6

Using Invasive Species to Study Evolution

CASE STUDIES WITH *DROSOPHILA* AND SALMON

Raymond B. Huey, George W. Gilchrist, and Andrew P. Hendry

*As invasive species spread through a new environment, they encounter novel selection pressures and challenges. Invasives thus offer rich opportunities to monitor the rate and predictability of evolution in the wild. Moreover, their evolutionary responses can alter their rate of spread as well as their interactions with native species; thus understanding whether invasive species evolve quickly or not is directly relevant to evolutionary biologists, ecologists, and conservation biologists. Here we review empirical studies of invasive species of fruit flies (*Drosophila*, focusing primarily on* D. subobscura*) and salmon (mainly* Oncorhynchus*). Both taxa have been introduced multiple times (the former by accident, the latter intentionally), offering replicated "experiments" of evolution in action. D. subobscura is an Old World fly that was introduced into both South and North America in the late 1970s. Studies pioneered by Catalonian and Chilean scientists document not only that some traits (e.g., chromosome inversions, wing size) evolved with extraordinary rapidity, but also that some (though not all) evolved predictably. Studies of introduced salmon have shown that most introductions fail; but when they succeed, many life history and morphological traits evolve quickly and (often) predictably. These and related studies show that invasive species can evolve remarkably quickly; therefore, evolutionary processes probably affect ecological*

ones. Future studies need to address how adaptive changes alter the spread of biological invaders and their interactions with native species, as well as how native species evolve in response to invaders.

Introduction

> *… for in all countries, the natives have been so far conquered by naturalised productions, that they have allowed foreigners to take firm possession of the land. And as foreigners have thus everywhere beaten some of the natives, we may safely conclude that the natives might have been modified with advantage, so as to have better resisted such intruders. (Darwin 1859, p. 83)*

Invasive species pose multiple threats to native species (Ruesink et al. 1995; Vitousek et al. 1996). An invader can add to the competitive load pressuring native species (Callaway and Ridenour 2004), disrupt the physical structure of natural habitats (Singer et al. 1984; Pollock et al. 1995), and sometimes introduce parasites or diseases that decimate natives (Daszak et al. 2000). Not surprisingly, invaders sometimes overwhelm native species, often with disastrous ecological and economic consequences (Wilcove et al. 1998). Because invasive species are growing in number around the globe, they are increasingly a major ecological concern.

Ecologists and conservationists have long drawn attention to the negative effects of introduced species (e.g., Elton 1958), but they have tended to focus on the ecological effects of invaders on the community dynamics of native species. Thus they have generally considered evolution to be largely irrelevant to the dynamics and consequences of invasion (see Thompson 1998). As a first approximation, this assumption is quite reasonable. To be sure, the initial damage caused by invasive species is often so rapid as to preclude any significant role for evolution. Moreover, invasive species might have a limited potential to evolve in general, simply because they *may* experience severe genetic bottlenecks during their introduction (e.g., Franklin and Frankham 1998; but see Goodnight 2000; Novak and Mack, this volume; Wares et al., this volume). Most importantly, however, evolution has until recently (Hendry and Kinnison 1999) generally been considered too slow to play a role in the dynamics of invasive species.

Despite such considerations, we argue here that invasive species are not just an ecological problem, but also an evolutionary one. As evidence, we review selected examples of invasive species that are evolving with extraordinary rapidity in their new environments. Moreover, parallel examples are accumulating (Diniz-Filho et al. 1999; Mooney and Cleland 2001; Palumbi 2001; Blair and Wolfe 2004; see also Drummond et al. 2003). Such rapid evolution by invaders is not just of academic interest, for it may have serious ecological and conservation consequences for native species (Stockwell et al. 2003). Consider a novel invader that harms native species. As the invader begins to adapt to the local environment, its effect on native species is likely to be exacerbated (Mooney and Cleland 2001; Lee et al. 2003). Furthermore, an invader’s spread can be accelerated by adaptation to its new environment (García-Ramos and Rodríguez 2002; Holt et al., this volume). Consequently, even though ecological interactions will dominate the initial effects of invaders on native species, local adaptation will eventually modify those interactions. Of course, native species could evolve in response to invaders (see the Darwin quote at the beginning of this chapter), so the long-term dynamics could be complex.

Invasive species cause many problems, but they nonetheless offer superb research opportunities to evolutionary biologists (Baker and Stebbins 1965). Joseph Grinnell (1919) was probably the first to suggest using invasive species to observe the dynamics of adaptation to new environments. Johnston and Selander (1964) implemented Grinnell's suggestion in their classic studies on the evolution of house sparrows (*Passer domesticus*) introduced to North America. Recently, the use of invasive species to study evolution has accelerated dramatically (Hendry and Berg 1999; Kinnison et al. 2001; Reznick and Travis 2001; Lee 2002; Parker et al. 2003; Blair and Wolfe 2004). Furthermore, the relevance of the evolution of invasive species to conservation issues is increasingly appreciated (Vermeij 1996; Mooney and Cleland 2001; Allendorf and Lundquist 2003; Stockwell et al. 2003).

Here we extend the Grinnellian perspective by turning an ecological problem into an evolutionary opportunity. Specifically, we show how introduced species can be used to address several issues of direct relevance to evolutionary biologists. We conclude by arguing that evolution feeds back on the ecology of interactions between native and invasive species and thus presents research opportunities to ecologists as well.

Invasive species can be used to address several general problems in evolution. We focus here on two:

1. How fast does evolution occur *in nature* (Darwin 1859; Simpson 1944; Hendry and Kinnison 1999)? In simple laboratory experiments, evolution is often extremely rapid (Rose et al. 1987; Lenski et al. 1991; Partridge et al. 1995). To determine whether evolution can also be fast in nature, one can monitor invasive species—or the native species with which they interact—and quantify changes in ecologically relevant traits over time scales of a few years, decades, or centuries.
2. Are patterns of evolution predictable (Gould 1989)? Laboratory or field experiments evaluate the predictability of evolutionary trajectories by setting up and monitoring replicate populations that are subject to some common selective factor (Reznick et al. 1990b; Travisano et al. 1995; Losos et al. 1998). Similarly, one can monitor the independent evolutionary responses of "replicate" introduced populations. If evolution is predictable, then the evolutionary responses of these replicate populations to specific environmental gradients (e.g., climate) should converge on those seen among ancestral populations. On the other hand, if evolution is unpredictable or highly sensitive to local conditions, then the responses of the replicate introduced populations may diverge from one another and from those of their ancestors.

To exemplify these issues, we focus on empirical studies of flies (*Drosophila*) and salmon (primarily *Oncorhynchus*). Both taxa have been repeatedly introduced around the world—the former by accident, the latter usually by intention. The repeated introductions of each taxon conveniently serve as replicated natural experiments (Ayala et al. 1989) that allow us to determine the rate, pattern, and predictability of evolutionary change in different venues and with biologically different players. Consequently, they offer an opportunity to explore the evolutionary roles of adaptation, chance, and history (Travisano et al. 1995).

