NOTES AND COMMENTS

PARALLEL SPECIATION BY NATURAL SELECTION

Natural selection plays a prominant role in most theories of speciation. Mayr (1963) and others viewed selection as one of the causes of genetic divergence between allopatric populations that yielded reproductive isolation as an incidental by-product. Selection is also invoked in models of parapatric (Endler 1977), reinforcement (Dobzhansky 1951), founder event (Barton 1989), and sympatric (Diehl and Bush 1989) speciation. Yet there is surprisingly little evidence from nature in support of its role in any scenario.

Our purpose here is to introduce an unappreciated form of evidence for natural selection that we call "parallel speciation." This we define as the repeated independent evolution of the same reproductive isolating mechanism. Below, we explain the phenomenon, list criteria needed to demonstrate it, and identify several possible examples from nature. We discuss broad implications of parallel speciation and review several mechanisms that can produce it. Throughout we use the concept of biological species (Mayr 1963): populations belong to the same species only if they are not reproductively isolated. We add the proviso that reproductive isolation between good species may be imperfect.

PARALLEL SPECIATION

We first review the concept of parallel evolution. This is a form of homoplasy in which the same trait evolves independently in separate closely related lineages (Futuyma 1986). For example, an ancestral species may give rise to two or more populations in a new type of environment in which independent transitions to smaller body size take place (fig. 1A). Or in a second scenario two new types of environments may be colonized multiple times, leading to repeated divergence in body size between populations in different environments (fig. 1B). The repetition of evolutionary changes in similar environments strongly implies that natural selection was the cause (Clarke 1975; Endler 1986) because genetic drift will not commonly produce concerted shifts in the same direction. This interpretation is strengthened if the environmental agents causing parallel evolution can be identified. Parallel evolution is common. Recent examples include parallel morphological and life-history evolution in cave amphipods (Jones et al. 1992; Kane et al. 1992; Culver et al. 1994), freshwater sticklebacks (Schluter and McPhail 1993),
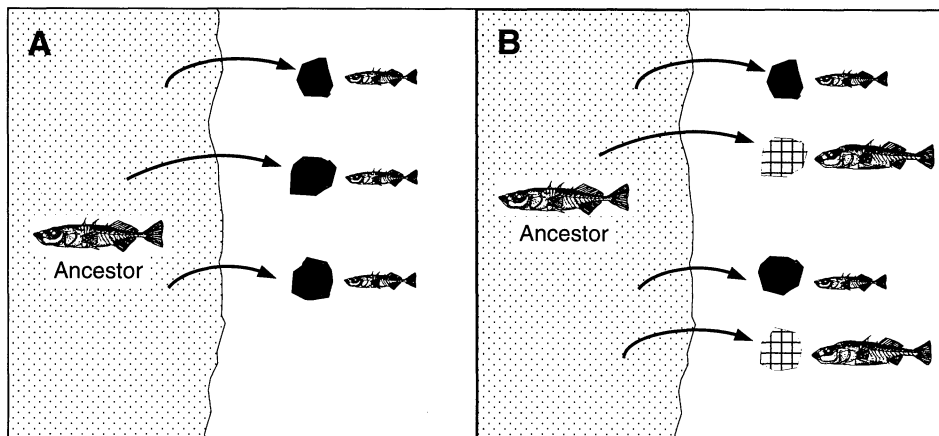
FIG. 1.—Example scenarios for parallel evolution and parallel speciation. Shaded areas are geographical ranges; shading type indicates environment type (e.g., habitat). Arrows indicate establishment of new daughter populations from a phenotypically uniform ancestral species. A, Colonization of replicate new environments leads to repeated evolution of small body size (and of mate preferences for small size). B, Colonization of two environment types causes repeated divergence in body size (and of mate preferences for body size) between daughter populations inhabiting different environments.

Anolis lizards (Losos 1992), and freshwater salmon (Foote et al. 1989). In some examples the sequence of steps that led to similar phenotypes in independent populations might be more accurately described as "convergence" rather than parallelism. This distinction is minor when dealing with closely related forms, and we use the term "parallel" for simplicity.

