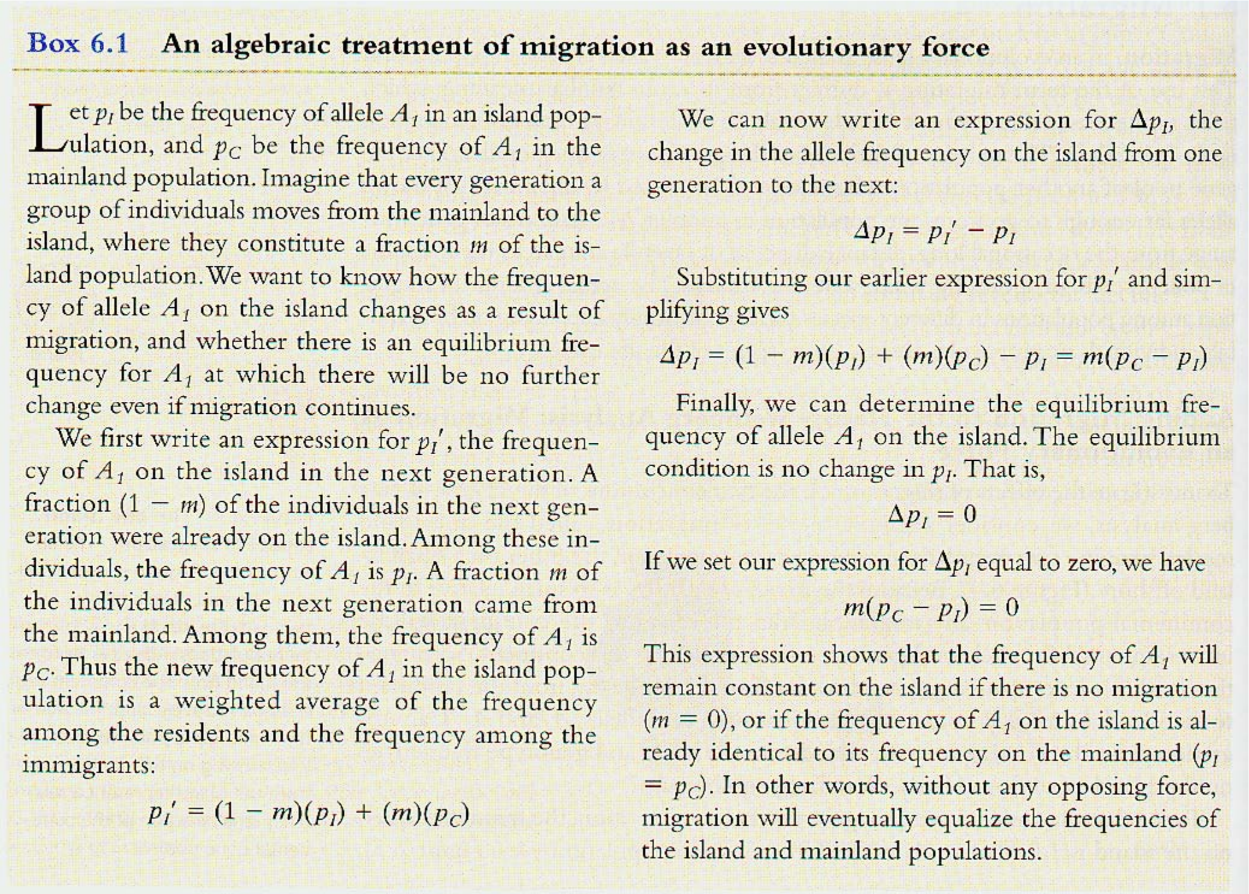
c. If selection favors unbanded snakes on the islands, then we would expect that the island populations would consist entirely of unbanded snakes. Why is this not the case? The answer, at least in part, is that in every generation several banded snakes move from the mainland to the islands. The migrants bring with them alleles for banded coloration. When the migrant snakes interbreed with the island snakes, they contribute copies of the banded allele to the island gene pool. In this example, migration is acting as an evolutionary force in opposition to natural selection, preventing the island population from becoming fixed for the unbanded allele!

References

King, R.B. 1993a. Color pattern variation in Lake Erie water snakes: inheritance. *Canadian Journal of Zoology* 71: 1985-1990.

King, R.B. 1993b. Color pattern variation in Lake Erie water snakes: predictions and measurement of natural selection. *Evolution* 47: 1819-1833.



Box 6.1 An algebraic treatment of migration as an evolutionary force

Let p_I be the frequency of allele A_1 in an island population, and p_C be the frequency of A_1 in the mainland population. Imagine that every generation a group of individuals moves from the mainland to the island, where they constitute a fraction m of the island population. We want to know how the frequency of allele A_1 on the island changes as a result of migration, and whether there is an equilibrium frequency for A_1 at which there will be no further change even if migration continues.

We first write an expression for p_I', the frequency of A_1 on the island in the next generation. A fraction $(1 - m)$ of the individuals in the next generation were already on the island. Among these individuals, the frequency of A_1 is p_I. A fraction m of the individuals in the next generation came from the mainland. Among them, the frequency of A_1 is p_C. Thus the new frequency of A_1 in the island population is a weighted average of the frequency among the residents and the frequency among the immigrants:

$$p_I' = (1 - m)(p_I) + (m)(p_C)$$

We can now write an expression for Δp_I, the change in the allele frequency on the island from one generation to the next:

$$\Delta p_I = p_I' - p_I$$

Substituting our earlier expression for p_I' and simplifying gives

$$\Delta p_I = (1 - m)(p_I) + (m)(p_C) - p_I = m(p_C - p_I)$$

Finally, we can determine the equilibrium frequency of allele A_1 on the island. The equilibrium condition is no change in p_I. That is,

$$\Delta p_I = 0$$

If we set our expression for Δp_I equal to zero, we have

$$m(p_C - p_I) = 0$$

This expression shows that the frequency of A_1 will remain constant on the island if there is no migration ($m = 0$), or if the frequency of A_1 on the island is already identical to its frequency on the mainland ($p_I = p_C$). In other words, without any opposing force, migration will eventually equalize the frequencies of the island and mainland populations.

In summary, migration is the movement of alleles from population to population. Within a single population, migration can cause allele frequencies to change from one generation to the next. For small populations receiving immigrants from large source populations, migration can be a potent mechanism of evolution. Across groups of populations, gene flow tends to homogenize allele frequencies. Thus, migration tends to prevent the evolutionary divergence of populations.