Drosophila are of interest in part because numerous laboratory studies have consistently shown them capable of evolving very rapidly under controlled conditions (Harshman and Hoffmann 2000; but see Hoffmann et al. 2003). Although *Drosophila* clearly have the genetic potential to evolve quickly, laboratory studies do not imply that flies will necessarily evolve as quickly in nature (Huey et al. 1991). After all, flies in nature face uncontrolled temporal variation in environments as well as selection pressures (e.g., predators, parasites, competitors) that are traditionally excluded from the benign and constant environments of laboratory cages. Moreover, gene flow among natural populations may constrain local adaptation (Lenormand 2002), and behavioral adjustments may buffer selection on physiological and morphological traits (Huey et al. 2003). In any case, established geographic patterns for natural populations provide an evolutionary baseline (Figure 6.1A) that can be used to predict the evolutionary trajectories of introduced species.

Salmon are of interest primarily because their strong philopatry results in thousands of isolated and locally adapted populations. By studying associations between traits and environments in native salmon populations (Figure 6.1B,C), biologists can predict how salmon will evolve when introduced into new locations. Introduced salmon will face many of the same challenges as introduced *Drosophila*, including uncontrolled temporal variation, multiple selective pressures, and ongoing gene flow. Nonetheless, the two taxa differ in at least one critical way: salmon have much longer generation times (2 to 7 years) than do *Drosophila* (a few weeks in warm seasons). As a result, salmon probably face greater challenges in adapting to local environments and interacting with native species. An additional advantage of studying salmon is that precise records of sources, numbers, and times of introductions are often available.

Terminology Issues

The terms "introduced," "invasive," and "colonizing" are often used somewhat interchangeably in the literature. Here we use "introduced" to imply an intentional introduction by humans (as with salmon), but otherwise we use "invasive." We do not use "colonizing" here, as this term should apply only to natural range expansions.

We use the term "rapid evolution" to imply observable genetic changes over a short time frame (a few decades), but caution that actual rates for such "rapid"

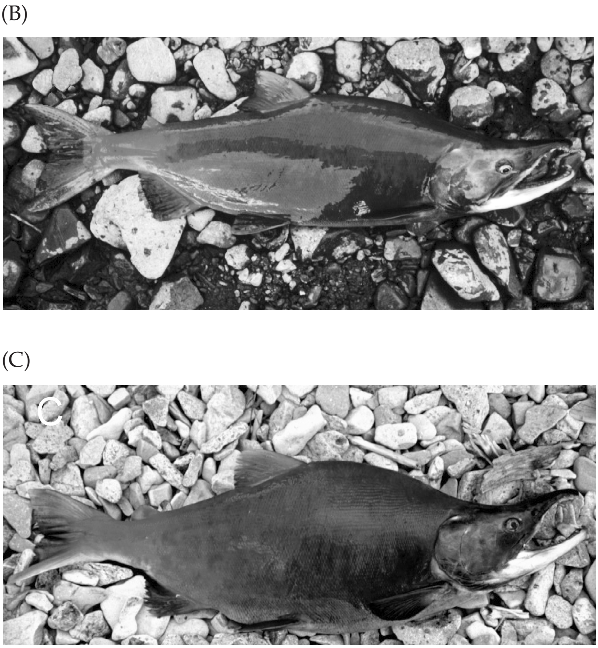

Figure 6.1 Geographic patterns in native populations provide predictive scenarios for how introduced species will evolve in new environments. (A) An example of latitudinal variation in size among Old World *D. subobscura*. As in many *Drosophila* species, high-latitude females (right) are substantially larger than low-latitude females. These flies are from Valencia, Spain (39°) and Aarhus, Denmark (56°). (B, C) Examples of morphological variation among populations of sockeye salmon in their native range. (B) A typical mature male from a medium-sized creek in Alaska (Lynx Creek). (C) A typical mature male from a beach site in Iliamna Lake, Alaska. Note the substantially deeper body of the beach male.

evolution may vary by orders of magnitude. For this reason, "contemporary evolution" has been suggested as the general term, with "rapid evolution" being reserved only for truly exceptional rates (Hendry and Berg 1999; Kinnison and Hendry 2001; Stockwell et al. 2003).

Case Study 1: Evolution of *Drosophila subobscura* on a Continental Scale

Many species of *Drosophila* are invasive (Parsons 1983), with *Drosophila melanogaster* at the forefront. This species is thought to be native to Africa, but (thanks to inadvertent human help) has successfully invaded broad ranges of latitude on all nonpolar continents. Many studies have shown that these invasive populations have evolved conspicuous and repeatable clines with latitude in diverse traits (David and Bocquet 1975; Cohan and Graf 1985; Boussy 1987; Simmons et al. 1989; James et al. 1995; Gilchrist and Partridge 1999; Hoffmann and Harshman 1999; van't Land et al. 1999). Nevertheless, *D. melanogaster* is not ideal for addressing the rate and predictability of evolution. For one thing, the initial introductions probably took place hundreds of years ago, such that we can now observe only the outcome of many generations of accumulated evolution. Moreover, repeated introductions to each continent have almost certainly taken place, contaminating and confounding evolutionary trajectories.

An alternative system for studying the rate and predictability of evolution involves *Drosophila subobscura*. The history of invasions of these flies has been well chronicled (Ayala et al. 1989), so we give only an outline here. The species is native to the Old World, where it is widespread from North Africa to Scandinavia and shows marked latitudinal clines in genetic markers and in many other traits (Krimbas 1993).

In the late 1970s, Chilean biologists discovered *D. subobscura* in the coastal city of Puerto Montt, Chile (Brncic and Budnik 1980). Very likely the flies had recently arrived by ship from the Mediterranean (Brncic et al. 1981; Ayala et al. 1989). The invaders spread rapidly; in less than a year they had colonized much of the habitable coast of Chile and had become the dominant *Drosophila* in many localities. Soon thereafter they crossed the Andes and are currently spreading in Argentina and Uruguay (Prevosti et al. 1983; Goñi et al. 1998).

In June 1982, Andrew Beckenbach discovered *D. subobscura* in central Oregon and on the Olympic Peninsula of Washington State. Intensive collecting soon thereafter revealed that the flies had already spread north into British Columbia and south to central California (Beckenbach and Prevosti 1986). As in Chile, mid- to high-latitude populations were (and still are) very abundant, and native *obscura*-group flies simultaneously became hard to collect (A. Beckenbach, personal communication). Abundant genetic evidence establishes that the North and South American populations were founded from a single stock (Ayala et al. 1989; Mestres and Serra 1995; Pascual et al. 2001).

