

females, but older birds were less likely to survive. Morphology did not differ with age. Nonsurvivors were not in poorer condition before the storm suggesting that selection acted on size and not condition. Larger birds apparently were favored in extreme cold weather due to the thermal advantage of larger size and the ability to store more body fat.

Examination of the adult progeny of the survivors indicated that mean body size of the population responded to the selective event caused by the storm. The body size of progeny was significantly greater than the body size of the population before the storm (Figure 8.11b). Thus body size had a substantially high heritability (see Section 2.2; Chapter 11).

#### Guest Box 8 Rapid adaptation and conservation

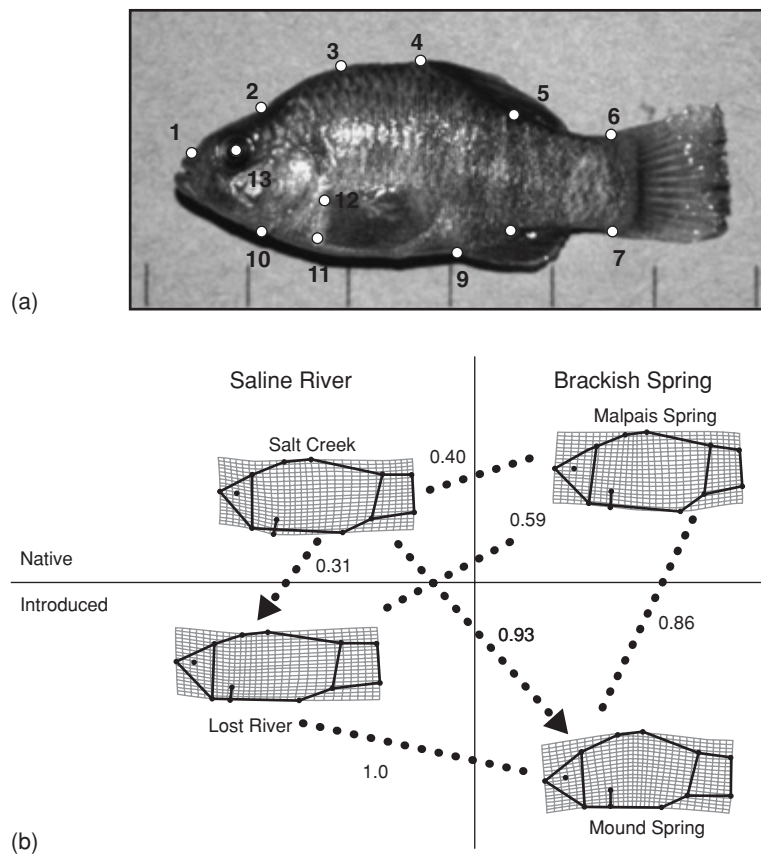
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Recent work has demonstrated that adaptive evolution often occurs on contemporary time scales (years to decades), making it of particular relevance to conservation planning (Ashley et al. 2003; Stockwell et al. 2003). Reports of rapid evolution span a variety of species, traits, and situations, suggesting that rapid adaptation is the norm rather than the exception (Stockwell et al. 2003). Furthermore, rapid adaptation is often associated with the same anthropogenic factors responsible for the current extinction crisis, including overharvest, habitat degradation, habitat fragmentation, and exotic species (Stockwell et al. 2003). Rapid evolution has crucial importance to conservation biology.

Here, we briefly discuss the implications of rapid adaptation for conservation biology in the context of exotic species and actively managed species. First, many case studies of rapid adaptation involve non-native species. For instance, introduced fish populations have been shown to undergo rapid adaptation in response to novel predator regimes and breeding environments (Stockwell et al. 2003). Further, exotic species may create novel selection pressures for native biota (see Chapter 19). Such is the case with the soapberry bug that apparently evolved shorter beak length in response to the smaller seed pods of the exotic flat-potted golden rain tree (Carroll et al. 2001). Finally, invasion dynamics may be influenced by the evolution of exotics as they encounter novel selection pressure(s) during invasion (García-Ramos and Rodríguez 2002).