We consider parallel speciation to be a special case of parallel evolution in which traits that confer reproductive isolation evolve independently in the same way in separate closely related lineages. The outcome of such multiple speciation events is an absence of reproductive isolation between independently derived populations in similar environments. For example, a preference for mates having small body size may accompany parallel transitions to small size (fig. 1A). Parallel speciation has then occurred because small-bodied daughter populations are reproductively isolated from their common ancestral form but are not reproductively isolated from one another. In the second scenario (fig. 1B) parallel speciation occurs when reproductive isolation evolves between populations in different environments but not between independent populations inhabiting similar environments.

Two selection experiments with *Drosophila* have resulted in parallel evolution of premating isolation (reviewed in Rice and Hostert 1993). Kilias et al. (1980) raised lines of *Drosophila melanogaster* in either a cold-dry-dark or a warm-damp-light environment, and Dodd (1989) placed flies in high-starch or high-maltose environments. In both studies some premating isolation evolved between lines in alternative environments, but none evolved between replicate lines experiencing the same environment. Reproductive isolation between divergent lines

was not complete (e.g., because more time may be needed), but the findings indicate the plausibility of full parallel speciation. The question we address is, Does it commonly happen in nature?

Three criteria must be satisfied to demonstrate parallel speciation. First, separate populations in similar environments must be phylogenetically independent, such that shared traits responsible for reproductive isolation evolved separately. Second, ancestral and descendant populations (or sets of descendant populations inhabiting different environments) must be reproductively isolated. Third, separate descendant populations inhabiting similar environments must not be reproductively isolated from one another. A fourth criterion is needed to establish that natural selection is the cause of parallel speciation: an adaptive mechanism must be identified and tested.

The fourth criterion is meant to distinguish parallel speciation by adaptive processes (which are our main interest here) from those caused by special genetic mechanisms such as polyploidy. For example, each of the tetraploid plant species *Tragopogon mirus* and *Tragopogon miscellus* and the tetraploid frog *Hyla versicolor* has arisen multiple times from diploid progenitors (Novak et al. 1991; Ptacek et al. 1994). Separate independent polyploids are parallel species if they are reproductively compatible with one another (which is suspected but not yet tested). However, each speciation event happened in a single step and natural selection played little role.

To our knowledge these four criteria have never been tested in natural populations. Hence, there are no unassailable examples of parallel speciation. We feel this is because little attention has heretofore been drawn to its theoretical significance. Nevertheless, data from at least four systems show promise, and we summarize these below.

We uncovered one other independent use of the term "parallel speciation" in the literature; it was used to refer to the repeated evolution of a distinct body morphology in closely related fish lineages (Goto and Andoh 1990). This is simply parallel evolution by our definition. We recommend that parallel speciation refer only to the parallel evolution of the same reproductive isolating mechanism. Parallel evolution of morphology accompanied by diverse mechanisms of reproductive isolation is not parallel speciation by our definition.

POSSIBLE EXAMPLES

Four possible cases were identified. They are incomplete mainly because they satisfy the third criterion above only indirectly: absence of reproductive isolation between independent daughter populations in similar environments is judged by whether they share traits known to determine isolation between species in different environments. The test is indirect because it lacks a direct measure of reproductive isolation between independent daughter populations.