Evolutionary geneticists immediately seized this opportunity (Brncic et al. 1981; Ayala et al. 1989), which they recognized as a "grand experiment in evolution" (Ayala et al. 1989). They recognized that the Old World populations, which probably have been evolving in place since the last glaciation, serve as an evolutionary baseline that establishes the long-term patterns of clinal evolution with latitude (see Figure 6.1A). Moreover, they recognized that the North and South American populations serve as independent evolutionary replicates. Finally, because the invasions probably took place in the late 1970s, they realized that the time frame for evolution in the New World was very short—just a few decades. Thus the invasions of *D. subobscura* offered special opportunities for monitoring rates and patterns of clinal evolution, essentially in real time (Prevosti et al. 1988).

Drosophila subobscura is a continuing focus of diverse evolutionary studies. For two traits (chromosomal inversions and wing length), several different sets of latitudinal samples have been made over time, generating a rare "time series" of evolution in action. Here we review the key points emerging from these studies, then discuss their implications for the themes of this chapter.

The bottleneck

Whether *D. subobscura* would show rapid evolution in the New World was initially debatable, simply because the genetic diversity of New World populations is greatly reduced in comparison with native European populations (Balanyà et al. 1994, 2003; Rozas et al. 1990; Mestres et al. 1992, 2004; Pascual et al. 2001). In fact, recent studies suggest that fewer than 15 individuals (probably from the Mediterranean: see Mestres et al. 2004) founded the New World populations (Pascual et al. 2001; Mestres et al. 2004). As shown below, the North and South American flies have rapidly evolved clinal patterns despite these major bottlenecks (Prevosti et al. 1985; Ayala et al. 1989; Huey et al. 2000; Pascual et al. 2001; Gilchrist et al. 2004). Nevertheless, those bottlenecks may be serving as a brake on the evolution of some traits (Balanyà et al. 2003) and may have influenced the evolutionary particulars of others (Gilchrist et al. 2001b).

Chromosomal inversions

The chromosomal arrangements that crossed to the New World are generally among the most common ones in Europe, occurring in 79% to 95% of all Old World samples (Balanyà et al. 2003). One interesting exception is the O_5 inversion, which is rare in Europe (~0.5%) but more common (6% to 7%) in the New World, and which is linked with a lethal allele in the colonizing, but not the ancestral, populations (Mestres et al. 1995). All 18 of the chromosomal arrangements that came over from the Old World were present in the first samples collected in South America in 1981 (Prevosti et al. 1985) and also in the first samples from North America collected in 1982–1983 (Beckenbach and Prevosti 1986). Furthermore, no new European chromosomal arrangements have appeared in subsequent New World collections (Balanyà et al. 2003). These facts, combined with the reduced diversity of microsatellites (Pascual et al. 2001) and DNA sequences (F. Mestres and M. Pascual, personal communication) observed in the New World, suggest that no further introductions are likely to have occurred since the initial colonization.

Most of the common (i.e., overall frequency greater than 0.01) chromosomal arrangements show significant latitudinal clines in the Old World (Menozzi and Krimbas 1992). Two alternative hypotheses have been suggested to explain these clines. First, latitudinal gradients in climate may favor different inversions at different latitudes (Prevosti et al. 1988). Second, the clines could reflect the chance colonization of northern Europe following the last glaciation by flies carrying certain inversions (Krimbas and Loukas 1980). Thus the hypotheses invoke either selection or historical contingency (e.g., phylogenetic history, founder effects, and genetic drift).

The invasion and rapid spread of *D. subobscura* in the New World provided a dramatic opportunity to test these competing hypotheses (Prevosti et al. 1988). Only 3 years after the discovery of *D. subobscura* in Puerto Montt, evolutionary geneticists collected flies from seven Chilean sites spanning 12° of latitude. They discovered that latitudinal clines in inversion frequencies were beginning to evolve (Brncic et al. 1981; Prevosti et al. 1985). Remarkably, clines for 17 of the 18 chromosomal arrangements were in the same direction with latitude as those in Europe! Collections in North America just a few years later (eight sites spanning 13°, 1985–1986) revealed clines that were again in the same direction with latitude as in Europe for 14 of 18 arrangements. Such rapidly evolving and concordant patterns on all three continents (Prevosti et al. 1988; Menozzi and Krimbas 1992) unambiguously suggest that the clines are driven by potent natural selection (Endler 1986), not by historical contingency (Krimbas and Loukas 1980).

Although the latitudinal patterns of inversion frequency are similar *in sign* on all three continents, slopes in the New World (regressing inversion frequency on latitude for Chile in 1999 and for North America in 1994) are generally far less steep than those in Europe (Balanyà et al. 2003). Climatic differences among the three continents may provide an explanation. Old World populations span more than 30° of latitude, whereas New World populations span only about 15° on each continent, suggesting that selection might be acting over a larger range of climates in the Old World. Moreover, seasonal variation in temperature at a given latitude is greater in Europe than in either New World continent, particularly South America (Addo-Bediako et al. 2000; Gilchrist et al. 2004). Thus climate-based selection might be stronger in the Old World, resulting in steeper slopes there.

Because flies had evolved shallow inversion clines within only 3 years of arriving in Chile, one might expect that the steepness of those clines would continue to converge on that of Old World clines. Surprisingly, a recent analysis of data from Chile spanning nearly two decades revealed no continued directional evolution of the clines since the early 1980s (Balanyà et al. 2003), contrary to an earlier suggestion (Prevosti et al. 1990). Apparently, the evolution of inversion clines was initially explosive, but stalled soon thereafter (Balanyà et al. 2003). This finding argues against the alternative explanation that clines might still be shallow simply because of insufficient time for divergence.

What drives latitudinal clines in inversion frequencies? Several lines of evidence suggest that temperature may be important. First, frequencies of inversions on the O chromosome of Spanish *D. subobscura* fluctuate seasonally in ways consistent with expectations based on their latitudinal patterns (Rodríguez-Trelles et al. 1996). Second, long-term shifts in frequencies have been detected within sites in Spain (Orengo and Prevosti 1996; Rodríguez-Trelles and Rodríguez 1998; Solé et al. 2002). Specifically, "southern" inversions are increasing in frequency, suggesting a response to documented climatic warming at these sites. Surprisingly, however, expected shifts in inversion frequencies have not been detected in laboratory stocks of *D. subobscura* currently evolving at three different temperatures (Santos et al. 2004), even though temperature has been shown to influence frequencies in *D. pseudoobscura* (Dobzhansky 1943; Wright and Dobzhansky 1946; Dobzhansky 1948).

In conclusion, the observed chromosomal inversion patterns in the New World conclusively resolve debates over the importance of selection versus historical contingency in this system (Prevosti et al. 1988; Ayala et al. 1989; Menozzi and Krimbas 1992). Moreover, the New World data provide a clear testament to the efficacy, speed, and repeatability of natural selection. They also show that the pace of clinal evolutionary change can be quite episodic, even over the span of a few decades. However, the hunt for unambiguous selective factors promoting latitudinal clines in inversion frequencies in *D. subobscura* (and in other *Drosophila*) continues to the present (Santos et al. 2004).