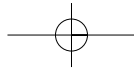
Rapid adaptation can also result in the evolution of less preferred phenotypes. For instance, selective harvest has been associated with evolution of smaller body size in harvested populations of fish (Olsen et al. 2004a) and bighorn sheep (see Guest Box 11; Coltman et al. 2003). Likewise, rapid adaptation of smaller egg size has been observed for a captive population of chinook salmon (Heath et al. 2003). In this case, wild populations supplemented with this stock have also shown a decrease in egg size (Heath et al. 2003).

Rapid adaptation may also occur for so-called **refuge populations** that are established as a hedge against extinction. For instance, a recently established population



**Figure 8.12** Body shape variation among native and recently established populations of White Sands pupfish. (a) A male pupfish is shown with the 13 anatomical landmarks used to calculate morphological distances from a generalized Procrustes analysis. These distances (on a relative scale) are shown in (b) along with deformation grids that depict shape change from an overall mean form. The directions of the arrows indicate that introduced populations were derived from Salt Creek. Experimental research (Collyer 2003) demonstrated that body shape variation in this system is strongly heritable, revealing that the evolutionary shape divergence of the Mound Spring population exceeded native shape divergence in as little as three decades. Modified from Collyer et al. (2005).

of the White Sands pupfish has undergone rapid adaptation in body shape (Figure 8.12). The native (Salt Creek) population is characterized by slender body shapes, indicative of adaptive streamlining because of high water flow during periodic flash floods at Salt Creek. The introduced population at Mound Spring has evolved a deep-bodied shape, presumably in response to the absence of high flows (Collyer et al. 2005). This evolution took place in less than three decades. The functional importance of body shape may preclude the refuge population's usefulness as a genetic replicate of the native population.



In all of these cases, evolutionary responses have occurred on limited time scales (often less than 50 years). Thus, for managed species, evolution may occur within the timeframe of a typical management plan. This in turn can influence the dynamics of population persistence. If selection is particularly harsh, a population may go extinct even as it evolves due to demographic stochasticity (Gomulkiewicz and Holt 1995). Further, rapid adaptation is likely to occur in the context of restoration efforts due to the fact that populations often encounter novel environmental conditions at restoration sites (Stockwell et al. 2005). These observations collectively suggest that an evolutionary approach to conservation is especially timely.

### Problem 8.1

The rate of evolution of a population adapting to a new environment is positively correlated with the genetic variability of a population. How does one measure “rate of evolution”, “adaptation”, and “genetic variability”?

### Problem 8.2

A population is in Hardy–Weinberg proportions at a particular locus. Do you think that it is valid to conclude that little or no natural selection is occurring at that locus? Remember to consider the effects of both differential survival and differential fertility.

### Problem 8.3

What is the expected equilibrium allele frequency ( $p^*$ ) in each of the following cases after an infinite number of generations in a population with two alleles? The initial allele frequency is  $p_0$ . Assume that only natural selection is affecting allele frequencies.

- (a)  $w_{11} = w_{12} = w_{22}$ ;  $p_0 = 0.40$ .
- (b)  $w_{11} > w_{12} = w_{22}$ ;  $p_0 = 0.01$ .
- (c)  $w_{11} = w_{22} = 0.9$ ,  $w_{12} = 1.0$ ;  $p_0 = 0.41$ .
- (d)  $w_{11} = 0.9$ ,  $w_{12} = 1.0$ ,  $w_{22} = 0.5$ ;  $p_0 = 0.41$ .
- (e)  $w_{11} = w_{22} = 1.0$ ,  $w_{12} = 0.5$ ;  $p_0 = 0.61$ .

### Problem 8.4

How would your answers for Problem 8.3 change if genetic drift was also acting because of small population size (say  $N_e = 20$ )? If more than one equilibrium is possible, identify which equilibrium frequency is more likely to be reached.