Threespine sticklebacks.—Populations of threespine sticklebacks (*Gasterosteus aculeatus* complex) that colonized freshwater from the sea at the end of the Pleistocene (ca. 13,000 yr B.P.) exhibit extensive parallel evolution. Very similar body forms have evolved multiple times in different watersheds. For example,
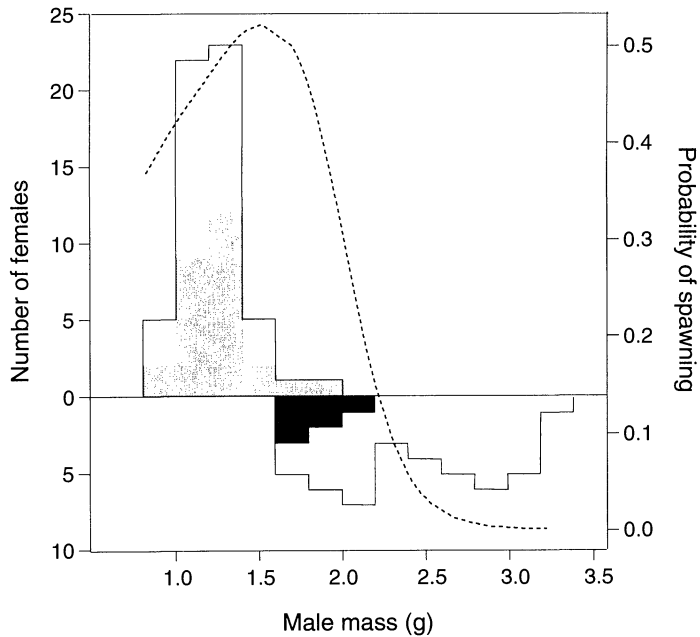
FIG. 2.—Spawning of female limnetic sticklebacks in relation to male body mass. Outlined histograms give mass distributions of male limnetics (*upright*) and male benthics (*inverted*) used in the experiment. The shaded portions indicate masses of males that spawned with females; dark regions indicate cross-species matings. The dotted curve gives overall probability of spawning as a function of male size, estimated using the cubic spline (Schluter 1988); $N = 99$. Data from Paxton and Priest Lakes were similar and are combined.

the large-bodied marine species has independently given rise to smaller-bodied freshwater forms throughout its holarctic range, of which a number are reproductively isolated from it (Bell 1976; Borland 1986; Ziuganov et al. 1987; McPhail 1993; Orti et al. 1994). Additionally, morphologically different sympatric species (a small, slender, "limnetic" and a larger, more robust, "benthic" species) exploit different habitats in several small coastal lakes of British Columbia, Canada. Each pair is thought to have diverged independently and in parallel from a common marine ancestor (Schluter and McPhail 1992; McPhail 1993; E. B. Taylor and J. D. McPhail, personal communication). We judged whether parallel speciation has also taken place by determining whether morphological differences are important to reproductive isolation.

Two studies suggest that size is important in premating isolation. First, mating is strongly size assortative where breeding distributions of large-bodied marine and smaller stream-resident sticklebacks overlap: stream-resident males mate preferentially with small females (Borland 1986). Second, mating is also size assortative in lakes containing two sympatric species that differ in size (fig. 2). These data are from a series of mating trials using wild fish from Priest and Paxton Lakes, British Columbia (Nagel 1994). A trial consisted of adding a single gravid

limnetic female to a 55-L aquarium containing a single male (limnetic or benthic species) actively displaying around his nest. After 30 min we recorded whether the pair had spawned. Probability of a limnetic female spawning with a male declined with increasing male size. Cross-species matings occurred only with the smallest benthic males—those most similar in size to limnetic males. Further analysis showed that cross-species matings also involved only the largest limnetic females—those most similar in size to the benthic species (Nagel 1994).

Mechanisms of postmating isolation may also be shared between separate species pairs. For example, hybrids between limnetic and benthic species have reduced feeding efficiency and slower growth in the wild, stemming from their intermediate morphology rather than from intrinsic genetic incompatibilities (Schluter 1993, 1994; T. Hatfield and D. Schluter, unpublished data). Intermediate morphology of hybrids is a feature shared among separate species pairs, and hence the mechanism of selection against them is also shared.

Sockeye salmon.—Pacific sockeye salmon (*Oncorhynchus nerka*) colonized freshwater in Asia and North America after the last glaciation. Adults usually migrate into lakes and tributaries to spawn and die, and their young remain in freshwater for 2 yr before migrating back to sea. This species independently gave rise to nonmigratory freshwater populations ("kokanee") in many drainages (Ricker 1940; Foote et al. 1989). These underwent parallel evolutionary shifts in various morphological and life-history characters (Wood and Foote 1990). Significant differences in allele frequencies between sympatrically breeding sockeye and kokanee suggest little gene flow between them (Foote et al. 1989). Among the most striking differences between the species is the smaller body size of kokanee (Foote and Larkin 1988). This difference results in a low number of cross species matings because assortative mating is size based (Foote and Larkin 1988). Thus, a trait that strongly affects premating isolation has evolved in parallel multiple times.