Evolutionary changes in wing size

Wing size varies across latitudinal clines in most species of *Drosophila*: flies from low latitudes have wings that are genetically smaller than flies from high latitudes (*D. melanogaster*: David and Bocquet 1975; Coyne and Beecham 1987; James et al. 1995; van't Land et al. 1999; Gilchrist and Partridge 1999; *D. obscura*: Pegueroles et al. 1995; *D. pseudoobscura*: Sokoloff 1966; *D. robusta*: Stalker and Carson 1947; *D. simulans*: David and Bocquet 1975; *Zaprionus indianus:* Karan et al. 2000). Prominent latitudinal size clines are also present in the ancestral European population of *D. subobscura* (Prevosti 1955; Misra and Reeve 1964; Pfriem 1983). Studies with *D. melanogaster* (cited above) have shown that size clines evolve predictably, at least over the course of several centuries, and that large size may be adaptive at low temperatures (Reeve et al. 2000). The invasion of the Americas by *D. subobscura* provided an opportunity to discover whether these clinal patterns could also evolve over a few decades.

Pegueroles and colleagues (1995) made the first comparative analysis of clinal variation in morphology across latitudes in populations of the ancestral and invading flies. They reared flies collected between 1986 and 1988 from seven sites in South America, six in North America, and four in Europe. They found ample clinal variation in wing size and tarsus length among the ancestral European flies, but no significant clines in either North or South America. Furthermore, wing and tarsus size were uncorrelated with environmental variables such as temperature and altitude. Thus, less than a decade after the discovery of *D. subobscura* in Chile, clines in morphology had not formed in the invading populations, even though clines in inversion frequencies had been detected earlier (as described above).

Limited evidence links wing size and chromosomal clines. Pfriem (1983) found that wing length was correlated with the frequencies of two classes of gene arrangements on the O chromosome, and Santos and colleagues (2004) recently found associations between gene arrangements and wing shape in laboratory stocks evolving at different temperatures. Nevertheless, the rapid evolution of chromosome clines in the New World (Prevosti et al. 1988) without a corresponding shift in wing length (Pegueroles et al. 1995) suggests that wing length is not inevitably influenced by gene arrangements.

About two decades after the introduction, Huey and colleagues reexamined variation in wing size along the New World and Old World clines (Huey et al. 2000; Gilchrist et al. 2001b; Gilchrist et al. 2004). Our motivation was to deter-

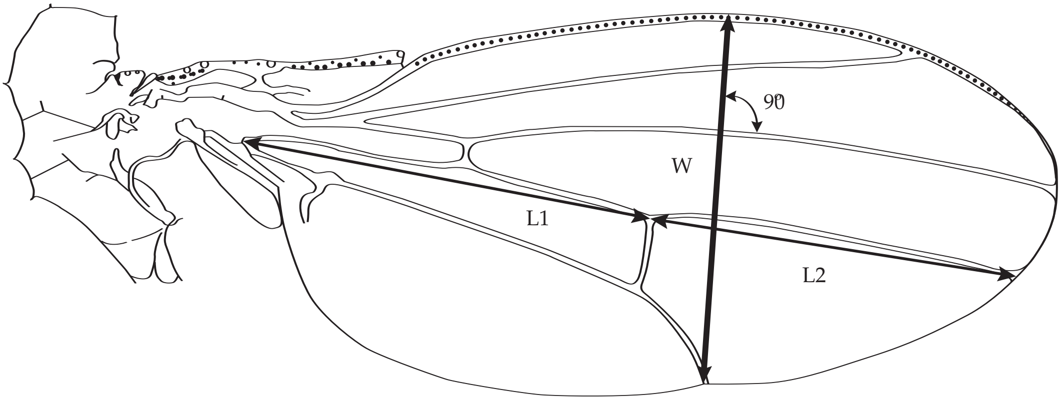

Figure 6.2 Wing of *Drosophila subobscura*, indicating the size dimensions used in our analyses.

mine whether size clines were finally detectable in the Americas. From 1997 to 1999, flies were collected from 10 sites in North America, 11 sites in Europe, and 10 sites in Chile. The sites spanned approximately 13° of latitude on each continent, were relatively near the west coast of each continent, and were below 525 m altitude. All flies were reared in a common garden in the laboratory for several generations before being measured. Three wing dimensions have been used in studies published to date: L1 is the length of the basal portion of the wing along vein IV, L2 is the length of the distal portion of the wing along vein IV, and W is the width of the wing, measured from the intersection of vein V and the trailing edge to the leading edge along a path perpendicular to vein III (Figure 6.2). These data were combined using principal components analysis. The first axis (PC1) explains about 70% of the variation in overall wing size. We also examined the component measurements independently to assess allometric change among the wing regions.

The repeatability of morphological evolution was assessed by comparing across continents the regression slopes of a given trait on latitude or on a local temperature index. Figure 6.3 shows the clinal pattern of PC1 and of the component wing traits as a function of latitude on all three continents. Slopes for females are statistically indistinguishable among the continents, although the latitudinal range in Chile is shifted approximately 6° toward the equator (probably reflecting the effect of the cold Humboldt Current: see Gilchrist et al. 2004). Thus, approximately two decades after colonization of the New World, natural selection has independently created similar patterns of geographic variation in both invading populations. But not everything is so elegantly repeated. North American males, for example, show less steep clines than do their European counterparts. The genetic correlation between male and female wing size has not been estimated in *D. subobscura*, but is essentially unity in *D. melanogaster* (Cowley et al. 1986; Reeve and Fairbairn 1996). If the genetic basis

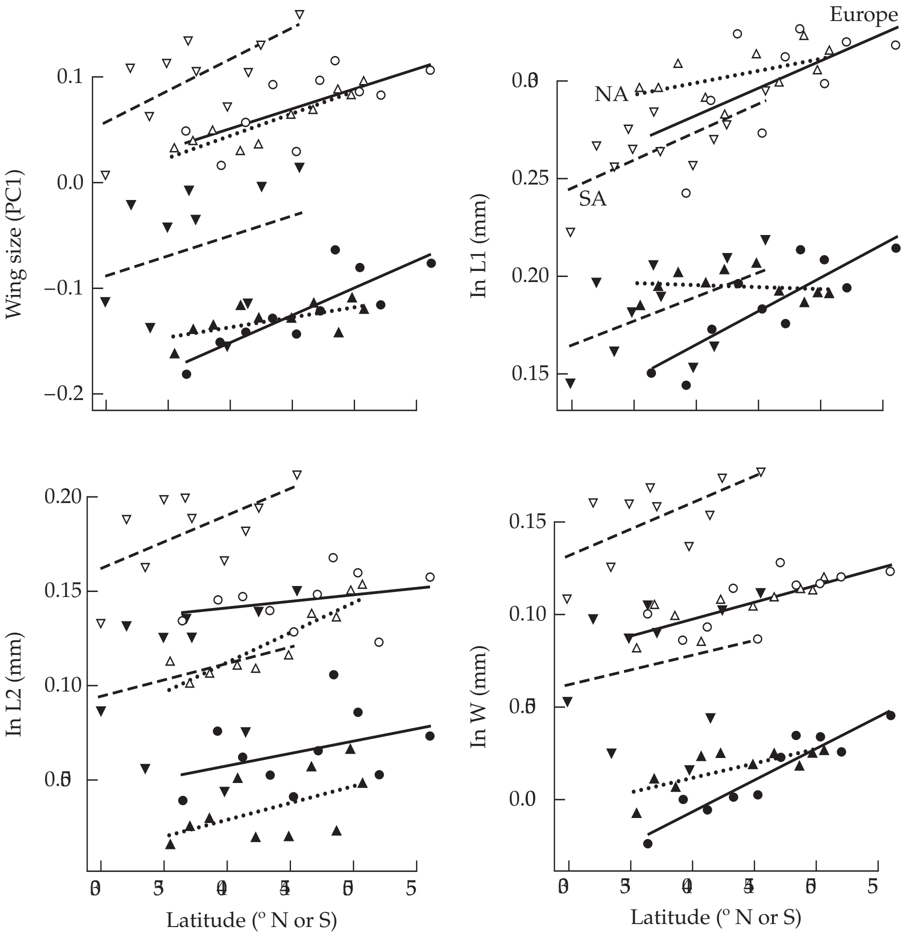

Figure 6.3 Wing size changes with latitude in Old World (circles), North American (triangles), and South American (inverted triangles) populations. Solid and open symbols represent females and males, respectively. PC1 refers to the first principal component of the three wing dimensions, L1, L2, and W (illustrated in Figure 6.2). (After Figure 2 in Gilchrist et al. 2004.)

of sexual dimorphism is similar in these two species, then the bottleneck in the founding population may have had a dramatic effect on the genetic architecture of sexual dimorphism. Additionally, males might face a different range of selection pressures in North America.

Morphological details of wing dimensions differ among continents (see Figure 6.3). The basal portion of the wing (L1) shows little clinal pattern for North American females or males, whereas it shows significant slopes in both the European ancestors and the South American invaders. South American females, but not males, tend to have shorter L1s than do European or North

American lines. In contrast, the length of the distal portion of the wing (L2) increases with latitude in both sexes in both New World populations, but shows little significant clinal pattern in Europe. Wing width (W) increases with latitude on all three continents, especially for females. South American flies of both sexes have longer and wider distal wings than their European and North American counterparts.

Concluding remarks on D. subobscura

Studies to date demonstrate that *D. subobscura* is undergoing extraordinarily rapid evolution on a continental scale. In less than 25 years, many traits have evolved—some strikingly so (see Figure 6.3). In fact, measured rates of evolution in this species are among the fastest ever documented in nature (Hendry and Kinnison 1999; Kinnison and Hendry 2001; Gilchrist et al. 2001b).

The observed patterns certainly highlight the predictability of evolutionary trajectories, but they simultaneously highlight some unpredictable aspects of evolution. Consider latitudinal clines in overall wing size (see Figure 6.3). Latitudinal patterns for females are predictable and always converge on the Old World pattern. However, those of males are much less predictable. Why patterns should differ between the sexes is unclear. Furthermore, the actual portion of the wing involved in size clines differs among the three continents (Gilchrist et al. 2004)! So even though the cline in total wing length is largely predictable, how that cline is achieved developmentally is decidedly not (Huey et al. 2000; Santos et al. 2004). Similarly, latitudinal shifts in inversion frequencies are predictable and usually converge on Old World patterns in sign, but not in magnitude (Balanyà et al. 2003).

We do not yet know whether these rapid changes will affect the competitive relations (Blossey and Nötzold 1995; Weber and Schmid 1998; Siemann and Rogers 2001) of *D. subobscura* with native species. To be sure, native *obscura*-group species, which were once abundant in the Pacific Northwest, are now hard to collect there. All in all, evolution is likely to have exacerbated the effect of this invader, but direct studies will be required to test this assumption. Surprisingly, *D. subobscura* fares poorly in competition with native species in the laboratory (Pascual et al. 1998; Pascual et al. 2000), in stark contrast to its apparent superiority in the field (Pascual et al. 1993). Nevertheless, field or outdoor-enclosure experiments remain to be done.

Case Study 2: Evolution in Introduced Salmon

At the outset of this chapter, we outlined two problems that can be addressed by studying introduced organisms: the rate and the predictability of evolution. Research on introduced salmonids (salmon, trout, char, and whitefish) readily informs both of these problems, but we concentrate here on the latter. Detailed reviews of salmonid evolutionary rates can be found elsewhere (e.g., Haugen and Vøllestad 2001; Hendry 2001; Quinn et al. 2001a; Koskinen et al. 2002; Kinnison and Hendry 2004). In brief, introduced salmonids evolve at rates typical of other introduced organisms (i.e., neither exceptionally fast nor exceptionally slow), which is itself surprising given the substantial ongoing gene flow among diverging populations.

Salmonids are well suited to a consideration of evolutionary predictability. First, they form a multitude of breeding populations that are reproductively isolated owing to strong philopatry (reviewed in Hendry et al. 2004a). Second, these populations typically adapt to their local environments (Taylor 1991; Quinn et al. 2001b). Third, groups of populations in different watersheds often have independent evolutionary origins, providing convenient replication of adaptive patterns (Wood 1995; Taylor et al. 1996; Waples et al. 2004). Fourth, salmonids have been introduced throughout the world and are now found on all major continents except Antarctica (Lever 1996). In several cases, natural dispersal after the initial introduction has generated multiple new populations, which now occupy environments that closely mirror those occupied by native (non-introduced) populations. These properties facilitate informed predictions as to how salmonids should evolve when introduced to new locations.

Research on introduced salmonids necessarily focuses on the successful introductions, but most introduction attempts have actually failed (Withler 1982; Wood 1995; Altukhov et al. 2000; Utter 2001). The record is particularly poor for anadromous salmon, which breed in fresh water but spend part of their lives in the ocean (Altukhov et al. 2000). In many cases, attempts to introduce anadromous salmonids have failed utterly despite massive and repeated efforts. Where such introductions have been successful, the new populations often forgo the anadromous life history, remaining in fresh water for their entire lives. The difficulty of establishing new populations, particularly anadromous ones, implies that introduced organisms (at least those with complex life cycles) often fail to adapt to novel environments. The successful introductions should therefore be viewed as exceptional, presumably succeeding either by chance or because environmental conditions were particularly favorable.