Traits causing postmating reproductive isolation may also have evolved in parallel in different drainages. Hybrids between the two forms have high viability and fertility when raised in the laboratory (Wood and Foote 1990). However, whereas kokanee and sockeye fry have synchronous emergence dates, F_1 hybrids emerge as free-swimming fry earlier or later in the season (depending on the cross that produced them) because of a subtle mismatch between maternal (egg size) and genetic components of offspring development rate (Wood and Foote 1990). Hybrids also have reduced capabilities in saltwater.

Cave amphipods.—The amphipod *Gammarus minus* has evolved reduced eyes, long antennae, and large body size independently in caves of several drainage basins (Kane et al. 1992; Culver et al. 1994). Allozyme differentiation is greater between cave and spring populations of the same drainage than between spring populations in different drainages (Kane et al. 1992), suggesting little current gene flow between adjacent caves and springs. The question is thus whether traits that confer reproductive isolation between cave and spring have also evolved in parallel.

Male mating success in caves increases with increasing antenna length and decreasing eye size, possibly reflecting differential ability of males to find mates

(Jones and Culver 1989; Jones et al. 1992). It follows that migrants between cave and spring would be selected against on the basis of eye size and antennal length but that migrants between caves would not. Body-size differences produce even stronger postmating isolation between cave and spring. A large immigrant from a cave to a stream would face a battery of size-selective fish predators; an immigrant of the small stream form to a cave is likely to be preyed on by the larger cave amphipods (Culver et al. 1994).

Size also confers premating isolation between independently evolved cave and spring forms. Small spring males are physically unable to amplex and mate with large cave females; cave males are highly likely to eat the small spring females rather than mate with them (Culver et al. 1994). Premating isolation has not been measured between different cave populations, but their similarity in size would not lead to the mating problems seen between cave and spring individuals.

Darwin's finches.—Galápagos ground finches provide one of the most vivid and carefully documented examples of natural selection's role in the evolution of size and shape (Boag and Grant 1981; Price et al. 1984; Grant 1986; Gibbs and Grant 1987; Grant and Grant 1989, 1993). Manipulations of body dimensions of stuffed female specimens presented to breeding males revealed that a large part of assortative mating between species is based on size and shape of the beak and body (Ratcliffe and Grant 1983). The implication is that a considerable degree of premating isolation between finch species has evolved along with morphological divergence (Grant 1986).

It is unknown whether size differences between species have evolved more than once. However, morphologically distinct species on a given Galápagos island are sometimes more similar electrophoretically to one another than are populations of same species on different islands (Yang and Patton 1981). This could mean that each morphological "species" has evolved more than once—a hypothesis not too farfetched in light of the observed speed of morphological evolution (Boag and Grant 1981; Price et al. 1984; Gibbs and Grant 1987). An alternative interpretation of the genetic data is that gene flow occurs between sympatric finch species (Grant and Grant 1992; Grant 1993).

DISCUSSION

The major implication of parallel speciation is that it provides strong correlative evidence for the role of environmental selection in the origin of species. Rice and Hostert (1993) summarized compelling evidence from laboratory experiments that divergent natural selection between populations can generate partial reproductive isolation. The examples above, if they withstand further scrutiny, show that similar events leading to virtually complete reproductive isolation have occurred in the wild.

A weakness of our examples is that none has direct evidence of whether independent daughter populations occurring in similar environments are reproductively isolated from one another. Fulfilling this criterion is essential for two reasons: replication is needed to establish whether traits causing reproductive isolation co-vary with environment, and crosses between daughter populations

occurring in similar environments are the surest (though not the only) means to establishing whether the measured traits are the actual cause of reproductive isolation. Presence of reproductive isolation between daughter populations in similar environments would imply that unique mechanisms of isolation are responsible for each speciation event, in which case no evidence would exist that environmental selection pressures played any role. Parallel speciation is thus a very conservative test: there are likely many cases in which natural selection has caused speciation, but this cannot be detected because replication is lacking.