Several successful salmonid introductions deserve special mention. Most striking among these has been the establishment of several Pacific salmon species in the North American Great Lakes (e.g., pink salmon, *Oncorhynchus gorbuscha*: Gharrett and Thomason 1987). Interestingly, these introduced fish have adopted a quasi-anadromous life history in which the Great Lakes substitute for the ocean. Successful introductions where the true anadromous life history has been retained include sockeye salmon (*O. nerka*) in Frazer Lake, Alaska (Burger et al. 2000), and Atlantic salmon (*Salmo salar*) on the Kerguelen Islands in the southern Indian Ocean (Ayllon et al. 2004). Successful introductions are much more common for nonanadromous salmonids (Lever 1996), but these have rarely been used to examine the rate or predictability of evolution. One exemplary exception is work on European grayling (*Tymallus thymallus*) introduced to Norwegian lakes (Haugen and Vøllestad 2001; Koskinen et al. 2002). In the following sections, we describe research on two successful introductions of anadromous salmon: Lake Washington sockeye salmon (*O. nerka*) and New Zealand chinook salmon (*O. tshawytscha*).

Lake Washington sockeye salmon

In the 1930s and 1940s, more than 3 million juvenile sockeye salmon from Baker Lake (in northwestern Washington State) were introduced into Lake Washington (near Seattle, Washington) (Hendry et al. 1996; Hendry and Quinn 1997). These fish soon established new anadromous populations in several different ecological environments, with the most striking contrast being that between a large river (Cedar River) and a lake beach (Pleasure Point). Strong divergent selection is expected between these environments over the approximately 13 subsequent generations (the typical life cycle is 4 years for this species). First, breeding adults experience strong water flows in the river, but not at the beach. Second, embryos incubating in gravel nests experience floods that cause gravel "scour" in the river, but not at the beach. Third, incubating embryos experience variable and cold temperatures in the river, but constant and warm temperatures at the beach (Hendry and Quinn 1997; Hendry et al. 1998). These and other putative selective agents, coupled with observed phenotypic variation among native (non-introduced) populations found in other watersheds, allow robust predictions of how deterministic evolution should proceed within the Lake Washington watershed. Deviations from these predictions would suggest that contingency may have played a role. Unfortunately, the ancestral Baker Lake population has not bred in its natural environment for more than a century (Hendry 2001), which precludes direct comparisons between Lake Washington populations and their ancestral source.

Perhaps the most obvious deterministic prediction relates to male body depth, a secondary sexual trait that increases dramatically with maturation (Hendry and Berg 1999). Deep-bodied males are favored by sexual selection because they are dominant during male-male competition for breeding females (Quinn and Foote 1994). In fast-flowing rivers, however, a deep body is hydrodynamically inefficient (Kinnison et al. 2003; Crossin et al. 2004), particularly because males often orient perpendicular to the flow of water during breeding competition. Accordingly, males from native beach populations consistently have deeper bodies at a common length than do males from native river populations (Blair et al. 1993; Quinn et al. 2001b) (see Figure 6.1B and C and Figure 6.4).

Has the same pattern evolved within Lake Washington? Males in this watershed generally have shallower bodies than males in the native populations surveyed thus far, but Pleasure Point (beach) males nevertheless have deeper bodies than Cedar River males at a common body length (Figure 6.4; Hendry and Quinn 1997; Hendry et al. 2000). Moreover, the relative difference in standardized body depth between beach and river males in Lake Washington (13.0%–13.8%) is similar to the relative difference between beach and river males in native populations (Hendry et al. 2000). For example, the mean difference in standardized body depth between beach and river males in Iliamna

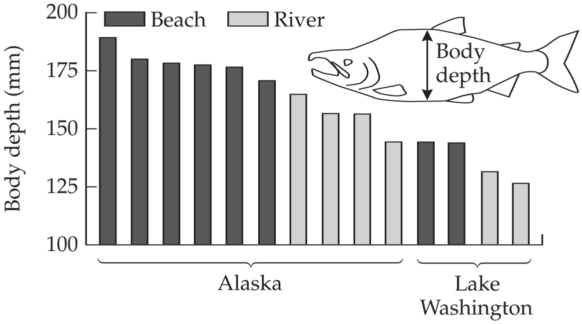

Figure 6.4 Average adult male body depths in beach and river populations from Alaska (native) and Lake Washington (introduced). (Data for Alaska from Quinn et al. 2001b; data for Lake Washington represent samples from two different years and are from Hendry and Quinn 1997 after standardization to the same body length [450 mm] used by Quinn et al. 2001b.)

Lake, Alaska, is 12.8% (Blair et al. 1993; Hendry 2001). Thus the evolution of male body depth seems to have been rapid and predictable, with a caveat that the relative contributions of genetic variation versus phenotypic plasticity are not yet known. Detailed considerations, however, suggest that adaptive divergence in male body depth within Lake Washington is at least partially genetically based (Hendry 2001), just as it is for populations of chinook salmon introduced to New Zealand (Kinnison et al. 2003).

Another deterministic prediction relates to female body length. Females oviposit into gravel nests, where their eggs then incubate for several months. High water flows during this period can mobilize the gravel and "scour" nests, causing high embryo mortality. Larger females can bury their eggs deeper in the gravel (Steen and Quinn 1999), which reduces the risk that their eggs will be lost to scour. Thus selection should favor larger females in high-scour environments. Within Lake Washington, the Cedar River is subject to strong gravel scour that causes high embryo mortality (Thorne and Ames 1987), whereas the Pleasure Point beach is largely devoid of scour. Matching this selective difference, Cedar River females are 5.5%–7.1% longer than Pleasure Point females (Hendry and Quinn 1997; Hendry et al. 2000; Hendry 2001). However, as with male body depth, a genetic basis for divergence in female length has not been unequivocally documented (Hendry 2001).

A third set of deterministic predictions relates to the effects of water temperature on the development of salmonid embryos incubating in the gravel. Conveniently, Pleasure Point beach and Cedar River embryos are exposed to very different temperature regimes. The former incubate in upwelling groundwater with a constant temperature of 10°C, whereas the latter incubate in temperatures that range from 8°C in mid-November to 4°C in the middle of winter and back up to 9°C by mid-April. Relying on observed patterns for native populations, we predicted that these temperature differences would cause local adaptation of survival, development rate, and developmental efficiency to river and beach sites within Lake Washington (see Hendry et al. 1998).

To test these predictions, we captured adults from both populations, used artificial fertilization to generate full-sib families, and then raised siblings from each family at 5°C, 9°C, and 12.5°C. Contradicting our prediction, river and beach embryos did not differ in survival or in development rates (Hendry et al. 1998). Matching our prediction, however, embryos from each population attained their largest size when incubating at the temperature closest to that which they would experience in nature (Hendry et al. 1998). This last result suggests the presence of genetic divergence in temperature-specific developmental properties that maximize embryo size, a critical trait in wild salmon (reviewed in Einum et al. 2004).

Did any aspects of the Lake Washington study system facilitate evolutionary divergence? Historical records are incomplete, but the original Baker Lake population seemingly contained both beach and river fish, with hatcheries then mixing both into a single panmictic group for about 10 generations preceding the Lake Washington introductions (Hendry 2001). This mixing of beach and river gene pools may have generated a highly variable group of introduced fish, thus facilitating evolutionary divergence following the colonization of beach and river environments in Lake Washington (for a detailed discussion, see Hendry 2001).

In summary, results for Lake Washington suggest that when evolutionary divergence occurs, it does so predictably. Each of the traits that *did* differ between the introduced populations did so in accordance with the expected role of divergent selection and with patterns previously documented in native populations. Moreover, the degree of differentiation between river and beach populations is similar for introduced and native populations. Thus divergent natural selection appears to generate predictable adaptive divergence in very short order—here, in fewer than 13 generations! Furthermore, the role of contingency seems limited to determining which traits evolve and which do not. As a caveat, however, trait divergence in Lake Washington has not been studied at the level of detail that was necessary to reveal a role for contingency in introduced *Drosophila* (Gilchrist et al. 2001a).

New Zealand chinook salmon

In 1901 and 1904–1907, juvenile chinook salmon from the Sacramento River, California, were introduced into the Hakataramea River on South Island, New Zealand (McDowall 1994; Quinn et al. 1996; Kinnison et al. 2002). Descendants of these fish then dispersed and established self-sustaining populations in other rivers on South Island. Environmental characteristics differ among these rivers, suggesting that selection might have promoted evolutionary diversification over the 26 subsequent generations (generation length for these populations is estimated at 3.2 years). Indeed, genetic differences among these populations have been confirmed for many phenotypic traits (reviewed in Quinn et al. 2001a). Here we focus on a single selective factor—migratory distance—that allows particularly clear interpretations.

Maturing salmon cease to feed when they enter fresh water. Their upstream migration, as well as all subsequent breeding activity, must then be fueled with stored energy (Hendry and Berg 1999). This strict energy budget leads to trade-offs among various aspects of reproductive investment and generates strong selection to maximize energy use efficiency. One axis of this trade-off is the amount of energy required for migration to the breeding grounds, which depends critically on the difficulty and length of the upstream migration. Accordingly, native populations that migrate longer distances typically (1) store more energy before entering fresh water, (2) use more energy during upstream migration, and (3) invest less energy in ovaries and have smaller eggs and smaller secondary sexual characteristics (e.g., Beacham and Murray 1993; Hendry and Berg 1999; Healey 2001; Kinnison et al. 2001; Crossin et al. 2004). Some of this variation probably reflects the proximate costs of migration (i.e., plasticity), but some of it probably also has a genetic basis (reviewed in Hendry et al. 2004b).

Research on chinook salmon introduced to New Zealand confirmed that upstream migrations are energetically costly. Juveniles were produced by artificial fertilization from two populations that differ in migration difficulty: Glenariffe (100 km and 430 m elevation) and Hakataramea (60 km and 200 m elevation). Representatives from each family were then released at two locations, one requiring a more difficult migration (Glenariffe) than the other (Silverstream, 17 km and 17 m elevation). The juveniles "imprinted" on the release sites, migrated to the ocean, and returned with strong fidelity to the release sites as adults. Sampling of the returning adults revealed that fish migrating the longer distance had substantially smaller ovaries, smaller eggs, smaller secondary sexual characteristics (hump size and snout length), and lower energy stores, but not fewer eggs, compared with their siblings migrating the shorter distance (Figure 6.5; Kinnison et al. 2001; Kinnison et al. 2003). Thus, migration imposed a substantial proximate cost, manifested as a phenotypically plastic reduction in the size of several traits.

Representatives from these same experimental families were also raised for their entire lives in a hatchery (i.e., a common garden), allowing a test for evolutionary divergence after 26 generations of potential adaptation to migration difficulty (Hakataramea vs. Glenariffe). In this common hatchery environment, the population adapting to the longer migration had relatively larger ovaries, more eggs, and smaller humps; however, the two populations had similar egg sizes, snout lengths, and energy stores (Kinnison et al. 2001; Kinnison et al. 2003) (see Figure 6.5). Thus adaptation to different migration distances led to substantial genetic changes in some traits, but not others.

How might these evolutionary changes (or the lack thereof) be interpreted in the context of natural selection? One predictable result was the genetically smaller hump size for the population migrating the longer distance (see also Crossin et al. 2004). Individuals with smaller humps should have enhanced migratory ability because they are more hydrodynamically efficient. Moreover, developing larger humps expends energy that might otherwise be used for migration or breeding. Supporting these ideas, hump size and somatic energy stores were negatively correlated for adults that migrated 100 km to Glenariffe, but not for those that migrated only 17 km to Silverstream (Kinnison et al. 2003).