Most of these examples found that pre- and postmating isolation is dependent on species differences in body size (though shape differences were also implicated in some cases). The apparent predominance of size may reflect a general tendency for reproductive isolation to depend on body morphology and the common tendency for closely related species to diverge in body size.

We think it is significant that our examples of parallel speciation are from local populations at the margins of the distribution of a more widespread parent species. Such a geographical setting is probably ideal because of the large number of daughter populations that may be spawned in new environments. This same setting was also suggested by Mayr (1963) to be conducive to "peripatric" speciation by founder events. It is difficult to imagine how founder events, which involve a large random component, would lead to parallel evolution of reproductive isolation in separate daughter populations. Consequently, parallel speciation may be strong evidence that founder events have played little role. Young, peripherally isolated species thus provide useful material for tests of alternative speciation modes.

Another implication is that since pre- and postmating isolation are contingent on divergent selection pressures, a reversal of selection can cause speciation to unravel. This mechanism of species diversity collapse is distinct from that caused by enhanced gene flow between species (e.g., following range changes or habitat disruption) because it results from a reversal in the direction of evolution and may happen in the absence of gene flow. A possible example is in the amphipod *Gammarus minus,* in which recent collapse of cave passages has reexposed segments of dark-adapted populations to light. The morphology of these cave populations has reverted wholly or partly to the original spring-inhabiting form (Culver et al. 1994), although the consequences for reproductive isolation are unknown. Such reversals are worthy of study (and even of initiating experimentally) as they would help reveal mechanisms of selection that caused species to form.

A final implication of parallel speciation is that true biological species (defined by the criterion of reproductive isolation rather than morphological criteria) may often be polyphyletic. That is, the traits that permit interbreeding between populations may have been acquired independently. Such cases are instructive for the processes that cause evolution but pose problems for systematists. Under the phylogenetic species concept (Cracraft 1989) each independent daughter population would instead be classified as a distinct species even if individuals from the different populations did not discriminate among one another when choosing a mate and even though the ecological fates of the different populations were similar. The very existence of polyphyletic species underscores the complete incompatibility between the biological and the phylogenetic species concepts.

Parallel evolution of reproductive isolation may occur through three classes of mechanisms (see also Endler 1989). In the first, traits causing premating isolation evolve nonadaptively because they are genetically correlated (via pleiotropy or linkage disequilibrium) with morphological or physiological traits under divergent natural selection. Rice and Hostert (1993) favored this interpretion for the buildup of assortative mating between divergent selected lines of *Drosophila,* but other explanations are possible. This by-product mechanism is also favored by some to explain the evolution of mate preferences in general (Kirkpatrick and Ryan 1991).

Second, mate preferences may be subject to direct selection. For example, phenotypic evolution in a population may cause a "chain of selection" in which mate preferences evolve to accommodate the new properties of available mates. Or new environments may directly favor changes to sensory mode for improved mate choice or detection of mates (Endler 1992; Marchetti 1993; Schluter and Price 1993; Culver et al. 1994). For example, dark habitats may cause individuals choosing mates to reduce their reliance on vision and increase their reliance on other sensory structures, producing premating isolation as a consequence.

Third, postmating isolation may evolve as a by-product of environmental selection pressures. For example, hybrids between divergent species may have an intermediate phenotype, which reduces their ability to harvest resources or otherwise exploit their environment.

Very little evidence has accumulated from natural populations to evaluate the importance of these alternative mechanisms for parallel speciation. Further study of suspected cases, along with a search for new examples, will yield much-needed answers to the question of how natural selection generates new species.

LITERATURE CITED

Barton, N. H. 1989. Founder effect speciation. Pages 229–256 *in* D. Otte and J. A. Endler, eds. Speciation and its consequences. Sinauer, Sunderland, Mass.

Bell, M. A. 1976. Evolution of phenotypic diversity in *Gasterosteus aculeatus* superspecies on the Pacific coast of North America. Systematic Zoology 25:211–227.

Boag, P. T., and P. R. Grant. 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galápagos. Science (Washington, D.C.) 214:82–85.

Borland, M. 1986. Size-assortative mating in threespine sticklebacks from two sites on the Salmon River, British Columbia. M.Sc. thesis. University of British Columbia, Vancouver.

Clarke, B. C. 1975. The contribution of ecological genetics to evolutionary theory: detecting the direct effects of natural selection on particularly polymorphic loci. Genetics 79(suppl.): 101–113.

Cracraft, J. 1989. Speciation and its ontology. Pages 28–59 *in* D. Otte and J. A. Endler, eds. Speciation and its consequences. Sinauer, Sunderland, Mass.

Culver, D. C., T. C. Kane, and D. W. Fong. 1994. Adaptation and evolution in caves. Harvard University Press, Cambridge, Mass.

Diehl, S. R., and G. L. Bush. 1989. The role of habitat preference in adaptation and speciation. Pages 345–365 in D. Otte and J. A. Endler, eds. Speciation and its consequences. Sinauer, Sunderland, Mass.

Dobzhansky, T. 1951. Genetics and the origin of species. 3d ed. Columbia University Press, New York.

Dodd, D. M. B. 1989. Reproductive isolation as a consequence of adaptive divergence in Drosophila pseudoobscura. Evolution 43:1308–1311.

Endler, J. A. 1977. Geographic variation, speciation, and clines. Princeton University Press, Princeton, N.J.

———. 1986. Natural selection in the wild. Princeton University Press, Princeton, N.J.

———. 1989. Conceptual and other problems in speciation. Pages 625–648 in D. Otte and J. A. Endler, eds. Speciation and its consequences. Sinauer, Sunderland, Mass.

———. 1992. Signals, signal conditions, and the direction of evolution. American Naturalist 139(suppl.):S125–S153.

Foote, C. J., and P. A. Larkin. 1988. The role of male choice in the assortative mating of anadromous and non-anadromous sockeye salmon (Oncorhynchus nerka). Behaviour 106:43–62.

Foote, C. J., C. C. Wood, and R. E. Withler. 1989. Biochemical genetic comparisons of sockeye salmon and kokanee, the anadromous and nonanadromous forms of Oncorhynchus nerka. Canadian Journal of Fisheries and Aquatic Sciences 46:149–158.

Futuyma, D. J. 1986. Evolutionary biology. 2d ed. Sinauer, Sunderland, Mass.

Gibbs, H. L., and P. R. Grant. 1987. Oscillating selection on a population of Darwin's finch. Nature (London) 327:511–513.

Goto, A., and T. Andoh. 1990. Genetic divergence between the sibling species of river-sculpins, Cottus amblystomopsis and C. nozawae, with special reference to speciation. Environmental Biology of Fishes 28:257–266.

Grant, B. R., and P. R. Grant. 1989. Evolutionary dynamics of a natural population: the large cactus finch of the Galápagos. University of Chicago Press, Chicago.

———. 1993. Evolution of Darwin's finches caused by a rare climatic event. Proceedings of the Royal Society of London B, Biological Sciences 251:111–117.

Grant, P. R. 1986. Ecology and evolution of Darwin's finches. Princeton University Press, Princeton, N.J.

———. 1993. Hybridization of Darwin's finches in Isla Daphne Major, Galápagos. Philosophical Transactions of the Royal Society of London B, Biological Sciences 340:127–139.

Grant, P. R., and B. R. Grant. 1992. Hybridization of bird species. Science (Washington, D.C.) 256:193–197.

Jones, R., and D. C. Culver. 1989. Evidence for selection on sensory structures in a cave population of Gammarus minus (Amphipoda). Evolution 43:688–693.

Jones, R., D. C. Culver, and T. C. Kane. 1992. Are parallel morphologies of cave organisms the result of similar selection pressures? Evolution 46:353–365.