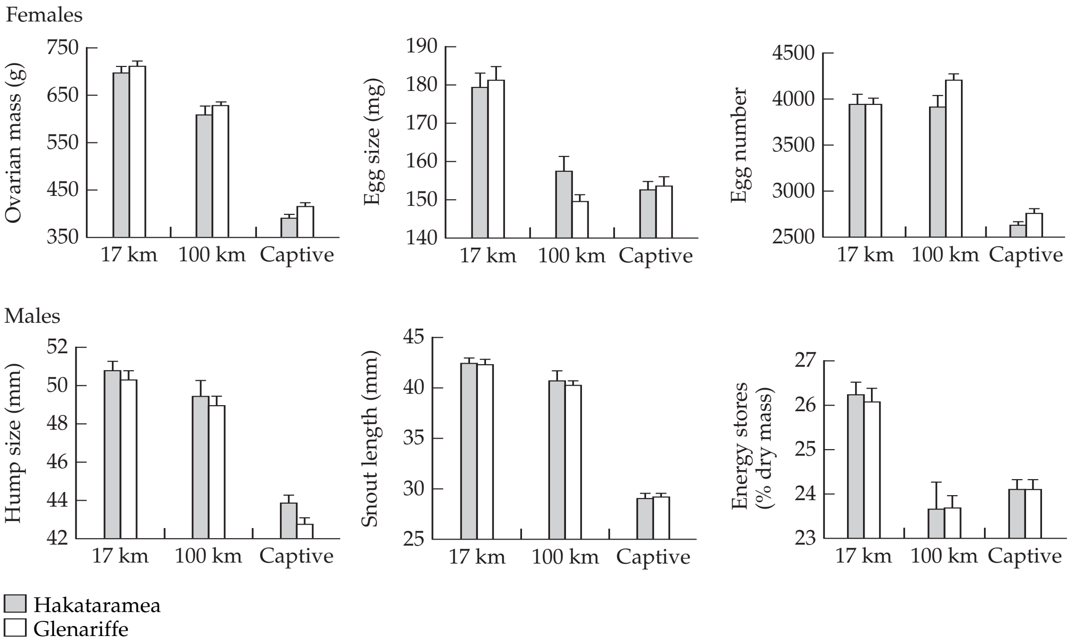

Figure 6.5 Reproductive traits for females of all ages and secondary sexual traits and energy stores for 2-year-old males from two New Zealand chinook salmon populations. The Hakataramea population naturally migrates 60 km before breeding, while the Glenariffe population naturally migrates 100 km. Juveniles were released at two river sites (100 km and 17 km from the ocean), where they imprinted, migrated to the ocean, and subsequently returned as adults. Representatives of the same families were also reared in a common hatchery environment (Captive). Mean trait values (with standard errors) are shown after standardization to a common body size. The difference between the 17 km and the 100 km migration treatments is significant ($P < 0.05$) for all traits. Comparisons between the migration treatments and the captive treatment were not performed because of entirely different diets and conditions. The difference between the two populations in the captive environment is significant ($P < 0.05$) for ovarian mass and hump size, and marginally significant ($P = 0.07$) for egg number. Comparisons between the two populations within each migration treatment were not performed because we cannot be sure they shared a common environment after release. (From Kinnison et al. 2001, 2003; and M. T. Kinnison, unpublished data.)

In addition, males experienced greater somatic energy losses than did females, presumably because males have larger humps (Kinnison et al. 2003).

Another predictable result was the genetically larger ovarian mass in the longer-migrating population, a difference that partially offsets the proximate cost of migration on this trait (see Figure 6.5). This result might seem to be in conflict with data from native populations, wherein ovary size and migration distance are negatively correlated. The work in New Zealand, however, shows that such phenotypic trends in wild populations are probably caused by proximate effects of migration that obscure an opposite trend in the genetic contribution to ovarian investment (i.e., countergradient variation). That is, longer-migrating populations have a genetic tendency to invest more energy in ovaries, but this tendency is not reflected in a higher ovarian mass at maturity because they also expend more energy during the migration itself.

Not all of the results for New Zealand chinook salmon were immediately predictable. Neither egg size, snout length, nor energy stores differed between the populations after rearing in a common hatchery environment, whereas egg number did. These results seem puzzling because each trait, *except* for egg number, was influenced by the proximate cost of migration. Interestingly, the genetic architecture of these traits may help explain the results for egg size and number. Specifically, the genetic correlation between ovary size and egg number appears greater than that between ovary size and egg size (Kinnison et al. 2001). As a result, selection to increase ovarian mass (to compensate for the proximate cost of migration) should lead to a greater initial increase in egg number than in egg size. This argument assumes little or no variation among populations in direct selection on egg size or number. Alternatively, smaller eggs may be favored in populations that migrate longer distances (Healey 2001; Kinnison et al. 2001). The lack of evolutionary divergence for snout length and somatic energy stores, however, currently remains unexplained.

Closing remarks on salmon

Studies of introduced salmon suggest that evolution is driven primarily by deterministic (predictable) processes such as natural selection. The role of contingency (e.g., phylogenetic history, founder effects, and genetic drift)at this taxonomic level appears related to which traits evolve and which do not. The importance of deterministic processes has also been confirmed for introduced European grayling (Koskinen et al. 2002). This is not to say that contingency does not have important effects. For example, it probably plays a substantial role in determining which populations survive the initial introduction. Moreover, patterns of life history variation show a signature of both deterministic and contingent events even among native salmon populations (Kinnison and Hendry 2004; Waples et al. 2004).

Parallel Opportunities That Can Be Exploited

We have highlighted some examples from studies of *Drosophila* and salmon, but we would be remiss not to mention that other introduced species offer similar opportunities. Indeed, diverse studies have recently documented rapid evolution of introduced and invasive species (Diniz-Filho et al. 1999; Losos et al. 2001; Maron et al. 2004), sometimes even involving reaction norms (Lee et al. 2003).

Many species of animals and plants are (like salmon) being intentionally introduced around the globe for agriculture or sport. For example, honey bees, trout, chickens, cattle, and sheep have been introduced into most continents;

these introductions provide biologists with many opportunities to study (often in replicate) adaptation to local environments. Of course, concomitant selective breeding may enhance (or sometimes confound) patterns of local adaptation of these species.

Similarly, although our focus has been on invasive species themselves, one could just as well look at the evolution of native species responding to an exotic. For example, the intentional introduction of predators into streams has had dramatic effects on the life history, morphology, behavior, and physiology of native guppies (Reznick et al. 1990a). Similarly, the introduction of exotic plants has led to the evolution of soapberry bugs (Carroll and Boyd 1992; Carroll et al. 2001) and of apple maggot flies (Filchak et al. 2000). The introduction of the European periwinkle *Littorina* into Connecticut prompted evolutionary shifts in the shell preferences of native hermit crabs (Blackstone and Joslyn 1984). Interestingly, plastic and genetic changes in the shell shape of *Littorina* have since been changed by an invasive crab (Trussell and Etter 2001).

Ecological Implications of Rapid Evolution

Our review of a few selected studies shows that the evolution of invasive and introduced species is often—though not always—rapid, predictable, and dramatic. These observations are directly relevant to classic debates in evolution (Darwin 1859; Simpson 1944; Gould and Eldredge 1977). In addition, they have profound significance for those attempting to monitor (as well as to blunt) the negative effects of introduced species on native species. Specifically, as introduced species rapidly adapt to local physical and biotic environments, their ecological effects are likely to grow. If they are "bad" just after arriving, they may well become even worse (Maron et al. 2004).

Even so, we can try to turn this problem to our advantage, at least from an academic perspective. Consider *D. subobscura*, which was probably introduced to the Americas from the Mediterranean (roughly 40° latitude) and which has now colonized much colder sites in both North (51°) and South America (46°). As these "southern" flies adapt to cold environments at high latitudes, their competitive effects on native, cold-adapted species might well increase. But does this actually occur? Currently no one knows. However, this possibility can be tested by setting up competition experiments, either in the laboratory (Pascual et al. 1998; Pascual et al. 2000) or in seminatural enclosures. At a high-latitude site in Washington State, for example, one might set up competition experiments involving native *Drosophila* versus local *subobscura*, versus *subobscura* from southern California, or perhaps even versus the presumed source Mediterranean population. If local adaptation has enhanced competitive ability since the introductions (see Bossdorf et al. 2004), then high-latitude *subobscura* should fare better in competition with native high-latitude congeners than should *subobscura* either from California or from the Mediterranean. Should that prove to be the case, it will further validate our central thesis; namely, that invasion is an evolutionary as well as an ecological problem.

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