Kane, T. C., D. C. Culver, and R. T. Jones. 1992. Genetic structure of morphologically differentiated populations of the amphipod Gammarus minus. Evolution 46:272–278.

Kilias, G., S. N. Alahiotis, and M. Pelecanos. 1980. A multifactorial genetic investigation of speciation theory using Drosophila melanogaster. Evolution 34:730–737.

Kirkpatrick, M., and M. J. Ryan. 1991. The evolution of mating preferences and the paradox of the lek. Nature (London) 350:33–38.

Losos, J. B. 1992. The evolution of convergent structure in Caribbean Anolis communities. Systematic Biology 41:403–420.

Marchetti, K. 1993. Dark habitats and bright birds illustrate the role of the environment in species divergence. Nature (London) 362:149–152.

Mayr, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, Mass.

McPhail, J. D. 1993. Speciation and the evolution of reproductive isolation in the sticklebacks (Gasterosteus) of southwestern British Columbia. Pages 399–437 in M. A. Bell and S. A. Foster, eds. Evolutionary biology of the threespine stickleback. Oxford University Press, Oxford.

Nagel, L. M. 1994. The parallel evolution of reproductive isolation in threespine sticklebacks. M.Sc. thesis. University of British Columbia, Vancouver.

Novak, S. J., D. E. Soltis, and P. S. Soltis. 1991. Owenby's *Tragopogon*s: 40 years later. American Journal of Botany 78:1586–1600.

Orti, G., M. A. Bell, T. E. Reimchen, and A. Meyer. 1994. Global survey of mitochondrial DNA sequences in the threespine stickleback: evidence for recent colonizations. Evolution 48:608–622.

Price, T. D., P. R. Grant, H. L. Gibbs, and P. T. Boag. 1984. Recurrent patterns of natural selection in a population of Darwin's finches. Nature (London) 309:787–791.

Ptacek, M. B., H. C. Gerhardt, and R. D. Sage. 1994. Speciation by polyploidy in treefrogs: multiple origins of the tetraploid, *Hyla versicolor*. Evolution 48:898–908.

Ratcliffe, L. M., and P. R. Grant. 1983. Species recognition in Darwin's finches (*Geospiza,* Gould). I. Discrimination by morphological cues. Animal Behaviour 31:1139–1153.

Rice, W. R., and E. E. Hostert. 1993. Laboratory experiments on speciation: what have we learned in 40 years? Evolution 47:1637–1653.

Ricker, W. E. 1940. On the origin of kokanee, a fresh-water type of sockeye salmon. Transactions of the Royal Society of Canada 34:121–135.

Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. Evolution 42:849–861.

———. 1993. Adaptive radiation in sticklebacks: size, shape and habitat use efficiency. Ecology 74:699–709.

———. 1994. Adaptive radiation in sticklebacks: trade-offs in feeding performance and growth. Ecology 76:82–90.

Schluter, D., and J. D. McPhail. 1992. Ecological character displacement and speciation in sticklebacks. American Naturalist 140:85–108.

———. 1993. Character displacement and replicate adaptive radiation. Trends in Ecology & Evolution 6:197–200.

Schluter, D., and T. Price. 1993. Honesty, perception and population divergence in sexually selected traits. Proceedings of the Royal Society of London B, Biological Sciences 253:117–122.

Wood, C. C., and C. J. Foote. 1990. Genetic differences in the early development and growth of sympatric sockeye salmon and kokanee (*Oncorhynchus nerka*) and their hybrids. Canadian Journal of Fisheries and Aquatic Sciences 47:2250–2260.

Yang, S. Y., and J. L. Patton. 1981. Genic variability and differentiation in Galápagos finches. Auk 98:230–242.

Ziuganov, V. V., G. Golovatjuk, K. A. Savvaitova, and F. F. Buganev. 1987. Genetically isolated sympatric forms of threespine sticklebacks, *Gasterosteus aculeatus,* in Lake Azabachije (Kamchatka-Peninsula, USSR). Environmental Biology of Fishes 18:241–247.

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